INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA - INPA

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# Efeito do contraste da plumagem com ambiente de fundo: o caso do Dançador-estrela (*Lepidothrix serena*, Aves: Pipridae) na Amazônia Central

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Manaus, Amazonas
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**Sinopse:**

Foram estudadas as predições da hipótese de favorecimento sensorial, pelas quais os machos selecionam locais e momentos de maior contraste, nos quais são mais aparentes para as fêmeas, para apresentarem seus rituais de corte.

**Palavras-chave:** Lepidothrix serena, Seleção sexual, Ecologia de populações, Comportamento.

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É nóis.

# RESUMO

A hipótese de favorecimento sensorial prevê que indivíduos selecionem locais e momentos nos quais são mais aparentes para as fêmeas para apresentarem seus rituais de corte. Esta hipótese foi levantada em diversos estudos com vertebrados, e é comprovada como promotora de evolução baseada em seleção sexual em espécies de peixes. No entanto, permanece não comprovada para espécies terrestres. Aqui testamos estas predições evolutivas da hipótese para uma espécie de passeriforme amazônico – o Dançador-estrela (Aves: Pipridae). Esta espécie foi fruto de diversos estudos comportamentais, inclusive da hipótese de favorecimento sensorial. No entanto, com o passar das décadas, novas técnicas de estimativas de cores surgiram, e novas conclusões podem ser distintas de resultados já publicados na literatura. Além disso, variações geográficas de comportamento podem resultar na comprovação da hipótese apenas para algumas populações da espécie. Aqui testamos algumas das predições da hipótese de favorecimento sensorial, com estimativas do contraste cromático à curta (entre plumagem e objetos do plano de fundo) e longa (entre plumagem e luz ambiente) distâncias, utilizando uma simulação de espaço de cor tetracromático proposto para visão de aves. Testamos o efeito dos principais tipos de ambientes de luz no habitat da espécie, bem como o efeito de cada mancha da plumagem no contraste dos machos. Estimamos ainda a variação em brilho, ambos entre locais e momentos utilizados na corte dos organismos. Por fim, aferimos o efeito do contraste de cor e do brilho total em variáveis comportamentais, como taxa de atividades e número de indivíduos presentes nos leks. As análises foram realizadas numa abordagem de máxima verossimilhança com modelos lineares mixtos generalizados. Nossos resultados mostram que o contraste de fêmeas é minimizado e o de machos maximizado durante a estação reprodutiva. Não houve variação no contraste a longa distância entre locais de lek e locais sem lek, e ainda não houve variação em contraste quando comparamos momentos usados pela espécie contra momentos não usados. O melhor modelo para variação de taxa de atividades foi o nulo. O contraste de longa distância foi explicado em função da taxa de atividade dos organismos, dos momentos com atividade, das áreas de estudo e do tipo de luz irradiante, sendo que as áreas de estudo diferem em tipo de luz, visto que uma tipologia luminosa fora apenas aferida em uma das áreas de estudo. O brilho a longa distância variou em função de tipo de luz, momentos com atividade e áreas de estudo. As análises de curta distância mostram que a atividade variou entre os locais e pela quantidade de indivíduos visitando os leks, enquanto não houve modelo de medida de contraste à curta distância que se destacasse em relação ao nulo. O brilho dos objetos do plano de fundo variou em função da saturação e da cor dos objetos, da região do substrato, do contraste cromático e das áreas de estudo, enquanto o contraste de cada mancha da plumagem foi função de sua cor e do tipo de luz. Nossos resultados mostram que a hipótese não promove seleção de hábitat que favoreça o contraste a curta distância, e que não há seleção de horários ou locais em resposta ao favorecimento sensorial. Em contrapartida, o período do ano com pico de atividades da espécie é aquele que promove maior contraste dos machos, e menor das fêmeas, apesar destes valores serem altos em ambos os casos e, portanto, os organismos serem bastante conspícuos dentro e fora da estação reprodutiva. Apontamos quatro forças seletivas não-exclusivas possivelmente associadas a tais resultados: 1) seleção natural para reduzir risco de predação de fêmeas e filhotes, uma vez que seus contrastes são reduzidos na estação, com maior frequência de ambientes com Sombra da Vegetação; 2) seleção natural para maior contraste dos machos, reduzindo o custo da busca de fêmeas por machos (de acordo com a hipótese do direcionamento sensorial); 3) seleção de fêmeas por períodos sem chuva, o que criaria vantagens adaptativas por menor gasto energético com reprodução; ou ainda 4) fatores estocásticos, como os promovidos pelo mecanismo de seleção runaway de Fisher. Além disso, variações no contraste da plumagem foram explicadas por propriedades inerentes das próprias plumagens, indicando que a sinalização de cores é mais dependente do organismo que do ambiente.

# ABSTRACT

## Effect of plumage contrast to the background: the White-fronted manakin case in central Amazon

The sensory Drive hypothesis has been widely tested, even if it is not confirmed as valid for any terrestrial species. This hypothesis proposes a mechanism of trait evolution considering that female energy spending for searching partners is minimized and evolution of conspicuous secondary sexual traits occurs. White-fronted manakin is one specie that has already been tested for Sensory Drive predictions and the results shows a male preference for performing displays under specific light conditions, which may promote higher contrast values. Although the estimation of colors via color space is a fast evolving area, our results may be different from what has already been published in researches, due to scientific computing techniques. Furthermore, this species may have geographical variations in its behavior, which *per se* justifies new studies. Here we provide several tests of Sensory Drive hypothesis, estimating short (plumage to objects) and long (plumage to ambient light) distance contrasts from the entire plumage to the background colors, using a simulated bird tetrachromatic vision color space. We used contrast values to test for discrimination between lek sites used by the specie and non-lek sites (not used sites), and also for comparing moments with and without activity. We have compared the effect of light environments of three most common irradiance conditions at the species habitat, and the effect of each plumage patch on the variability of male contrast. We also estimated the variability in total brilliance of backgrounds. As noted by other authors, when simulating color vision in terrestrial vertebrates irradiant light makes no difference for contrast calculations. This way, we have performed our long distance analysis comparing irradiant light as a background color, with a white standard light as an illuminant. Our results emphasizes no selection of habitats in response to ambient light conditions, but they suggest that these birds may reproduce in a period of the year in which chromatic contrast of the male plumage is maximized, and chromatic contrast of females is minimized, although all values were well above thresholds. However, measured courtship activity was higher at one visited area, indifferently of light environment. Courtship activity was performed more at ground level, in a darker background environment. Furthermore, leks with higher activity levels had lower chromatic contrast values at short distance analysis. Brilliance at short distance was influenced by object color, substrate in which object is located, study area and saturation (chroma) of the object, showing that background brilliance is highly variable among areas and objects. Our data shows that Sensory Drives has no strength, in short or long distances contrasts, for habitat selection of the White-fronted manakin populations of Central Amazon. The suggested selection of main reproductive period, only possible effect of Sensory Drive mechanism, may be a consequence of, at least, four non-exclusive selective forces: 1) females may be favored by natural selection for breeding under Forest Shade moments, because this ambient light promotes lower contrast values for females plumages while 2) increases contrast of males, thus reducing search cost to females (in accordance to the Sensory Drive predictions); 3) Individuals may be favored by natural selection for lower female reproductive investment, since the season with higher Forest Shade frequency has lower rainfall; 4) selection of breeding season may be a consequence of Fisherian runway selection, or other stochastic factors. Furthermore, variations in contrast values are consequences of inherent properties of plumages, indicating higher importance of plumage properties than environments in signaling behavior.

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# SUMÁRIO

# INTRODUÇÃO

Poliginia de *lek* é um sistema reprodutivo caracterizado pela agregação de machos em sítios de apresentação. Estes territórios são visitados por fêmeas que buscam prioritariamente a fertilização de ovos (Bradbury e Gibson 1983). Neste contexto, um *lek* é a área na qual ocorrem de um a vários territórios reprodutivos, os quais são defendidos por machos e não possuem valor de recursos para as fêmeas (Bradbury 1981, Prum 1994).

Fêmeas de espécies poligínicas mostram unanimidade na seleção de machos (Kirkpatrick e Ryan 1991). Assim, a pressão de seleção de parceiros gera uma grande variação no sucesso reprodutivo de machos de espécies poligínicas (Elmen e Oring 1977, revisão em Höglund e Alatalo 1995). Fêmeas poligínicas parecem ter preferência por parceiros que possuam caracteres sexuais secundários mais exagerados e/ou vistosos (Kirkpatrick e Ryan 1991), como os complexos rituais de corte apresentados por machos de piprídeos (e.g. McDonald 1989).

Uma vez que no sistema de poliginia de leks os machos não apresentam cuidado parental (Anderson 1994), muito se hipotetizou acerca da origem e manutenção da poliginia de *lek*, tendo em vista que as fêmeas selecionam machos dos quais aparentemente não obtém vantagens diretas, como auxílio no cuidado à prole (Höglund e Alatalo 1995). Dentre as linhas de pesquisa sobre poliginia de *lek*, destacam-se trabalhos que buscam fatores determinantes do sucesso reprodutivo e do desvio do sucesso reprodutivo entre os machos (e.g Pruett-Jones e Pruett-Jones 1991), mecanismos de preferências de fêmeas (e.g. Behler e Foster 1988), organização social de *leks* (e.g. Durães 2009) e sobre a própria evolução deste sistema reprodutivo (e.g. Prum 1997, Jones e Quinnell 2002).

Este sistema está presente em diversos taxa de invertebrados (e.g. coleóptera em Lloyd 1972; lepidóptera em Alcock 1983; díptera em Spieth 1978, Jones e Quinnell 2002) e nas quatro classes de vertebrados (e.g. peixes ciclídeos em McKayle 1983; anuros em Ryan 1983; quirópteros em Bradbury 1977; cervídeos em Balmford *et al.* 1993; aves em Snow 1963). Entre os vertebrados, a poliginia de *lek* ocorre em pouco mais de 1,4% das espécies de aves (138 espécies em 14 famílias) e em apenas 0,2% das espécies de mamíferos (13 espécies em cinco famílias; Höglund e Alatalo 1995). Por ser relativamente bem distribuída entre as aves, a poliginia de *lek* é amplamente estudada neste grupo.

Dentre as aves que apresentam poliginia de lek, destaca-se a família Pipridae, passeriformes frugívoros conhecidos principalmente por seus elaborados rituais de corte (Sick 1997, revisão em Snow 2004). Nesta família a poliginia de lek é uma característica ancestral (Prum 1994), que foi aparentemente favorecida pela abundância de frutos com alta riqueza energética, permitindo o investimento em aquisição de elevado número de cópulas em detrimento de defesa de recursos alimentares e cuidado parental (Snow 1963, Sick 1997).

Na familia Pipridae, muitas espécies parecem ter preferência por apresentarem rituais de corte em condições luminosas que favoreçam seu contraste com o ambiente (e.g. Heindl e Winkler 2003a, 2003b). A preferência por ambientes luminosos pode ser um indício da importância da hipótese de favorecimento sensorial (do inglês *Sensory Drive*, Endler e McLellan 1988, Basolo e Endler 1995) nas espécies de piprídeos (Uy e Endler 2004, Anciães 2005, Anciães e Prum 2008). Esta hipótese propõe um mecanismo de evolução de preferência de características sexuais, como coloração conspícua e vôos elaborados, através de seleção natural atuando na preferência (e.g. Marchetti 1993, Johnsgard 1994, Théry e Vehrencamp 1995, Endler e Théry 1996, Macedonia 2001, Scott 2001, Leal e Fleishman 2002, 2004, revisões em Ryan 1990, Andersson 1994, Basolo e Endler 1995, Prum 1997, Savalli 2001).

O mecanismo proposto pela hipótese de favorecimento sensorial prediz que características que ampliem a atividade sensorial do parceiro sexual possuem maior possibilidade de se fixarem em populações (Ryan 1990). Assim, o ambiente físico e a interpretação neural do sinal seriam fatores determinantes na evolução da sinalização. Desta forma, a hipótese prevê que variações na sinalização de espécies ocorrem em resposta a um aumento da conspicuidade de machos no ambiente, reduzindo o tempo de busca das fêmeas (Uy e Endler 2004, Seehausan *et al.* 2008, Anciães e Prum 2008).

Apesar de ter sido indicada diversas vezes em piprídeos, a hipótese de que o favorecimento sensorial levou ao surgimento de novidades evolutivas na família Pipridae foi refutada ao menos para um clado da família (Anciães 2005, Anciães e Prum 2008). Uma das espécies de piprídeos com potencial para estudos relacionados à hipótese de favorecimento sensorial é o uirapuru-estrela (*Lepidothrix serena*). Esta espécie apresenta variações locais de adensamento e de comportamento entre populações (Théry 1990; Endler e Théry 1996) e tais variações de adensamento e de localização de *leks* foram sugeridas como respostas a variações na cor ambiental (Théry 1990).

Endler e Thery (1996) sugerem que fêmeas de *L. serena* se baseiam no contraste visual (diferença entre cor de indivíduos e cor ambiental) durante a corte para a escolha de parceiros, e que machos selecionam condições luminosas e de coloração dos objetos do ambiente que favoreçam sua sinalização. Assim, os indivíduos maximizariam seu contraste em relação ao ambiente de fundo durante as apresentações de corte, enquanto sua plumagem e seu comportamento reduzem a conspicuidade quando os indivíduos estão fora do *lek* ou não estão se apresentando. O padrão diário de atividade desta espécie estaria, portanto, associado à variação da cor do ambiente ao longo do dia. Além disso, Endler e Théry (1996) verificaram que, em uma população da espécie na Guiana Francesa, na qual leks estão localizados em um sopé de montanha, machos mudam a localização dos leks ao longo do dia em resposta às condições luminosas, e segundo seus resultados selecionam o ambiente que maximiza o contraste entre plumagem dos machos e o ambiente de fundo. No entanto, apesar destas conclusões, este efeito de seleção de hábitat pode ser um artefato da técnica utilizada. Considerando que as técnicas de computação científica para a estimativa de cores, na forma como as aves enxergam, se desenvolveu a passos largos nos últimos anos, e que pode haver variações geográficas que mudem os padrões de seleção de hábitat entre populações da espécie, novos estudos são necessários para verificar se de fato a hipótese é válida para a espécie.

A cor é dependente de diferenças qualitativas em ondas de luz que são refletidas, transmitidas ou emitidas por um objeto. No entanto, cor não é sinônimo de comprimento de onda e não pode ser inferida com base no espectro de luz que vem de um objeto. A cor é uma capacidade psicofísica dos organismos, e depende da capacidade dos animais perceberem e compararem comprimentos de onda vindos do ambiente (Jacobs 1981, revisão em Cuthill *et al.* 2000). Podemos, assim, definir cor como uma medida comparativa e interpretativa dos comprimentos de onda.

A percepção de cores pode ser crucial para a compreensão do comportamento, ecologia e especiação de animais (Ödeen e Håstad 2003). A visão de mamíferos é uma exceção dentre os vertebrados, visto que possuem menor quantidade de fotorreceptores (dois ou três) e menor espectro de visão quando comparados aos outros grupos de vertebrados, como aves e alguns peixes que possuem quatro fotorreceptores (Goldsmith 1990, Jacobs 1993, revisões em Hart 2001, Hart e Hunt 2007). Pelo fato de possuírem um cone fotorreceptor a mais que humanos, espécies tetracromatas (e.g. aves) possuem a capacidade teórica de enxergar duas vezes mais cores que os humanos (Losey *et al*. 1999).

Diante das diferenças entre os sistemas visuais de mamíferos e demais vertebrados, a percepção de cores pelos humanos não deve ser utilizada para estimar a percepção de cores para outros animais (Cuthill 2006). Um dos métodos mais usados para se fazer uma boa estimativa da visão de cores em aves é a simulação da captura de fótons pelos quatro cones fotorreceptores (revisão Cuthill 2006). O uso de espectrofotômetros e de computação estatística permite simular o sistema visual de aves e fazer boas estimativas de como indivíduos vêem e contrastam cores, mesmo para comprimentos de onda fora do espectro de visão humana (e.g. ultravioleta).

As medidas de contraste são aferidas usando duas distâncias distintas, ou aproximações: longa distância e curta distância (e.g. Doucet *et al.* 2007). As análises a curta distância estimam o contraste entre a plumagem da espécie-alvo e os objetos localizados no ambiente de fundo, que de forma geral são aferidos com reflectância de folhas verdes (Endler e Théry 1996, Heindl e Winkler 2003a). As análises de longa distância são, por sua vez, realizadas, estimando o contraste entre plumagem e irradiância, sendo que a irradiância pode ser usada nos cálculos como iluminante (e.g. Heindl e Winkler 2003b, Anciães 2005) ou como um objeto no plano de fundo (e.g. Anciães e Prum in prep., este trabalho).

O contraste, para visão em aves, é estimado em ambientes visuais tetracromáticos, como o proposto por Goldsmith (1990). Estes diversos espaços de cores utilizam distâncias nem sempre relacionadas ao contraste percebido pelos animais (Pike 2012), o que pode gerar interpretações incorretas. Aqui usamos um espaço de cor proposto por Stoddard e Prum (2008), o qual implementa métricas exclusivas para resumir as propriedades colorimétricas das cores conforme vistas pelas aves, e também cálculos de contraste via modelo baseado no ruido em canais de oposição (“Receptor Noise”, Vorobyev e Osorio 1998).

# OBJETIVOS

Nossos objetivos no presente estudo, portanto, são: testar as predições da hipótese do favorecimento sensorial para o dançador-estrela (*Lepidothrix serena*), estimando o contraste à longa distância e curta distância dos machos. Desta forma, pretendemos, numa aproximação baseada em verossimilhança, verificar: a) se as taxas de atividade da espécie são respostas às condições de contraste; b) se o contraste varia em função do local, da atividade e brilho do ambiente de fundo; e c) quais fatores são determinantes para a variação de brilho, comparando ainda os resultados aqui obtidos com demais resultados da literatura.

# CAPÍTULO 1

Medeiros, W. & Anciães, M. A role of plumage contrast to the background: testing Sensory Drive effects on the White-fronted manakin in Central Amazon. Artigo em preparação para *Behavioral Ecology*

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# A ROLE OF PLUMAGE CONTRAST TO THE BACKGROUND: TESTING SENSORY DRIVE EFFECTS ON THE WHITE-FRONTED MANAKIN IN CENTRAL AMAZON

## ABSTRACT

Sensory Drive has being widely tested, even it has not been confirmed as a mechanism of trait evolution for terrestrial animals. White-fronted manakin has already been tested for this hypothesis, showing that display behavior may be an answer to Sensory Drive. Although, the species may have geographical variation and color estimation techniques has changed throughout time, enabling different results than those published. Here we provide tests of the hypothesis using a tetrachromatic color space to compare entire plumage color contrasts at lek and non-lek sites, and at some moments with and without activity. We have also compared three light environments measured at the species habitat; tested the effect of each plumage patch on the variability of male contrast; and estimated the variability in total brilliance of backgrounds. There was no selection of habitats, although birds breed in a season that maximizes male and minimizes female contrast to the background. Leks with higher activity presented lower contrast at short distance. Long distance brilliance did not explain variation in displays. Brilliance at short distance was highly variable among study areas and objects. Possible selection of a breeding season may result from, at least, four non-exclusive forces: 1) natural selection on females for breeding when ambient light promotes lower contrast while 2) increases males' contrast, thus reducing search cost to females; 3) natural selection for lower reproductive investment, during dry season; 4) Fisherian runaway selection, or other stochastic factors. Finally, plumage colors were more important than environments for explaining variations in visual signals.

Keywords: sensory drive, sexual selection, habitat selection.

# INTRODUCTION

Lek polygyny is a rare reproductive system whereas males defend display territories, called leks, and their reproductive investment are all spermatic (Hoglund and Alatalo 1995). Leks are visited by females due to egg fertilization (Breadbury and Gibson 1983), and there is strong divergence in male reproductive success (Elmen and Oring 1977). Despite its rarity, this breeding system is widespread among animals, being present in invertebrate taxa such as Coleoptera (Lloyd 1972), Lepidoptera (Alcock 1983) and Diptera (Spieth 1978, Jones and Quinnell 2002), and in all vertebrate classes, e.g. in Cichlid fish (McKayle 1983), anuran Amphibia (Ryan 1983), Chiroptera (Ryan 1983), Cervidae (Balmford *et al.* 1993), and birds (Snow 1963). Within vertebrates, lek polygyny is most common in Aves and Mammalia, occurring in 1.4% of birds (136 species in 14 families) and in 0.2 % of mammalian species (13 species in five families, Höglund and Alatalo 1995).

In polygynyc reproductive systems, females seems to prefer partners which displays more complex secondary sexual traits (Kirkpatrick and Ryan 1991), as complex ritual courtships in lekking species (e.g. McDonald 1989). This female preference for complex ritual courtships may be a result of stochastic driven preferences due to Runaway process (Fisher 1930), preference for patches which signals for male quality (Hamilton and Zuk 1992) or by fixation of conspicuous signals which are best fitted neurologically and reduces female energy costs for searching males, as proposed by Sensory Drive hypothesis (Endler and McLellan 1988, Endler1990, 1992, Endler and Basolo 1998, review in Savalli 2001).

Birds within the family Pipridae are likely to be the better known taxa with lek polygyny and a well-studied model group. This Neotropical bird family is characterized by strong sexual divergence and complex courtship (Sick 1997, Snow 2004). Females and juveniles are usually olive-green and adult males are bright colored (Snow 2004). Males of some species seems to prefer specific light conditions for performing courtships (Endler and Théry 1996, Heindl and Winkler 2003a, 2003b, Uy and Endler 2004, Uy and Stein 2007, Anciães and Prum 2008), and species from at least two genera clean their display arenas (*Corapipo* and *Manacus*, Uy and Endler 2004, Anciães 2005) which, in *Manacus*, has been attributed to higher visual contrast values between bird plumage patches and the background (Uy and Endler 2004). Such preferences for light habitats and background patterns has been pointed as an indication of the importance of Sensory Drive mechanism for Pipridae species.

Sensory drive is a verbal evolutionary model that predicts that traits which could maximize sensory stimulation in the partner, as conspicuous signals, are more likely to be fixed in populations (Ryan 1990, Boughman 2002). Biophysics, neurological interpretation and signaling environment can guide the direction of traits evolution by Sensory Drive (review in Endler 2000). This way, Sensory Drive may be an evolutionary mechanism for minimizing energy spending by females during males search. Several studies, across all vertebrate groups, has focused on the selection of behaviors and display habitats (e.g. Johnsgard 1994, Basolo and Endler 1995, Marchetti 1995, Théry and Vehrencamp 1995, Endler and Théry 1996, Macedonia 2001, Scott 2001, Leal and Fleishman 2002, 2004, reviews in Ryan 1990, Andersson 1994, Basolo and Endler 1995, Prum 1997), although evolutionary predictions of sensory drive are tested in few studies (Seenausan *et al.* 2008, Anciães and Prum 2008). Despite being indicated many times in Pipridae, Sensory Drive evolutionary pressure, in response to changes in the environment colors, within species of the family, has been refuted (see Anciães and Prum 2008). Cummings (2007), in a comparative study with Superperch fishes, shows that Sensory Drive can promote visual system evolution when the sister-species occupies distinct light environments. Single-species studies may not test the evolutionary predictions of Sensory Drive, like animal colors or visual system evolution, but they add up to tests at the macroevolutionary level. Here we ask if the extant species' behavior is a response to the signaling environment, such as the ambient light or the background objects, that maximizes visual contrast to males plumage.

We specifically test if the behavior of White-fronted manakin (*Lepidothrix serena*, Aves: Pipridae), in Central Amazon, is a response to higher contrast values promoted by ambient light and background objects used at lek sites and during display activity. This species and a congeneric have already been subject of others sensory ecology studies in other geographical region. Some studies indicate that Sensory Drive mechanism may promote habitat selection on Pipridae species, as a response to supposed vertical gradients of light conditions (Heindl and Winkler 2003b) or via selection of specific light conditions for performing displays (Endler and Théry 1996). This way, we believe White-fronted manakin is a good model species for testing Sensory Drive predictions. In French Guiana, the White-fronted manakin presents local variation in aggregation, and such variation is argued to result from variation in ambient irradiance light and the background foliage color that maximizes visual contrasts of the bird plumage colors (Théry 1990, Endler and Théry 1996). Males in this population occupy a mountain slope and lek location changes along the day (Théry 1990) in response to ambient light changes (Endler and Théry 1996). In central Amazon there is no movement in lek territories locality, between near localities (Medeiros and Anciães in. prep.). This indicates that the species presents geographical variation in behavior and suggests that possible advantages in visual contrast among sites in contiguous areas in Central Amazon would be either site specific or a response in timing of display activity within lek sites. Besides the variation in aggregation and behavior, the contrast calculation is a fast-evolving area, so replicating similar tests with the same species can lead to different results.

Simulations of psychophysics environments were used in many researches with birds (Endler and Théry 1996, Heindl and Winkler 2003a, Anciães and Prum 2008), and this approximation is necessary, as birds see color that humans cannot see (review in Hart and Hunt 2007). Human color vision is provided by three cone types, and vision ranges from 400 to 700 nm. Avian color vision is provided by four cone types, being tetrachromatic, as reptiles and some fishes. This way, tetrachromatic color vision incorporates ultraviolet spectra, when compared to humans, so birds can see between 300 to 700 nm or between 320 to 700 nm, depending on visual type of the eye (review in Hart and Hunt 2007). This ability on discriminating UV colors make birds see twice more colors than humans do (Losey *et al.* 1999). Here we estimate short (background objects) and long (light environments) distance chromatic contrast of bird plumage colors against background colors for the White-fronted manakin (*Lepidothrix serena*) in Central Amazon, using a tetrachromatic color space as proposed by Goldsmith (1990) and implemented in TetraColorSpace (Stoddard and Prum 2008) to test predictions of the Sensory Drive hypothesis.

We test the specific predictions that 1) males White-fronted manakin performs courtships in moments when light environment maximizes its contrast to the bird plumage colors; 2) lek sites present overall ambient light conditions that maximizes its contrast to the bird plumage colors; and 3) birds uses display perches with background foliage color that maximizes its contrast to the bird plumage color. We also assessed the variation in activity rate, the variability in total brilliance from backgrounds and variability in chromatic contrast explained by individual plumage patches as alternatives.

## MATERIALS AND METHODS

### Study species: White-fronted manakin

As other species of family Pipridae, White-fronted manakin presents strong sexual dimorphism (Sick 1997). Young individuals and females are green, whereas adult males are black with white, yellow, orange and blue insertions (Figure 1, Prum 1994, per. obs.). During the peak of the reproductive station, males stay at the lek about 90% of daytime (Prum 1985), so one can believe sexual selection has a strong force in this species. The main reproductive period occurs in the dry season, between May and November, however female visitations and reproduction occurs all over the year (Anciães pers. com.; pers. obs.). White-fronted manakin has Amazonian distribution, and its limits ranges are Guianas' Shield (north), Amazonas River (south) and Negro River (west; Snow 2004). The species occupies terra-firme areas of French Guiana, Suriname and Brazilian states of Amazonas, Pará and Amapá (Prum 1994, Snow 2004). The species is known for its variation in aggregation and territory size, which goes from classical (4-6m of diameter; Théry 1990) through exploded (30-40m; Prum 1985, present study) and solitary leks (80-150m, present study). Théry (1990) proposed that variation in aggregation can be a result of differences in habitat luminous conditions among distinct regions occupied for the species.

### Study areas and selection of leks

The study was conducted at FRAD (Forest Reserve Adolpho Ducke, 02º55'S 59º57'W) and BDFFP (Biologic Dynamics of Forest Fragments Project) regions, both located at north Manaus, Brazil. Both regions are composed of tropical humid terra-firme forest with uniform canopy (Guillaumet and Kahn 1982). Leks were found searching for the main vocalization of the species ("wee" calls, *sensu* Prum 1985). At the two regions we selected a total of three study areas. In FRAD we selected a plot of 2,000 ha of continuous forest, where we actively searched for leks between July and August 2011. In BDFFP we selected two areas, farm Dimona (10 ha fragment and secondary area, 02º20’S 60º05’W) and farm Esteio (continuous forest, 02º26’S 59º45’W). At Dimona area, we actively searched for leks at November 2010. At Esteio, leks were located via autonomic radio recorders of another project, which were active during 2010 reproductive station. The autonomic radio recorders are placed at the forest for four days in each point (each radio approximately 400m from the next), and they have a range of 250 meters. They automatically record the forest sounds between 6:00 and 10:00 A.M. Then, at lab, researchers identifies the bird species by the vocalizations. For the autonomic radio recorders, we considered leks, all listening points where “wee” calls were performed for two or more days. All leks located via these both methods (actively search and autonomic radio recorders) were found in 2012 fieldwork, corroborating traditionality in leks occupancy in the genus, as shown in Durães *et al.* (2007).

## Behavioral data

A total of 25 leks were visited between February and April 2012. Even not being the main reproductive period, during activity peaks vocalization rates were similar to others fieldworks with the species (Prum 1985, Théry 1990). Behavioral data were collected via continuous focal observation in 5 minutes intervals, following Martin and Bateson (2007). The same two observers collected behavioral data in leks between 7:00 A.M and 2:00 P.M. If activity was high (> 20 vocalizations per minute for more than five intervals of 10 minutes), the observation were extended until 4:00 P.M. Behavioral data was used for two analyzes: Long Distance analysis, which incorporates light conditions and behavior at the leks, and was used only when irradiance light was collected, and Short Distance analysis, which incorporate the background object color properties and the behavior at leks. Long and short distance analyzes will be best explained at Contrast Analyzes section.

Activity data was transformed into instantaneous activity rate – number of vocalizations in each 10 minutes intervals divided by 10; and daily activity rate – integrals of vocalizations for each day, divided by total time of observation on that day. Instantaneous vocalization allows comparing behavioral rates along the day, and daily vocalization rates allows comparing activity rates between days. Moreover, the numbers of individuals present in leks were measured for each five-minute interval. The individual presence data was transformed into instantaneous individuals' presence rate, which was measured for each 10 minutes interval – number of individuals measured at each 10 minutes interval; and daily presence rate – integral of the number of individuals at each observational interval divided by all observational intervals along the day. We collected data of four vocalizations types, five stereotyped flights and three display postures, in a total of twelve behaviors. Of the total behaviors found, six are new for the species and will be described elsewhere. For minimizing the observer effects, only two observers (WM and TB) performed all behavioral data collecting. Also, all behavioral analysis were made with three more conspicuous vocalizations, as we believe these data has minor error chance.

## Contrast analyzes

We performed two types of contrast analyzes: long distance analysis (LD) and short distance analysis (SD). For LD analysis we intended to simulate contrast when conspecifics see the birds at a long distance (e.g. > 10m). For such analysis, we compared differences between plumage patch colors and irradiance light, using irradiant light as a background color. For SD analysis we simulated contrast at short distance (e.g. < 3m), in which individuals see conspecifics in front of the background leaves and branches. Because White-fronted manakin males perform reproductive behaviors at the foliage level and near the ground (Prum 1985, pers. obs.), we measured SD contrast as the difference between plumage patches and reflectance spectra of objects located in two different substrates: foliage and soil.

## Spectral data

Plumage spectra were obtained using an USB-2000-UV-VIS spectrophotometer, attached to a bifurcated optic fiber (R400-2-UV-VIS) and connected to a PX2-Pulsed Xenon Light Source. Standard spectra were obtained using a spectralon standard (WS-1-SL). All spectroscopy equipment and software used here are made by Ocean Optics Inc. Plumage reflectance data was obtained of museum specimens (Four males and five green individuals) of National Institute for Amazonian Research and National Museum of Federal University of Rio de Janeiro. Anciães (2005) shows little variation in reflectance spectra among individuals of the same species. We selected nine areas of adult male plumages (crown, back, throat, wing, rump, tail, rump chin, breast, belly,) and six areas of green individuals (juveniles or adult females) plumages (crown, back, throat, breast, belly and rump). The selected areas provide all possible human-based color variation in the White-fronted manakin. For the spectrophotometric readings, the probe was located 6 mm away of the feather, and then Spectrasuite software performed 20 scans, with no boxcar interval (interval between susceptive scans), and saved the average.

Reflectance spectra data of objects, used for SD Analysis, was obtained from a random sample of 12-20 objects (e.g. leaves) collected at leks, at two heights (soil and foliage). The foliage background was collected about 1.5 – 2 m high, approximately at the height the birds vocalize. Soil background was collected near the ground, and was composed mainly of decomposing leaves. Reflectance measures of the objects were obtained using the same spectrophotometer, Y fiber and white standard, although the light source used was a DH2000 deuterium halogen lamp. Lamp changing provides imperceptible changes in measured spectra, and we change the selected light source due to availability of the lamp. Each object had its reflectance measured with Spectrasuite software, from an average of five scans and six readings of boxcar width. The probe was located at 5 mm away from the object.

Irradiation spectra data, used for LD analysis, were collected using the same spectrophotometer, this time connected to a simple optic fiber (P400-2-UV-VIS) attached to a cosine corrected probe (CC3-UVS) aimed upwards. Energy was standardized using LS-1-CAL light source. The software Spectrasuite performed the readings of the ambient light. Spectra were collected at 10 minutes intervals, starting at 7:00 and stopping when the netbook battery got off, usually near 12:00. Irradiation measures were collected from one to 20 seconds of integration time, varying in response to irradiance intensity (the bigger the irradiance, the smaller the integration time). Light spectra were collected at leks and at non-random not lek sites. The not lek sites were placed in contiguous areas, located about 200m or more from the edge of the focal lek, at places with similar vegetal structure (e.g. Plato with similar canopy open), and not occupied by another male of the species. This design allow us comparing spectra of lek with non-lek sites, and also spectra of moments with activity and moments without activity, allowing us testing if the species select areas and moments of activity in response of higher contrast values. We followed Endler (1990) for converting energy flux into photon flux, but here we chose another unit, uMols . cm^-2 . s^-1, for showing our results. The change was done because this unit represents our data with less zeros (e.g. 18 in opposition to 180,000) and also because it is being used in other works (e.g. Anciães and Prum in prep.).

### Spectral analyses

We interpolate spectral data using Avicol (Gomez 2006) and also used interpolated spectra for calculation of two contrast metrics in a tetrachromatic color space: Span (euclidian distance in a tetrachromatic color space) and JNDS (just noticeable differences, Vorobyev and Osorio 1998), as implemented in TetraColorSpace (TCS; Stoddard and Prum 2008). We selected a violet eye type, with photoreceptor proportions of 1:2:2:4. Anciães (2005) shows, for Pipridae, little variation in color perception due variations in photoreceptor proportions. For Span, TCS compares hue and chroma for each plumage color to the background ambient, which could be irradiance spectra, for LD analysis, or the objects spectra, for SD analysis. For JNDS, TCS calculates the receptor noise model proposed by Vorobyev and Osorio (1998), and this metric needs three inputs: irradiance light, patch color and background color. After calculating JNDS values, we noticed that some black plumages had high values (65-75 JNDS), and we decided excluding these patches from our analysis. We used a white standard light as illuminant, and irradiant light or objects spectra as the background color. This choice was done because distinct types of unsaturated lights (as all types of terrestrial irradiance lights) did not make perceptible differences in the total photon catch at each class of cone receptors and therefore in contrast values (Anciães 2005, Stoddard and Prum 2008). Thus, using different types of irradiance light as illuminant in Vorobyev-Osorio model, for terrestrial ambient, is indifferent. We transformed JNDS and Span values per plumage patch into average values of the patches, for SD and LD analyzes, despite the fact that having equal number of analyzed plumages of adult males and green individuals (six patches used). This choice permits us to compare all plumage colors of the bird with the background, and also comparing green and adult male individuals. We also used the TCS metric “r” for best fitted model selection. TCS plots all spectra in a tetrahedron, as proposed by Goldsmith (1990), and some characteristics of the points may be used as metrics. “R” metric is a measure of distance between the achromatic origin and the point where the plumage is represented, so, as it is an informative of how saturated a color is and thus a predictor of ambient light type. “R” values ranges from 0 to 1, and small values means points near the origin and high values means the color is near one of the tetrahedron vertices. As Forest Shade has more unsaturated color than Small Gaps or Cloudy environments, this type of light is more saturated and has a higher “r” value. For more about “r” and other TCS metrics, see Stoddard and Prum (2008). Furthermore, we performed brilliance analysis of plumages, objects and irradiances, using Avicol. Brilliance is simply the integration of all values of a spectra, and spectra with low brilliance values seems darker for humans.

## Statistical analyses

Basics statistical analysis (e.g. regressions) and selection of models were implemented in R (R Development Core Team 2008). We used a likelihood approach for testing multiple hierarchical models (Burnham and Anderson 2002) using Generalized Linear Mixed Models (glmm), and we built all possible models on each approach. The best explanatory variables explaining the tested response variables models were implemented using R packages BBLME (Bolker and R Development Core Team 2012) and LME4 (Bates *et al*. 2012)

We selected best fitted glmm models using three data sets – firstly for LD analysis, secondly for SD analysis and the last for individual plumage patch analysis. We decided to add individual plumage patch analysis because the results of other analysis may have some influence of plumage patch (e.g. crown plumage influencing more the data than other plumages). For all analyses, random effect was the place of data collecting, each lek or non-lek site. This way, we isolated part of the variation due only of intrinsic characteristics of the study sites. We tested a total of eight response variables and 17 explanatory variables, which are presented in detail in table 1.

## RESULTS

We performed 5,320 5-minutes observation's intervals, summing a total of 443h20min of observation, during 50 days of field work. Activity moments represent less than 11% of observed time, varying between areas (table 2), and it occurred mainly early in the morning. Correlation between individuals rate and vocalization rate is positive and moderate (adjusted R squared = 0.674, $p<0.0001$). The reflectance spectra of the 15 plumage patches measured for the species are shown in figure 2. We collected 320 background objects (examples in figure 3), which were divided into two classes – soil objects and foliage objects. We also collected a total of 657 irradiance spectra, in leks and non-leks sites, and these spectra did not vary in function of study area or activity rate, but vary in function of type of light – Forest Shade and Cloudy (figure 4). We added data of another possible ambient light, Sunny Gap, which was not measured is this study. The Sunny Gap irradiance spectra were measured in two of the same study areas of the present study, at BDFFP region, and are presented at figure 4 (courtesy of M. Anciães). Irradiance brilliance varies among study areas and type of light, as shown in figure 5. The distinct types of light promoted distinct contrast values, and, in general, Forest Shade provides higher contrast values for adult male plumage than Cloudy, as shown in table 3.

All measured spectra can be showed in a tetrahedral color space, simulating the colors as birds see them (figure 6). Panels A and B represents plumage colors of males and females, and shows that colors are widely distributed throughout the color space, and so males and females may be highly visible among environments. Panel C shows a sample of the colors of background objects, which occupies green and brown colors. Panel D shows the irradiance spectra measured in moments with activity. The two groups formed in panel D represents the two measured ambient lights – Cloudy conditions, which are represented close to the origin, and Forest Shade, the group represented close to the green vertex of the tetrahedron. Unfortunately the program do not allow us to change the font of distinct points on the tetrahedrons, what would simplify the interpretation of these data.

JNDS and Span values are very similar (adjusted R squared = 0.8756, $p<0.0001$), and we selected JNDS for further analysis because it is based on a physiological calculation and relates to how animals perceive and discriminate colors (Osorio and Vorobyev 1998, Pike 2012). JNDS variation explaining vocalization rate in LD and SD analyzes are shown in figure 7. Panel A, showing long distance analysis, presents 2 groups of JNDS values, one for Forest Shade and another for Cloudy conditions. Forest shade ambient shows highest contrast values. The panel B, showing short distance analysis, indicates an inverse correlation between activity rate and contrast values, a result against our expectations. Panel B also shows that contrast promoted by soil objects is not different from contrast promoted by foliage objects.

The best fitted models and the effects of explanatory variables on each response variable are showed at table 4. Tables showing all models are shown as supplement material (tables S1 to S8). Best fitted glmm for instantaneous vocalization rate was a null model (weight = 100%). JNDS score contrast for adult male plumage, as a response variable, was best fitted by a model which incorporates moment, area and “r” metric for irradiant light (weight = 96.33%). Moments without activity were negatively related to JNDS values, Dimona and Esteio areas had minor contrast values and “r” metric positively influenced the contrast values. Ambient light brilliance were best explained by model including study area, activity rate and r metric for irradiant light (weight = 100%). Moments without activity had higher brilliance values than moments with activity, Dimona and Esteio had lower brilliance values than Ducke and “r” metric of irradiant light influenced positively the brilliance values, in spite of having high standard error.

Daily vocalization rate was best explained by a model composed by daily individuals presence rate and area (weight = 63.06%), with positive and strong correlation. For average JNDS contrast at short distance analysis, best models fitted for adult male individuals (best model weight = 35.79%) and green plumage individuals (best model weight = 29.8%) had low weight, although in both groups best models are composed by object color and “r” metric for objects, with black objects promoting higher contrast values for both, green and black individuals. Also, saturation of background object color, measured by “r” metric, was positively correlated to JNDS values, and so, contrast is higher when the object is more saturated. Objects brilliance were best explained by the more complex model (weight = 100%), which includes “r” metric of object, study area, substrate (soil or foliage) and object color. Dimona and Esteio has slightly darker backgrounds, and yellow leaves are brighter than black, brown and green ones. The more saturated an object, the darker it looks to human eyes. Also, soil is a brighter environment than foliage.

Best fitted model for explaining contrasts of individual plumage patches has "r" metric for light habitat, color of patch and "r" metric for plumage as explanatory variables (weight = 100%). Blue, white and black plumages promotes higher JNDS values than yellow plumages. Metric “r” for light habitat and for plumage has both positive relations with JNDS values, being plumage saturation four times more important for contrast values than ambient light saturation.

## DISCUSSION

Our data shows little or no influence of Sensory Drive mechanisms on habitat selection of the species. Instantaneous vocalization rates varies stochastically, daily vocalization rates varies in response to visiting behavior, being higher when there are other individuals at leks, indifferently of contrast or brilliance promoted by incident light, or contrast or brilliance promoted by background objects. Our glmm shows no best model for JNDS variation at short distance, but JNDS at long distance analysis varied in function of study area, moments with or without activity and type of light. Light brilliance varied in function of study area, moments with or without activity and type of light, and background objects brilliance varied in function of area, object color, object saturation (“r” metric) and substrate. JNDS variation for each plumage patch varied in function of saturation of light ("r" metric), saturation of object ("r" metric), and object color.

### Chromatic contrasts on leks and during activity

Plumage contrasts against light environments (long distance contrast) had no variation in function of lek sites or activity moments, but showed strong differences in function of type of light (figures 4 and 6). For short distance analysis our data shows weak inverse relationship between JNDS contrast values and activity rate (figure 7). It indicates, for short distance analysis, that the relationship between contrast values and activity rate is inverse, opposing to Sensory Drive prediction.

Our best fitted model for contrast values at long distance analysis shows that contrast values changed in function of study area, moment with or without activity and saturation of light (“r” metric for irradiant light). Contrast values were slightly higher in moments of activity, probably because percent activity under Forest Shade was higher than percent activity under Cloudy conditions (table 2). These results may be an artifact, because of the higher influence of the Forest Shade moments in the result, since Ducke was the only area whereas Forest Shade was measured. Thus, Ducke area has higher contrast values than other areas, and also more intervals with activity (table 2), creating this apparent correlation between moments with activity and higher contrast values. Saturation of light is related to the areas, again because Forest Shade was only measured at Ducke site, and so Ducke site had higher contrast and higher “r” values than Dimona and Esteio (table 4).

For short distance analysis, we did not found models with high weight for explaining JNDS variation (table 4). We performed two glmm analyzes groups for contrast variation in short distance analysis, one for JNDS of adult males plumages and another for JNDS of green individuals plumages, and each had two best models. In both cases the same explanatory variables composed the best models (area, object color and “r” metric of object), whereas saturation of the objects influences more the contrast values. Black and brown objects promotes higher contrast values than yellow and green ones, and Dimona area has more contrasting leks. As already shown in figure 7, soil objects do not promote higher contrast values than foliage objects. As the species display is done at soil level, these results show no preference of White-fronted manakin for displaying under better contrast conditions, in opposition to Sensory Drive hypothesis.

## Variation in activity

Instantaneous vocalization rate is best explained by null model (table 4), indicating no influence of individual presence rate, playback, JNDS values or type of light in this approximation. This result shows that momentary variation on activity rate is stochastic or under other factors unanalyzed. As shown in table 2, there were more intervals with activity at Ducke site, independently of type of light. Individual presence rate was expected to have effect on instantaneous vocalization rate, showing relation between activity and visitors presence at leks, but this expectation was not met by the models. On the other hand, daily vocalization rate was best explained by individual presence rate (table 4, table S4). Prum (1985) asserted that probably males’ activity is response of female presence at leks. The three vocalization types used in this study may be used by the species in agonistic and in non-agonistic group interactions. This way, the vocalization rates are higher while there is females or possible females (green juveniles) visiting leks, and while there are more adult males visiting leks.

## Variation in brilliance

Best fitted brilliance models shows that total brilliance of background light varies in function of area, activity rate and "r" values for irradiance (table 4). Maybe our result is skew because areas of study and "r" values are correlated. This correlation is an artifact of our fieldwork, because, as already said, Forest Shade light environment was only measured in our last campaign, which occurred in Ducke area (table 2). All irradiance measures in Dimona and Esteio areas were taken under Cloudy condition. Forest Shade environment presents lower intensity than Cloudy moments, but Ducke area under Cloudy conditions were brighter than the other areas under the same climatic conditions (figure 5). This way, Ducke presented high average brilliance values than Dimona or Esteio. Moments without activity, in response of its main occurrence under Cloudy conditions, had higher brilliance than moments with activity. Metric “r” for irradiant light also influenced brightness, in a moderate and positive correlation, indicating more saturated lights (Forest Shade) had higher brilliance values, however the standard error of this variable is high.

Brilliance variation at short distance analysis was explained by all variables used on the models – “r” metric for object, area of study, substrate (foliage or soil) and object color. Metric “r” is negatively correlated to brilliance, showing objects with more saturated colors are darker. This way, black objects reduces the brilliance of a substrate, and yellow ones amplify the brilliance. Soil is composed mainly of yellow and brown objects, so it is a more brighter environment than foliage, thus soil is positively correlated to brightness values. Also, brightness is a response of "r" metric, indicating that more saturated objects are darker. Ducke area had slightly more bright substrate ambient than Dimona and Esteio. These results show brilliance at short distance analysis is a response to many variables and it is difficult to control its values and direction.

Our data show achromatic values at long distance analysis are high variable along the day, the seasons and study areas, having a proportional range of variation of 1:1300 times. Plumages vary in brilliance between 1:300 times and objects between 1:60 times in achromatic values. Because there is such high variation in achromatic cues, we believe achromatic contrast promoted by radiating light or background objects has low or no influence on habitat selection and on the reproductive behavior of the species. Achromatic contrast cues are not used in this work and therefore not investigated, but the high variability in total brilliance suggests that it would be difficult to represent a selective force on a stereotyped behavior. We found no indications of advantages for White-fronted manakin for displaying at soil level as a response to brilliance values, and so, probably the selection of ground level is not correlated to the brightness of the decomposing leaves.

The importance of achromatic cues for birds is not well defined. Goldsmith and collaborators (1981) showed that hummingbirds cannot discriminate color of feeders based only on achromatic signals. On the other hand, Osorio and collaborators (1999) showed that domestic chicken uses achromatic signals for small objects recognition. Data on passerine birds are lacking, although the double cones, responsible for achromatic vision, has low variation among the birds (Hart and Hunt 2007), so we could expect low variation in importance of such contrast characteristic among bird groups. The presented models suggests no selection on brighter habitats, in opposition to Endler and Théry (1996) results. White-fronted manakin at Ducke presents higher activity rates (table 2), and this area has a brighter Cloudy environment and also the only measured Forest Shade environment (figure 5). No statistical variance on brightness occurs between lek and non-lek areas, or between moments with or without activity. Therefore, this variation in display activity, in response to brighter conditions among areas, may be a result of stochastic behavioral variation among populations, and so might be misleading.

Our results show no relationship between background brightness and White-fronted manakin activity rates, as the activity rate is higher at one study area, independently of its luminous conditions (table 2). This results are not confirming behavioral data of Endler and Théry (1996), who concluded that White-fronted manakin prefer darker environments. In French Guiana, the species follows the darker areas shaded by a mountain (Théry 1990), and, when sun is not blocked by the mountain, males prefer to perform displays under Cloudy conditions. Cloudy light condition is assumed by the authors to be darker than Forest Shade, in opposition to our results (Figure 5). This way, Endler and Théry (1996) showed that the species prefer darker environments, either Cloudy environments or mountain shade, which are two quite different things in terms of spectral properties and likely in terms of contrast values.

## Type of light environment

Regarding chromatic contrast, our results show that contrast of White-fronted manakin is higher in Forest Shade than in Cloudy or Sunny Gap conditions (table 3). Therefore, the behavior of following a mountain, if the Sensory Drive prediction is true for White-fronted manakin French Guianan population, may be a result of avoiding Sunny Gaps. The selection of Cloudy moments for performing displays observed in French Guiana is, though, opposite to Sensory Drive prediction. Furthermore, we found leks in large gaps areas (unfortunately Sunny Gap light condition was unmeasured due to Cloudy conditions), indicating that males of Central Amazon population have low or none preference for darker areas. For example, one lek, which is occupied at least since 2010, was divided into two by a dirt road, showing that this male is probably not highly affected by this bright habitat.

Considering the entire plumage, the large variation in contrast values between ambient types of light (table 3) can be used for turn males more conspicuous during the main breeding season. In a general, males are 30% more conspicuous (average JNDS values increasing from 15.60 to 20.32) and females 20% less conspicuous (contrast values decaying from 21.76 to 17.30 JNDS) in Forest Shade environment, while comparing with Cloudy environments (table 2). This variation can be proposed as the primary cause for reproductive activity being higher at dryer months, when Forest Shade environment is preeminent. If the Sensory Drive prediction is true for the studies population, Females might prefer reproducing in a period when males are more conspicuous, and might also avoid possible predators by selecting a period of the year when they are more camouflaged. Therefore, we do not know if nest predation is high for the species, so, the possible behavior of females avoiding a period of the year whereas they are more inconspicuous may be cue of other selective forces or simply a stochastic behavior. Physiological cues can be another cause for this preference of females for reproduction under dryer conditions, since females may have less energy spending for feeding juveniles in the rainy season, as a result of avoiding hypothermic conditions and lower feeding resources. Non-adaptive preferences, as Fisherian Runaway process (Fisher 1930), can be another explanation for variation in activity between seasons.

## Color contrast of plumage patches

Plumage reflectance spectra shows a high reflective curve for the white front-head plumage (figure 2, panel A). This spectra is also highly affected by modifications in ambient light (table 3), having contrasts values 3.4 times higher under Forest Shade light, in comparison with Cloudy environments. Other adult male plumage which presents large variation in contrast values are the black chin and black breast. Breast is not shown during displays, but chin and front-head are areas shown during courtship. We cannot conclude if these patches are shown in displays as a response to its higher contrast values. If JNDS values are higher than 2, the patches are distinguishable, as shown by Defrize and collaborators (2010). Therefore, the contrast values of the main variable plumage patches are above thresholds for discrimination (average values > 2 JNDS) and we do not know if showing these patches could represent a big advantage for the species.

The five regions with black plumages have different curve shapes (figure 2, panel B), and also distinct variation in JNDS values (table 3). TCS considers black plumages achromatic when relative brilliance is less than 3%, but this is an arbitrary cut. We do not know if birds would see colors in these patches, since these five plumages seems black to human eyes, but only three were considered achromatic for TCS calculations. JNDS values were overlapped for three of this plumages (wing, throat and back), and was distorted when comparing with Span values, so we did not use these plumages on the average JNDS values used on the glmm. Although, we do not know if this high values of JNDS for achromatic plumages are real or just artifacts, especially because black colors and white irradiant lights follows near the tetrahedral origin, and this way we could expect that black and white colors presents lower JNDS values among each other (like front head and chin patches present in our calculations). Other distortions in JNDS occur when the patch has saturated color – as orange throat patch and females blue-green back (figure 2). This distortion may be result of JNDS calculation, which uses log normal values in its calculations (Stoddard and Prum 2008), and so it calculates high values for some colors. The highly contrasting the green individual plumage is located at an area without any object or light spectra, thus this spectra has the highest contrast values for Long Distance analysis of all plumages analyzed, as shown in table 3.

Best glmm model for explaining individual plumage patch contrast has color of plumage patch, “r” metric of plumage patch and “r” metric of irradiance light as explanatory variables. Irradiance light is divided in two contrast group values – Forest Shade and Cloudy conditions, which has distinct values and represents two isolated groups (figure 3, panel D), and “r” metric for irradiant light incorporates such variation, as already discussed. Plumage color and “r” metric for plumage color are related, as “r” represents the saturation of such color (e.g. a black plumage has an unsaturated achromatic color and a white plumage has a saturated achromatic color). We could represent a color by other TCS metrics, as angles phi and theta, which measures the vector direction in a tetrachromatic color space and add information on Ultra Violet range (Stoddard and Prum 2008). But we preferred to choose color like humans see because it is a categorical variable of simple interpretation which incorporates the variation of the hue angles and, mainly, because White-fronted manakin does not have two plumages metameric for human eyes. Here we show that plumage characteristics are more relevant for discriminating colors and that illuminant and objects background has little or no influence on contrast values, and also show that intrinsic characteristics of plumage (color and saturation) are more important for contrast values than background ambient (table 4). The influence of plumage color and "r" of plumage color in JNDS variation between the plumage patches indicates that variation in JNDS score values are highly influenced by each plumage patch, partly corroborating Anciães (2005) conclusions and Stoddard and Prum predictions (2008) that plumage reflectance is important and that environment colors are not important for chromatic contrast discrimination.

## Conclusions

With little variation on spectral properties of irradiant light, high variation in brilliance properties and moderate variation on brilliance of background object colors, we should expect Sensory Drive is not a highly influencing force on habitat selection of the White-fronted manakin in Central Amazon. The species population of Central Amazon shows no selection for performing displays under specific moments or at specific places as response to higher chromatic contrast values. Daily vocalization rates are result of presence of other individuals at leks, but our models failed proposing primary causes of instantaneous variation in vocalization, and a stochastic null model is the best model for explaining such variation.

Endler and Théry (1996) proposed White-fronted manakin, in French Guiana, follows a mountain shade and prefer to perform displays under Cloudy conditions due supposed high contrast values under these conditions. Application of Vorobyev-Osorio physiological model (1998) for estimating contrast values of the species shows that, if the Sensory Drive hypothesis is true, the species should prefer Forest Shade environment. So, we propose the behavior of following a mountain shade could be an adaptation of avoiding sunny gaps environments, if Sensory Drive promotes habitat selection on the White-fronted manakin in French Guiana. Because central Amazon has few mountains, the behavior of avoiding sunny gaps may not have evolved in this population. Furthermore, White-fronted manakin in Central Amazon seems to be low affected by more brightly habitats. We encourage future researches on this population preference for using distinct light habitats, even without measuring light spectra, since we failed measuring behavior during main reproductive station and we do not know if the species prefer a specific light condition for performing displays. A population could prefer performing courtships due stochastic preference, as Runaway Fisherian selection (Fisher 1930), and variation between populations should be expected, as it occurs between Suriname, French Guiana and Central Amazon populations of White-fronted manakin.

Our data show that Sensory Drive has no force in short or long distances contrasts for habitat selection of the White-fronted manakin populations of Central Amazon, and the Sensory Drive mechanisms may influence these populations on the selection of the main reproductive period. The suggested selection of main reproductive period may be a consequence of, at least, four non-exclusive selective forces: 1) females may be favored by natural selection for breeding under Forest Shade moments, because this ambient light promotes lower contrast values for females plumages while 2) increases contrast of males, thus reducing search cost to females (in accordance to the Sensory Drive predictions); 3) Individuals may be favored by natural selection for lower female reproductive investment, since the season with higher Forest Shade frequency has lower rainfall; 4) selection of breeding season may be a consequence of Fisherian runway selection, or other stochastic factors. On the other hand, plumage contrast models shows high influence of plumage color and plumage saturation in JNDS values of each patch. This result indicates that high part of variation is due plumage properties, and ambient selection may be of low importance in how these organisms see conspecifics. This way, ambient light spectra and objects background color would be of low or none importance for habitat selection on this species.

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## FIGURE LEGENDS

**Figure 1.** Photographs of the White-fronted manakin. A – adult male in front posture, note white insertion in front-head, orange insertion in breast and yellow color of belly. Photograph by JA Alves, available at http://www.wikiaves.com.br/683788. B – adult male in back posture, note iridescent blue rump. Photograph by K Okada, available at http://www.wikiaves.com.br/6980701. C – green individual (female or juvenile) in side posture. Note olive-green of wing and brightest area on front-head. Photograph by JA Alves, available at http://www.wikiaves.com.br/686372. D – green individual in backside posture. Note olive-green wing and tail, blue-green back and brightest front-head. Photograph by B Salavori, available at http://www.wikiaves.com.br/713077.

**Figure 2.** Reflectance spectra of plumages. Panel A – reflectance spectra of colored patches of adult male plumages. Panel B – reflectance of black plumages of adult male individuals. Panel C – plumage patches of green individuals.

**Figure 3.** Examples of reflectance spectra of background objects. Color lines represents how human see the objects.

**Figure 4.** Normalized brilliance (for integrals = 1) of irradiance spectra (Mean +- SD) of three classes of ambient light – Forest Shade (N=34), Cloudy (N=50) and Sunny Gap (N=24).

**Figure 5.** Brilliance variation between areas and type of light. FS – Forest Shade, CL – Cloudy. All measurements at Dimona and Esteio were taken under cloudy conditions.

**Figure 6.** Tetrahedral projection of colors as birds see them. A – Variation in plumage spectra of adult males (nine regions; volume – 3,5394^-4, B – Variation of green individual plumage (six regions; volume = 1,6463^-4, C – sample of 254 objects of background (volume

= 9,8988^-3); 4 – Activity light, D – irradiance spectra in moments of activity (84 points; volume = 1,8366^-4) showing grouping in two classes – forest shade (down) and cloudy (top) ambient lights.

**Figure 7.** JNDS variation explaining vocalization rates at long (panel A) and short distance (panel B) analysis.

## TABLES

**Table 1.** Description of answer variables and explanatory variables used in glmm models.

| **Answer variables** | **Explanatory variables** | **Description** |
|---|---|---|
| Instantaneous vocalization rate | | Rate of vocalizations per each ten minutes interval |
| | Instantaneous individual rate | Rate of individuals per 10 minutes interval |
| | Irradiance brilliance | Irradiance brilliance |
| | Average JNDS | Average JNDS for six adult males patches |
| | Playback | Presence or absence of playback in the day |
| | “r” of light | Irradiant light “r” metric |
| Average JNDS | | |
| | Area | Study area |
| | Irradiance brilliance | |
| | Lek | If the measurement point is at a lek or non-lek site |
| | Moment | Moment with or without activity |
| | “r” of light | |
| Irradiance brilliance | | |
| | Area | |
| | Lek | |
| | Moment | |

| | | |
|---|---|---|
| | “r” of light | |
| Daily vocalization rate | | Rate of vocalizations for each day |
| | Area | |
| | Daily individual rate | Rate of individuals all long the day |
| | Average JNDS | |
| | Object brilliance | Brilliance of the background object |
| | Object color | Color of the background object |
| | “r” of object | Background object “r” metric |
| JNDS average for adult individual | | Average JNDS for black individuals |
| | Area | |
| | Object brilliance | |
| | Object color | |
| | “r” of object | |
| | Substrate | Substrate of analysis - soil or foliage |
| JNDS average for green individual | | Average JNDS for green individuals |
| | Area | |
| | Object brilliance | |
| | Object color | |
| | “r” of object | |
| | Substrate | |
| Object brilliance | | |
| | Area | |
| | Object color | |

| | | |
|---|---|---|
| | “r” of object | |
| | Substrate | |
| Plumage patch contrast | | JNDS values for each plumage patch |
| | Distance | Distance analysis of the JNDS values (short or long distance) |
| | Object color | |
| | Plumage brilliance | Brilliance of the plumage patch |
| | Plumage color | Color of the plumage patch |
| | “r” of light | |
| | “r” of object | |
| | “r” of plumage | “r” metric of plumage patch |

**Table 2.** Percentage of observed intervals with activity, per area and type of light.

| | **Dimona** | **Ducke** | | **Esteio** |
|---|---|---|---|---|
| Type of light | Cloudy | Forest Shade | Cloudy | Cloudy |
| Percentual of intervals with activity | 7,49 | 16,00 | 16,96 | 7,31 |

**Table 3.** Variation in contrast values (JNDS) for each plumage patch in different ambient lights. Values: average JNDS +- SD. *as human see, ** courtesy of Anciães, [1]male plumage, [2]green plumage.

| **Plumage patch** | **Color *** | **Cloudy (N=50)** | **Forest Shade (N=34)** | **Sunny Gap** (N=24)** |
|---|---|---|---|---|
| Back[1] | Black | 59.52+-1.50 | 69.72+-1.60 | 62.58+-0.91 |
| Crown[1] | White | 4,81+-1.39 | 16.25+-1.96 | 5.00+-0.98 |
| Chin[1] | Black | 3.35+-1.03 | 11.91+-1.94 | 1.23+-0.65 |
| Throat[1] | Orange | 37.17+-1.74 | 27.11+-1.59 | 34.66+0.90 |
| Wing[1] | Black | 54.32+-1.85 | 62.22+-1.86 | 57.01+-0.99 |
| Tail[1] | Black | 59.49+-1.51 | 69.75+-1.61 | 62.54+-0.91 |
| Rump[1] | Blue | 22.24+-1.51 | 33.10+-1.72 | 25.26+-0.91 |
| Belly[1] | Yellow | 15.21+-1.49 | 10.76+-0.66 | 12.71+-0.74 |
| Breast[1] | Black | 10.76+-1.70 | 22.78+-1.84 | 13.63+-0.96 |
| Head[2] | Green | 14.35+-5.08 | 6.81+-1.01 | 9.74+-0.79 |
| Back[2] | Blue-green | 70.29+-3.50 | 65.17+-1.02 | 68.24+-0.74 |
| Throat[2] | Green | 10.48+-4.39 | 3.39+-0.59 | 3.04+-0.81 |
| Breast[2] | Green | 8.91+-2.00 | 6.63+-1.49 | 6.04+-0.37 |
| Rump[2] | Green | 17.00+-3.37 | 12.15+-0.58 | 14.61+-0.58 |

| | | | | |
|---|---|---|---|---|
| Belly[2] | Yellow | 9.52+-1.20 | 9.63+-1.48 | 7,65+-0.67 |

**Table 4.** Effects of variables on the best fitted models. Acronyms: Df – degrees of freedom, dAIC – delta AIC, Std. Dev. – standard deviation, Std. Error – standard error, vocl – vocalization rate for each ten minutes interval, iind – instantaneous individual presence rate, pb – playback (presence or absence), rlt – irradiance light “r” metric, jna – average JNDS, mom – moment with or without activity, area – study area, brir – irradiance brilliance, vocs – vocalization rate for each day, rob – irradiant light “r” metric, dind – daily individual presence rate, jnab – average JNDS of adult male plumage patches, corob – object color as human see, rob – object “r” metric, jnag – average JNDS of green individual plumage patches, brob – object brilliance, subs – substrate of each object (soil or foliage), plum – JNDS values for each plumage patch, copl – color of plumage as human see, rpl – plumage patch “r” metric, brpl – plumage brilliance. *This null model has no fixed or random effects, since it was built based only on the response variable.

| **Response variable** | **Models** | **Weight** | **Random effects** | | | **Fixed Effects** | | |
|---|---|---|---|---|---|---|---|---|
| | | | **Groups name** | **Variance** | **Std. Dev.** | **Groups name** | **Estimate** | **Std. Error** |
| Instantaneous vocalization rate | Null* | 1 | - | - | - | - | - | - |
| Average JNDS | jna_mom_area_rlt | 0.9663 | Point (Intercept) | 0.47635 | 0.69018 | (Intercept) | 1.46791 | 0.35989 |
| | | | Residual | 0.64470 | 0.80293 | WithoutActivity | -0.03087 | 0.11524 |
| | | | | | | Dimona | -1.22806 | 0.40829 |
| | | | | | | Esteio | -1.51773 | 0.49713 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | | | “r” of light | 25.71593 | 1.56988 |
| Irradiance brilliance | brir_area_mom_rlt | 1 | Point (Intercept) | 5928090 | 2434.8 | (Intercept) | 1805.3 | 991.7 |
| | | | Residual | 1351293 | 1162.5 | Dimona | -1143.2 | 1369.5 |
| | | | | | | Esteio | -988.8 | 1692.6 |
| | | | | | | WithoutActivity | 180.9 | 168.2 |
| | | | | | | "r" of light | 1737.6 | 2391.7 |
| Daily vacolization rate | vocs_dind | 0.6306 | Point (Intercept) | 0.14306 | 0.37823 | (Intercept) | -0.0005495 | 0.0937650 |
| | | | Residual | 0.88636 | 0.94147 | tx_ind | 3.5811466 | 0.0974155 |
| JNDS average for adult male individuals | jnab_corob _rob | 0.35781 | Point (Intercept) | 1.0373 | 1.0185 | (Intercept) | 13.0968 | 0.3258 |
| | | | Residual | 4.2235 | 2.0551 | Brown_obj | 1.2484 | 0.2985 |
| | | | | | | Black_obj | 3.1481 | 0.6488 |
| | | | | | | Green_obj | 1.0316 | 0.1985 |
| | | | | | | “r” of object | 34.4155 | 1.0944 |
| | jnab_corob_area_rob | 0.35755 | Point (Intercept) | 0.21191 | 0.46033 | (Intercept) | 27.83839 | 0.23570 |
| | | | Residual | 2.32678 | 1.52538 | Brown_obj | 1.09649 | 0.22135 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | | | Black_obj | 1.71587 | 0.47974 |
| | | | | | | Green_obj | -0.92345 | 0.14678 |
| | | | | | | Dimona | 0.42955 | 0.28451 |
| | | | | | | Esteio | 0.07892 | 0.27160 |
| | | | | | | "r" of object | 38.18987 | 0.80215 |
| JNDS average for green individuals | jnag_corob_rob | 0.2980 | Point (Intercept) | 1.2108 | 1.004 | (Intercept) | 17.1347 | 0.3734 |
| | | | Residual | 6.1604 | 2.482 | Brown_obj | 1.3138 | 0.3603 |
| | | | | | | Black_obj | 4.1600 | 0.7829 |
| | | | | | | Green_obj | -1.8792 | 0.2395 |
| | | | | | | "r" of object | 34.6072 | 1.3188 |
| | jnag_corob_area_rob | 0.2650 | Point (Intercept) | 1.2164 | 1.1029 | (Intercept) | 16.7778 | 0.4705 |
| | | | Residual | 6.1594 | 1.4818 | Brown_obj | 1.3215 | 0.3608 |
| | | | | | | Black_obj | 4.1941 | 0.7833 |
| | | | | | | Green_obj | -1.8719 | 0.2397 |
| | | | | | | Dimona | 0.9339 | 0.6473 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | | | Esteio | 0.3881 | 0.6149 |
| | | | | | | "r" of object | 34.5732 | 1.3193 |
| Object brilliance | brob_rob_area_subs_corob | 1 | Point (Intercept) | 539777 | 734.7 | (Intercept) | 5838.0 | 320.0 |
| | | | Residual | 2809729 | 1676.1 | “r” of object | -15142.7 | 891.0 |
| | | | | | | Dimona | -282.0 | 433.0 |
| | | | | | | Esteio | -143.2 | 411.3 |
| | | | | | | Soil | 911.1 | 331.2 |
| | | | | | | Brown_obj | -556.4 | 243.8 |
| | | | | | | Black_obj | -4466.6 | 564.5 |
| | | | | | | Green_obj | -933.4 | 165.4 |
| Plumage patches contrast | plum_rlt_copl_rpl | 1 | Point (Intercept) | 0.41715 | 0.64587 | (Intercept) | -18.9710 | 0.6242 |
| | | | Residual | 24.85674 | 4.98565 | "r" of light | 31.9572 | 2.2885 |
| | | | | | | "r" of plumage | 132.5928 | 1.7884 |
| | | | | | | Blue plumage | 17.0548 | 0.3238 |
| | | | | | | White plumage | 17.7950 | 0.5245 |

| | | |
|---|---|---|
| Black plumage | 12.9433 | 0.4218 |

**FIGURES**

Figure 1 .

Figure 2.

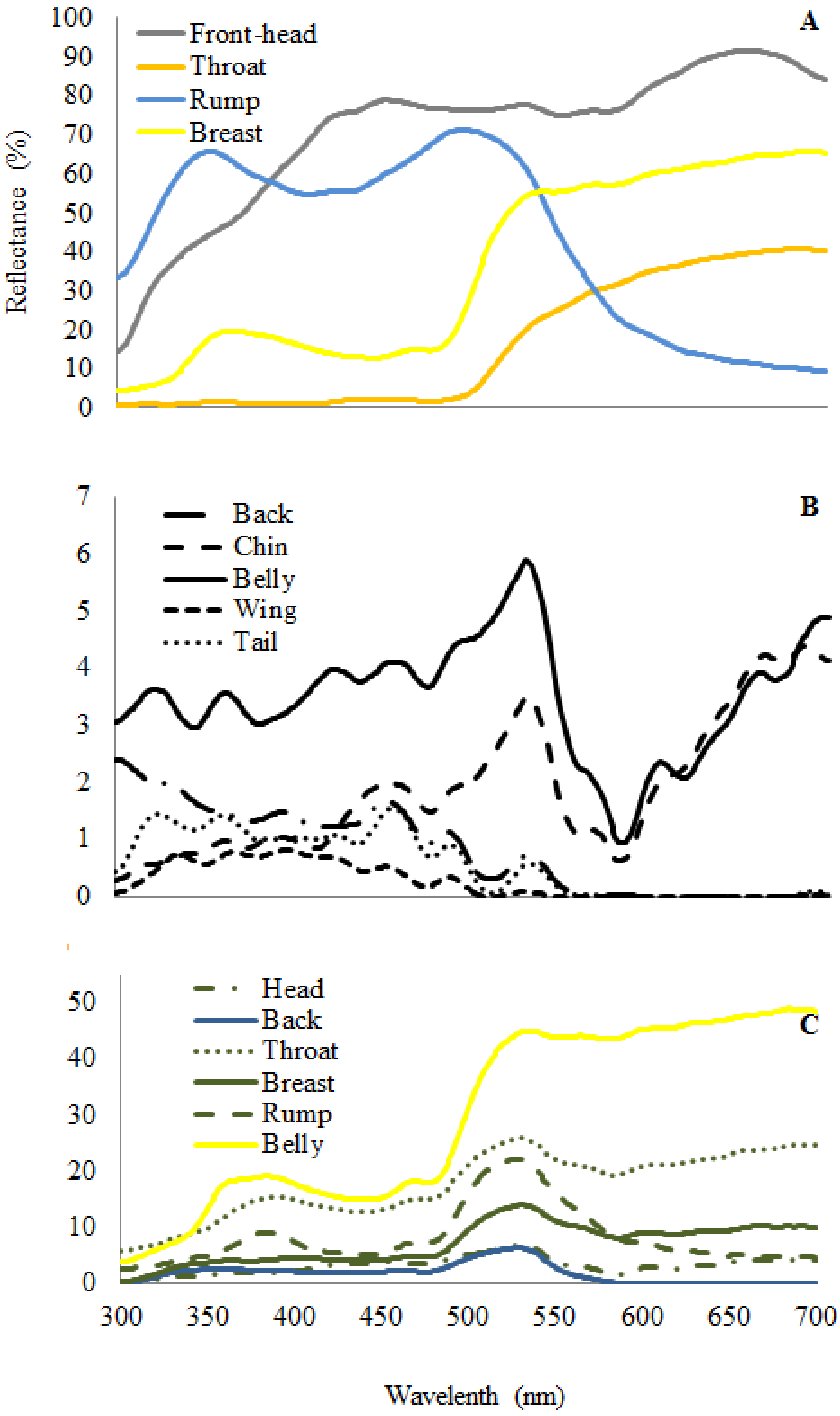

A
Front-head
Throat
Rump
Breast
Reflectance (%)
100
90
80
70
60
50
40
30
20
10
0
B
Back
Chin
Belly
Wing
Tail
7
6
5
4
3
2
1
0
C
Head
Back
Throat
Breast
Rump
Belly
50
40
30
20
10
0
300
350
400
450
500
550
600
650
700
Wavelenth (nm)

Figure 3.

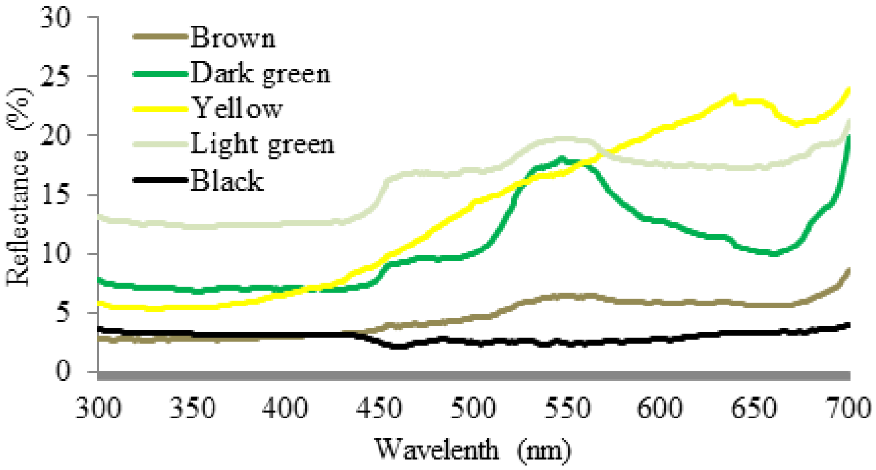


Figure 4.

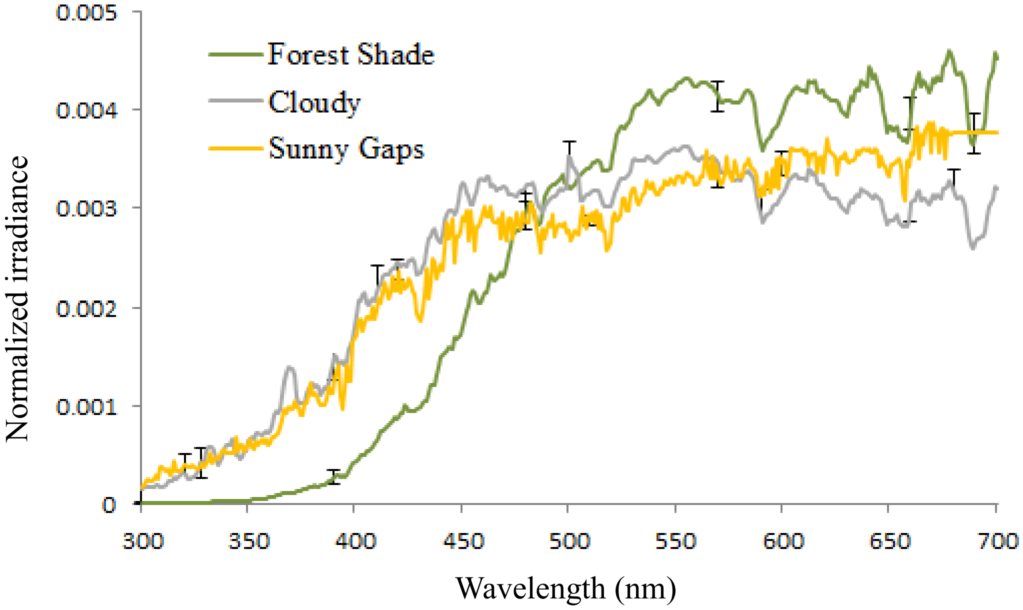


Figure 5.

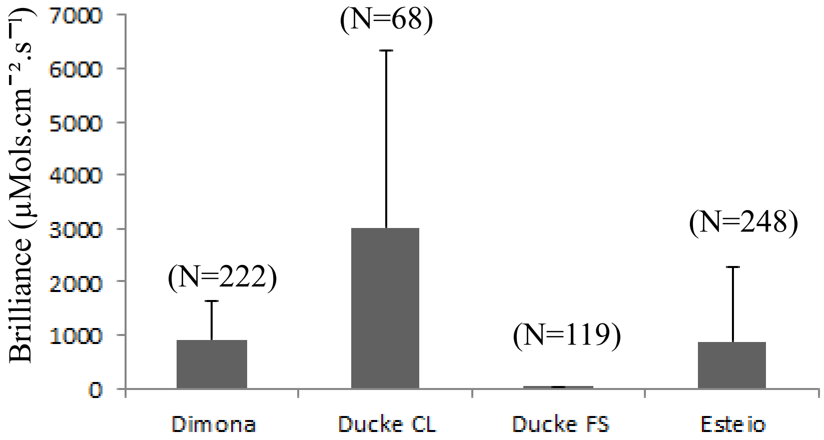


Figure 6.

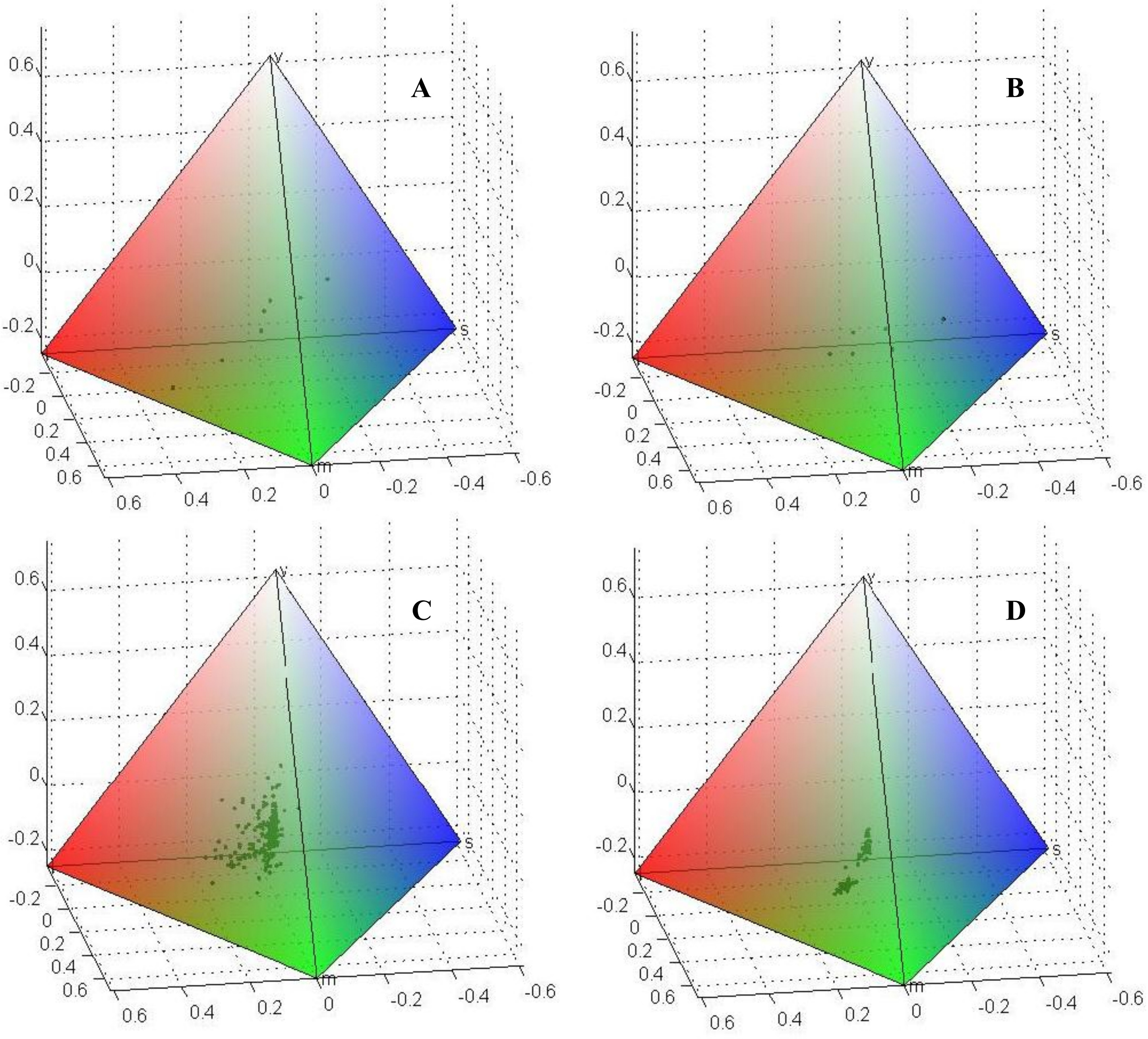
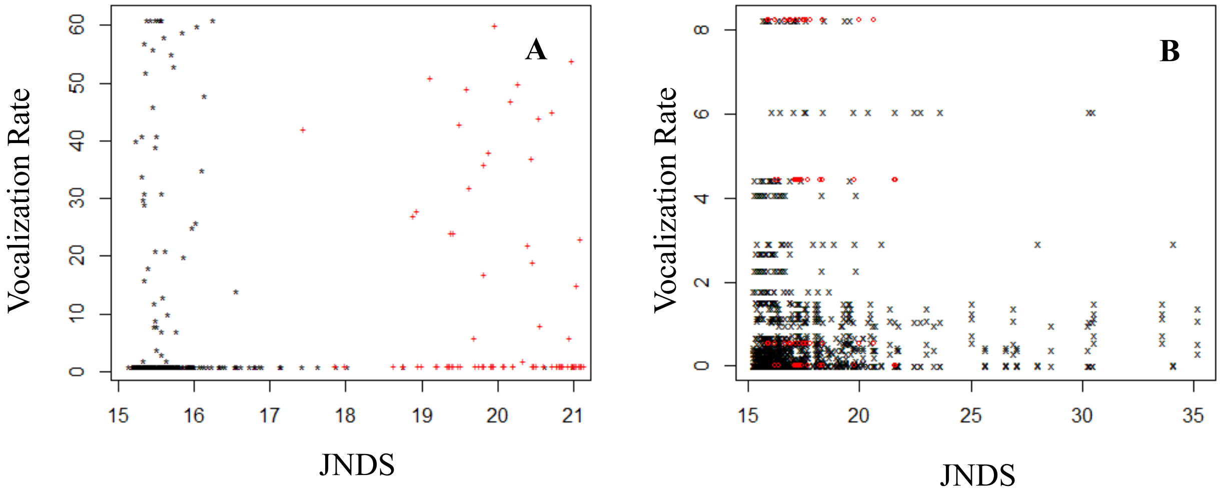


Figure7.


A
Vocalization Rate
0
10
20
30
40
50
60
15
16
17
18
19
20
21
JNDS
B
Vocalization Rate
0
2
4
6
8
15
20
25
30
35
JNDS

## SUPPLEMENTS

**Table S1.** Models testing effects of explanatory variables on variation of vocalization rates. Best fitted model is null, weight = 100%. Acronyms: vocl – vocalization rate for each ten minuts interval, iind – instantaneous individual presence rate (for each ten minutes), pb – playback (presence or absence), rlt – irradiance light “r” metric, jna – average JNDS for six plumage patches of adult males, brir – irradiance brilliance, Df – degrees of freedom, dAIC – delta AIC. Detailed explanations for variables and null models are described in the text.

| **Models** | **AIC** | **Df** | **dAIC** | **Weight** |
|---|---|---|---|---|
| Null1 | 2 | 0 | 0 | 1 |
| vocl_iind_pb_rlt | 2397.8 | 6 | 2395.8 | <0.001 |
| vocl_iind_pb_rlt_jna | 2400.8 | 7 | 2398.8 | <0.001 |
| vocl_iind_pb | 2401.5 | 5 | 2399.5 | <0.001 |
| vocl_iind_pb_jna | 2405.2 | 6 | 2403.2 | <0.001 |
| vocl_iind_brir_pb_rlt | 2415.5 | 7 | 2413.5 | <0.001 |
| vocl_iind_brir_pb_rlt_jna | 2418.5 | 8 | 2416.5 | <0.001 |
| vocl_iind_brir_pb | 2419.2 | 9 | 2417.2 | <0.001 |
| vocl_iind_brir_pb_jna | 2423.0 | 7 | 2421.0 | <0.001 |
| vocl_pb_rlt | 2627.5 | 5 | 2625.5 | <0.001 |
| vocl_pb_rlt_jna | 2629.2 | 6 | 2627.2 | <0.001 |
| vocl_pb | 2631.9 | 4 | 2629.9 | <0.001 |
| vocl_pb_jna | 2634.6 | 5 | 2632.6 | <0.001 |
| vocl_brir_pb_rlt | 2643.5 | 6 | 2641.5 | <0.001 |
| vocl_brir_pb_rlt_jna | 2645.4 | 7 | 2643.4 | <0.001 |

| | | | | |
|---|---|---|---|---|
| vocl_bril_pb | 2647.9 | 5 | 2645.9 | <0.001 |
| vocl_brir_pb_jna | 2650.8 | 6 | 2648.8 | <0.001 |
| vocl_iind_rlt | 3532.4 | 5 | 3530.4 | <0.001 |
| vocl_iind | 3535.1 | 4 | 3533.1 | <0.001 |
| vocl_iind_rlt_jna | 3536.5 | 6 | 3534.5 | <0.001 |
| vocl_iind_jna | 3539.4 | 5 | 3537.9 | <0.001 |
| vocl_iind_brir_rlt | 3550.9 | 6 | 3548.9 | <0.001 |
| vocl_iind_brir | 3553.7 | 5 | 3551.7 | <0.001 |
| vocl_iind_brir_jna | 3558.4 | 6 | 3556.4 | <0.001 |
| vocl_rlt | 3913.2 | 4 | 3911.2 | <0.001 |
| vocl_rlt_jna | 3916.2 | 5 | 3914.2 | <0.001 |
| Null2 | 3916.6 | 3 | 3914.6 | <0.001 |
| vocl_jna | 3920.4 | 4 | 3918.4 | <0.001 |
| vocl_brir_rlt | 3931.0 | 5 | 3929.0 | <0.001 |
| vocl_brir_rlt_jna | 3934.1 | 6 | 3932.1 | <0.001 |
| vocl_brir | 3934.4 | 4 | 3932.4 | <0.001 |
| vocl_brir_jna | 3938.2 | 5 | 3936.2 | <0.001 |

**Table S2.** Generalized linear mixed models for long distance contrast values (average JNDS). Best fitted model includes vocalization rate, moment, localization (area) and irradiance light “r” metric, weight = 96.33%. Acronyms: area – study area (e.g. Dimona), lek – lek or not-lek sites, mom – moments with or without activity, else see table S1.

| **Models** | **AIC** | **Df** | **dAIC** | **Weight** |
|---|---|---|---|---|
| jna_mom_area_rlt | 1051.9 | 7 | 0 | 0.9633 |
| jna_mom_rlt | 1058.6 | 5 | 6.7 | 0.0337 |
| jna_mom_area | 1245.5 | 6 | 193.7 | <0.001 |
| jna_mom | 1254.0 | 4 | 202.1 | <0.001 |
| jna_area_rlt | 1742.9 | 6 | 691.0 | <0.001 |
| jna_area_rlt_lek | 1745.2 | 7 | 693.3 | <0.001 |
| jna_rlt | 1746.8 | 4 | 694.9 | <0.001 |
| jna_rlt_lek | 1749.0 | 5 | 697.2 | <0.001 |
| jna_area | 1995.6 | 5 | 943.7 | <0.001 |
| jna_area_lek | 1996.6 | 6 | 944.7 | <0.001 |
| Null2 | 2002.4 | 3 | 950.5 | <0.001 |
| jna_lek | 2003.6 | 4 | 951.7 | <0.001 |
| Null1 | 2893.6 | 1 | 1841.7 | <0.001 |

**Table S3.** GLMM for irradiance brilliance. Best fitted model includes area, moment and irradiance light "r" metric, weight = 100%. Acronyms: see tables S1 and S2.

| **Models** | **AIC** | **Df** | **AIC** | **Weight** |
|---|---|---|---|---|
| brir_area_mom_rlt | 7041.9 | 7 | 0 | 1 |
| brir_area_mom | 7057.9 | 6 | 15.9 | <0.001 |
| brir_mom_rlt | 7071.5 | 5 | 29.6 | <0.002 |
| brir_mom | 7087.5 | 4 | 45.6 | <0.003 |
| brir_area_lek_rlt | 11170.0 | 7 | 4128.0 | <0.004 |
| brir_area_rlt | 11182.8 | 6 | 4140.9 | <0.005 |
| brir_lek_rlt | 11197.5 | 5 | 4156.0 | <0.006 |
| brir_area_lek | 11198.1 | 6 | 4156.2 | <0.007 |
| brir_rlt | 11210.7 | 4 | 4168.8 | <0.008 |
| brir_area | 11210.9 | 5 | 4169.0 | <0.009 |
| brir_lek | 11227.3 | 4 | 4185.4 | <0.010 |
| Null2 | 11240.0 | 3 | 4198.1 | <0.011 |
| Null1 | 11629.0 | 1 | 4587.0 | <0.012 |

**Table S4.** GLMM for vocalization rate in short distance analysis. Best fitted model includes individual presence rate and localization (area), weight = 63.06%. Acronyms: vocs – daily vocalization rate, dind – daily individual presence rate, rob – objects “r” metric, corob – object color as human see (category), brob – object brilliance, else see tables S1 and S2.

| **Models** | **AIC** | **Df** | **dAIC** | **Weight** |
|---|---|---|---|---|
| vocs_dind | 2856.9 | 4 | 0 | 0.63060 |
| vocs_rob_dind | 2858.4 | 5 | 1.5 | 0.29522 |
| vocs_dind_area | 2862.3 | 6 | 5.4 | 0.04173 |
| vocs_rob_dind_area | 2863.9 | 7 | 7.0 | 0.01932 |
| vocs_dind_jna | 2866.2 | 5 | 9.3 | 0.00612 |
| vocs_rob_dind_jn | 2867.1 | 6 | 10.2 | 0.00384 |
| vocs_corob_dind | 2868.9 | 7 | 12.0 | 0.00156 |
| vocs_corob_dind_rob | 2870.4 | 8 | 13.4 | <0.001 |
| vocs_dind_area_jna | 2871.6 | 7 | 14.7 | <0.001 |
| vocs_rob_diind_area_jna | 2872.6 | 8 | 15.7 | <0.001 |
| vocs_corob_dind_area | 2874.4 | 9 | 17.4 | <0.001 |
| vocs_corob_dind_area_rob | 2875.8 | 10 | 18.9 | <0.001 |
| vocs_corob_dind_jna | 2878.1 | 8 | 21.2 | <0.001 |
| vocs_corob_dind_jna_rob | 2879.0 | 9 | 22.1 | <0.001 |
| vocs_brob_dind | 2879.3 | 5 | 22.3 | <0.001 |
| vocs_rob_brob_dind | 2880.6 | 6 | 23.7 | <0.001 |
| vocs_corob_diind_area_jna | 2883.6 | 10 | 26.7 | <0.001 |
| vocs_corob_rob_diind_area_jna | 2884.5 | 11 | 27.6 | <0.001 |
| vocs_brob_dind_area | 2884.7 | 7 | 27.8 | <0.001 |

| | | | | |
|---|---|---|---|---|
| vocs_rob_brob_dind_area | 2886.0 | 8 | 29.1 | <0.001 |
| vocs_brob_dind_jna | 2888.4 | 6 | 31.4 | <0.001 |
| vocs_rob_brob_dind_jna | 2889.2 | 7 | 32.3 | <0.001 |
| vocs_corob_brob_dind | 2891.2 | 8 | 34.3 | <0.001 |
| vocs_corob_brob_dind_rob | 2892.4 | 9 | 35.5 | <0.001 |
| vocs_brob_dind_area_jna | 2893.8 | 8 | 36.9 | <0.001 |
| vocs_rob_brob_dind_arrea_jna | 2894.7 | 9 | 37.8 | <0.001 |
| vocs_corob_brob_dind_area | 2896.7 | 10 | 39.7 | <0.001 |
| vocs_corob_brob_dind_area_rob | 2897.9 | 11 | 41.0 | <0.001 |
| vocs_corob_brob_dind_jna | 2900.3 | 9 | 43.4 | <0.001 |
| vocs_corob_brob_dind_area_jna | 2905.8 | 11 | 48.8 | <0.001 |
| vocs_corob_brob_dind_area_jna_rob | 2906.5 | 12 | 49.6 | <0.001 |
| vocs_area | 3698.3 | 5 | 841.4 | <0.001 |
| vocs_rob_area | 3699.1 | 6 | 842.1 | <0.001 |
| Null2 | 3699.1 | 3 | 842.2 | <0.001 |
| vocs_rob | 3699.4 | 4 | 843.0 | <0.001 |
| vocs_area_jna | 3706.8 | 6 | 849.9 | <0.001 |
| vocs_rob_area_jna | 3706.9 | 7 | 850.0 | <0.001 |
| vocs_jna | 3707.6 | 4 | 850.7 | <0.001 |
| vocs_rob_jna | 3707.8 | 5 | 850.9 | <0.001 |
| vocs_corob_area | 3707.9 | 8 | 851.0 | <0.001 |
| vocs_corob_area_rob | 3708.6 | 9 | 851.7 | <0.001 |
| vocs_corob | 3708.7 | 6 | 851.8 | <0.001 |
| vocs_corob_rob | 3709.4 | 7 | 852.5 | <0.001 |
| vocs_corob_area_jna | 3716.4 | 9 | 859.5 | <0.001 |

| | | | | |
|---|---|---|---|---|
| vocs_corob_area_jna_rob | 3716.4 | 10 | 859.5 | <0.001 |
| vocs_corob_jna | 3717.2 | 7 | 860.3 | <0.001 |
| vocs_corob_jna_rob | 3717.3 | 8 | 860.3 | <0.001 |
| vocs_brob_area | 3719.8 | 6 | 862.9 | <0.001 |
| vocs_rob_brob_area | 3720.4 | 7 | 863.5 | <0.001 |
| vocs_brob | 3720.6 | 4 | 863.7 | <0.001 |
| vocs_rob_brob | 3721.5 | 5 | 864.3 | <0.001 |
| vocs_brob_area_jna | 3728.2 | 7 | 871.3 | <0.001 |
| vocs_rob_brob_area_jna | 3728.2 | 8 | 871.3 | <0.001 |
| vocs_brob_jna | 3729.0 | 5 | 872.1 | <0.001 |
| vocs_rob_brob_jna | 3729.1 | 6 | 872.2 | <0.001 |
| vocs_corob_brob_area | 3729.4 | 9 | 872.4 | <0.001 |
| vocs_corob_brob_area_rob | 3729.8 | 10 | 872.9 | <0.001 |
| vocs_corob_brob | 3730.2 | 7 | 873.3 | <0.001 |
| vocs_corob_brob_rob | 3730.7 | 8 | 873.8 | <0.001 |
| vocs_corob_brob_area_jna | 3730.7 | 10 | 880.8 | <0.001 |
| vocs_corob_brob_jna_rob | 3738.5 | 9 | 881.6 | <0.001 |
| vocs_corob_brob_jna | 3738.5 | 8 | 881.6 | <0.001 |
| Null1 | 4097.2 | 1 | 1240.3 | <0.001 |

**Table S5.** GLMM for contrast (average JNDS) of adult male plumages in short distance analysis. Acronyms: jnab – average JNDS for adult male plumage. Best model includes object color, substrate and object “r” metric, but this model has low weight (45.13%). Acronyms: subs – substrate, else tables S1, S2 and S4.

| **Models** | **AIC** | **Df** | **dAIC** | **Weight** |
|---|---|---|---|---|
| jnab_corob_subs_rob | 3843.9 | 8 | 0.0 | 0.4215 |
| jnab_corob_rob | 3844.2 | 7 | 0.3 | 0.3916 |
| jnab_corob_area_rob | 3847.4 | 9 | 3.5 | 0.0790 |
| jnab_corob_subs_area_rob | 3847.6 | 10 | 3.6 | 0.0733 |
| jnab_corob_brob_subs_rob | 3864.3 | 9 | 20.4 | < 0.001 |
| jnab_corob_brob_rob | 3864.3 | 8 | 20.4 | < 0.001 |
| jnab_corob_brob_area_rob | 3867.6 | 10 | 23.7 | < 0.001 |
| jnab_corob_brob_subs_area_rob | 3868.0 | 11 | 24.1 | < 0.001 |
| jnab_corob_brob_vocs_rob | 3871.3 | 9 | 27.4 | < 0.001 |
| jnab_corob_brob_subs_area_vocs_rob | 3875.0 | 12 | 31.0 | < 0.001 |
| jnab_rob_subs | 3973.1 | 5 | 129.1 | < 0.001 |
| jnab_rob_subs_area | 3975.5 | 7 | 131.6 | < 0.001 |
| jnab_rob | 3977.8 | 4 | 133.9 | < 0.001 |
| jnab_rob_subs_vocs | 3979.9 | 6 | 136.0 | < 0.001 |
| jnab_rob_area | 3981.1 | 6 | 137.1 | < 0.001 |
| jnab_rob_subs_area_vocs | 3982.3 | 8 | 138.4 | < 0.001 |
| jnab_rob_vocs | 3984.6 | 5 | 140.6 | < 0.001 |
| jnab_rob_area_vocs | 3987.7 | 7 | 143.8 | < 0.001 |
| jnab_rob_brob_subs | 3994.0 | 6 | 150.1 | < 0.001 |

| | | | | |
|---|---|---|---|---|
| jnab_rob_brob_subs_area | 3996.5 | 8 | 152.5 | < 0.001 |
| jnab_rob_brob | 3998.8 | 5 | 154.9 | < 0.001 |
| jnab_rob_brob_area | 4002.1 | 7 | 158.2 | < 0.001 |
| jnab_corob_brob | 4875.1 | 7 | 1031.2 | < 0.001 |
| jnab_corob_brob_subs | 4876.4 | 8 | 1032.5 | < 0.001 |
| jnab_corob_brob_area | 4877.1 | 9 | 1033.2 | < 0.001 |
| jnab_corob_brob_subs_area | 4878.3 | 10 | 1034.3 | < 0.001 |
| jnab_corob | 5031.7 | 6 | 1187.8 | < 0.001 |
| jnab_corob_area | 5032.1 | 8 | 1188.1 | < 0.001 |
| jnab_corob_subs | 5033.0 | 7 | 1189.1 | < 0.001 |
| jnab_corob_subs_area | 5033.4 | 9 | 1189.5 | < 0.001 |
| jnab_brob_subs | 5045.0 | 5 | 1201.1 | < 0.001 |
| jnab_brob_subs_area | 5045.5 | 7 | 1201.6 | < 0.001 |
| jnab_brob | 5055.7 | 4 | 1211.8 | < 0.001 |
| jnab_brob_area | 5056.9 | 6 | 1213.0 | < 0.001 |
| jnab_subs_area | 5167.3 | 6 | 1323.3 | < 0.001 |
| jnab_subs | 5167.8 | 4 | 1323.9 | < 0.001 |
| Null2 | 5176.1 | 3 | 1332.2 | < 0.001 |
| jnab_area | 5176.2 | 5 | 1332.2 | < 0.001 |
| Null1 | 5320.9 | 1 | 1477.0 | < 0.001 |

**Table S6**. GLMM for contrast (average JNDS) of green individual plumages in short distance analysis. Acronyms: jnag – average JNDS for green individuals. Best fitted model includes object color and "r" metric of objects, though the weight is not high (29.8%). For other acronyms legends see tables S1, S2, S4 and S5.

| **Models** | **AIC** | **Df** | **dAIC** | **Weight** |
|---|---|---|---|---|
| jnag_corob_rob | 4855.3 | 7 | 0.0 | 0.298 |
| jnag_corob_area_rob | 4855.5 | 9 | 0.2 | 0.265 |
| jnag_corob_subs_rob | 4855.7 | 8 | 0.4 | 0.244 |
| jnag_corob_subs_area_rob | 4856.1 | 10 | 0.9 | 0.193 |
| jnag_corob_vocs_rob | 4861.2 | 8 | 6.0 | < 0.001 |
| jnag_corob_subs_vocs_rob | 4861.6 | 9 | 6.4 | < 0.001 |
| jnag_corob_rob_subs_area_vocs | 4862.1 | 11 | 6.8 | < 0.001 |
| jnag_corob_brob_rob | 4875.1 | 8 | 19.9 | < 0.001 |
| jnag_corob_brob_area_rob | 4875.4 | 10 | 20.2 | < 0.001 |
| jnag_corob_brob_subs_rob | 4875.6 | 9 | 20.4 | < 0.001 |
| jnag_corob_brob_subs_area_rob | 4876.1 | 11 | 20.8 | < 0.001 |
| jnag_rob_subs_area | 5005.0 | 7 | 149.7 | < 0.001 |
| jnag_rob_subs | 5005.7 | 5 | 150.5 | < 0.001 |
| jnag_rob | 5020.0 | 4 | 164.8 | < 0.001 |
| jnag_rob_area | 5020.4 | 6 | 165.1 | < 0.001 |
| jnag_rob_brob_subs_area | 5025.0 | 8 | 169.8 | < 0.001 |
| jnag_rob_brob_subs | 5025.7 | 6 | 170.5 | < 0.001 |
| jnag_rob_vocs | 5025.8 | 5 | 170.5 | < 0.001 |

| | | | | |
|---|---|---|---|---|
| jnag_rob_brob | 5040.1 | 5 | 184.8 | < 0.001 |
| jnag_rob_brob_area | 5040.4 | 7 | 185.2 | < 0.001 |
| jnag_corob_brob_area | 5301.4 | 9 | 446.2 | < 0.001 |
| jnag_corob_brob | 5301.6 | 7 | 446.3 | < 0.001 |
| jnag_corob_brob_subs_area | 5302.4 | 10 | 447.2 | < 0.001 |
| jnag_corob_brob_subs | 5302.6 | 8 | 447.4 | < 0.001 |
| jnag_corob_area | 5379.4 | 8 | 524.2 | < 0.001 |
| jnag_corob_subs_area | 5380.4 | 9 | 525.2 | < 0.001 |
| jnag_corob | 5380.6 | 6 | 525.3 | < 0.001 |
| jnag_corob_subs | 5381.6 | 7 | 526.3 | < 0.001 |
| jnag_brob_subs_area | 5490.4 | 7 | 635.2 | < 0.001 |
| jnag_brob_subs | 5492.1 | 5 | 636.8 | < 0.001 |
| jnag_brob_area | 5511.7 | 6 | 656.5 | < 0.001 |
| jnag_brob | 5512.3 | 4 | 657.0 | < 0.001 |
| jnag_subs_area | 5552.9 | 6 | 697.6 | < 0.001 |
| jnag_subs | 5555.1 | 4 | 699.8 | < 0.001 |
| jnag_area | 5571.5 | 5 | 716.3 | < 0.001 |
| Null2 | 5572.9 | 3 | 717.6 | < 0.001 |
| Null1 | 5747.5 | 1 | 892.2 | < 0.001 |

**Table S7.** GLMM models for brilliance in short distance analysis. Best fitted model has all variables – r metric of objects, area, substrate, object color and average JNDS. Weight = 100%. For acronyms legends see tables S1, S2, S3, S4 and S5.

| **Models** | **AIC** | **Df** | **dAIC** | **Weight** |
|---|---|---|---|---|
| brob_rob_area_subs_corob | 18185.8 | 10 | 0.0 | 1 |
| brob_rob_area_corob | 18204.8 | 9 | 19.0 | <0.001 |
| brob_rob_subs_corob | 18209.9 | 8 | 24.0 | <0.001 |
| brob_rob_corob | 18229.3 | 7 | 43.5 | <0.001 |
| brob_rob_area_subs | 18302.9 | 7 | 117.1 | <0.001 |
| brob_rob_area | 18316.3 | 6 | 130.5 | <0.001 |
| brob_rob_subs | 18326.9 | 5 | 141.1 | <0.001 |
| brob_rob | 18340.4 | 4 | 154.6 | <0.001 |
| brob_area_subs_corob | 18453.2 | 9 | 267.4 | <0.001 |
| brob_area_corob | 18469.0 | 8 | 283.2 | <0.001 |
| brob_subs_corob | 18478.6 | 7 | 292.8 | <0.001 |
| brob_corob | 18494.8 | 6 | 309.0 | <0.001 |
| brob_area_subs | 18529.0 | 6 | 343.2 | <0.001 |
| brob_area | 18540.7 | 5 | 354.9 | <0.001 |
| brob_subs | 18554.5 | 4 | 368.7 | <0.001 |
| Null2 | 18556.2 | 3 | 380.4 | <0.001 |
| Null1 | 18719.6 | 1 | 533.8 | <0.001 |

**Table S8.** GLMM for contrast (JNDS) in each plumage patch. Best fitted model has variables “r” metric of irradiance light, plumage color and “r” metric of plumage, weight = 100%. Acronyms: plum – JNDS of plumage each patch, copl – color of the plumage patch, rpl – “r” metric of the plumage patch, brpl – brilliance of the plumage patch, dist – distance analysis (SD or LD), else see tables S1 and S4.

| **Models** | **AIC** | **Df** | **AIC** | **Weight** |
|---|---|---|---|---|
| plum_rlt_copl_rpl | 23967.2 | 8 | 0.0 | 1 |
| plum_rlt_brpl_copl | 24227.3 | 8 | 260.1 | <0.001 |
| plum_rlt_brpl_rpl | 26087.7 | 6 | 2120.5 | <0.001 |
| plum_rlt_rpl | 26163.5 | 5 | 2196.1 | <0.001 |
| plum_rlt_copl | 27402.4 | 7 | 3435.2 | <0.001 |
| plum_rlt_brpl | 30227.1 | 5 | 6259.9 | <0.001 |
| plum_rlt | 30228.8 | 4 | 6261.5 | <0.001 |
| plum_rob_brpl_corob_copl_rpl | 92998.3 | 13 | 69031.1 | <0.001 |
| plum_rob_copl_corob_rpl | 94170.9 | 12 | 70203.2 | <0.001 |
| plum_rob_copl_rpl | 94199.4 | 9 | 70232.2 | <0.001 |
| plum_rob_brpl_copl_rpl | 94215.7 | 10 | 70248.5 | <0.001 |
| plum_copl_corob_rpl | 94595.6 | 11 | 70628.4 | <0.001 |
| plum_rob_corob_rpl | 97850.7 | 8 | 73883.5 | <0.001 |
| plum_rob_brpl_corob_rpl | 97867.7 | 9 | 73900.5 | <0.001 |
| plum_rob_rpl | 97871.4 | 5 | 73904.1 | <0.001 |
| plum_rob_brpl_rpl | 97887.7 | 6 | 73920.5 | <0.001 |
| plum_brpl_corob_rpl | 97997.7 | 8 | 74030.5 | <0.001 |
| plum_corob_rpl | 98172.6 | 7 | 74205.4 | <0.001 |

| | | | | |
|---|---|---|---|---|
| plum_ brpl_copl _corob | 102155.6 | 11 | 78188.4 | <0.001 |
| plum_ rob_copl _corob | 103370.0 | 11 | 79402.8 | <0.001 |
| plum_rob_copl | 103382.7 | 8 | 79415.5 | <0.001 |
| plum_rob_brpl_copl_corob | 103386.6 | 12 | 79419.4 | <0.001 |
| plum_rob_brpl_copl | 103398.9 | 9 | 79431.7 | <0.001 |
| Plum_copl_corob | 103584.4 | 10 | 79617.2 | <0.001 |
| plum_brpl_corob | 104650.0 | 7 | 80682.8 | <0.001 |
| plum_rob_corob | 104957.1 | 7 | 80989.9 | <0.001 |
| plum_rob | 104968.2 | 4 | 81001.0 | <0.001 |
| plum_rob_brpl_corob | 104973.6 | 8 | 81006.4 | <0.001 |
| plum_rob_brpl | 104984.3 | 5 | 81017.1 | <0.001 |
| plum_corob | 105148.3 | 6 | 81181.1 | <0.001 |
| plum_brpl_copl_rpl | 121116.3 | 9 | 97149.1 | <0.001 |
| plum_copl_rpl_dist | 121867.0 | 9 | 97899.7 | <0.001 |
| plum_copl_rpl | 122015.8 | 8 | 98048.6 | <0.001 |
| plum_brpl_rpl_dist | 126998.7 | 7 | 103031.5 | <0.001 |
| plum_rpl_dist | 127059.8 | 5 | 103092.6 | <0.001 |
| plum_brpl_rpl | 127063.8 | 5 | 103096.5 | <0.001 |
| plum_rpl | 127148.8 | 4 | 103181.6 | <0.001 |
| plum_brpl_copl_dist | 131358.0 | 9 | 107390.7 | <0.001 |
| plum_brpl_copl | 131420.8 | 8 | 107453.5 | <0.001 |
| plum_copl_dist | 133697.8 | 8 | 109730.6 | <0.001 |
| plum_copl | 133734.3 | 7 | 109767.0 | <0.001 |
| plum_brpl_dist | 135953.0 | 5 | 111985.8 | <0.001 |
| Plum_brpl | 135957.8 | 4 | 111990.6 | <0.001 |

| | | | | |
|---|---|---|---|---|
| plum_dist | 136422.7 | 4 | 112455.5 | <0.001 |
| Null2 | 136454.3 | 3 | 112487.1 | <0.001 |
| Null1 | 136527.0 | 1 | 112559.7 | <0.001 |

# CONCLUSÃO

O trabalho aqui apresentado mostra que a hipótese de favorecimento sensorial não explica a seleção de hábitats para a aproximação de curta distância. Além disso, mostramos, para esta análise, que a seleção apenas de objetos verdes não é uma boa aproximação, e que o ambiente de fundo pode variar entre áreas próximas.

Para a aproximação de longa distância, nossos grupos de análises não mostraram influência dos mecanismos de favorecimento sensorial na escolha de leks, tão pouco na seleção de horários de apresentação nestes territórios. Por outro lado, a variação de contraste ao longo das estações reprodutivas é forte. A condição de iluminação ambiental durante as estações reprodutivas (Sombra da Floresta, ou “Forest Shade”) promove valores mais altos de contraste para machos e mais baixos para fêmeas. Assim, o mecanismo pode estar favorecendo a seleção de estação reprodutiva para a espécie.

Por outro lado, esta variação no contraste durante a estação reprodutiva pode ter outras explicações: seleção natural para reduzir as taxas de predação de fêmeas em ninhos, uma vez que estas estão menos conspícuas durante a estação reprodutiva; seleção natural para reduzir o gasto energético de fêmeas durante a estação reprodutiva, uma vez que as chuvas podem redobrar os custos reprodutivos das fêmeas (perda de ninhos, controle homeotérmico e diminuição de alimentos), ou ainda ação de mecanismos estocásticos, como a seleção Runaway proposta por Fisher (1930).

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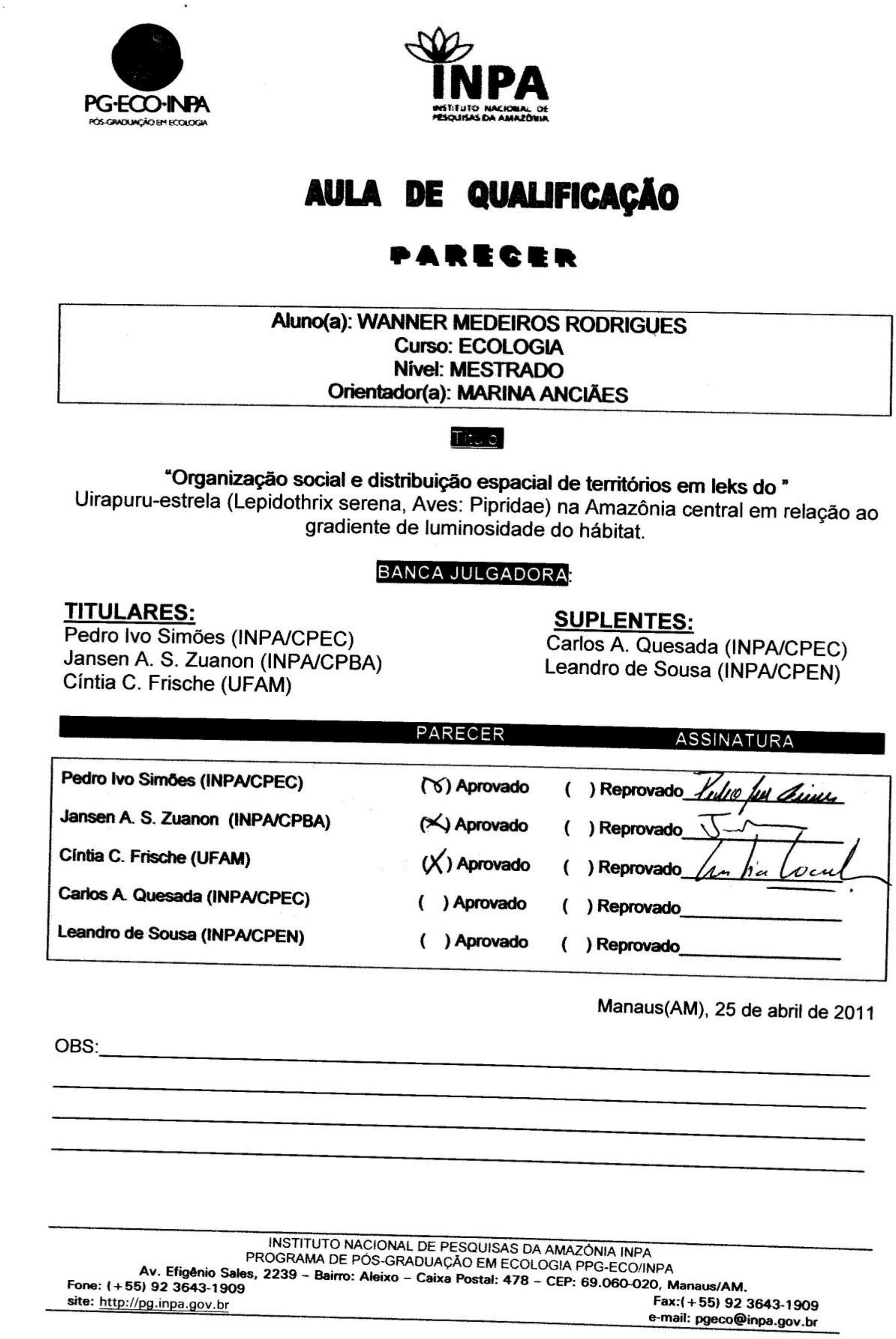
# APÊNCICE A – ATA DE AULA DE QUALIFICAÇÃO



PG-ECO-INPA
PÓS-GRADUAÇÃO EM ECOLOGIA

INPA
INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA

## AULA DE QUALIFICAÇÃO

### PARECER

**Aluno(a): WANNER MEDEIROS RODRIGUES**
**Curso: ECOLOGIA**
**Nível: MESTRADO**
**Orientador(a): MARINA ANCIÃES**

Título

**"Organização social e distribuição espacial de territórios em leks do "**
Uirapuru-estrela (Lepidothrix serena, Aves: Pipridae) na Amazônia central em relação ao gradiente de luminosidade do hábitat.

BANCA JULGADORA:

**TITULARES:**
Pedro Ivo Simões (INPA/CPEC)
Jansen A. S. Zuanon (INPA/CPBA)
Cíntia C. Frische (UFAM)

**SUPLENTES:**
Carlos A. Quesada (INPA/CPEC)
Leandro de Sousa (INPA/CPEN)

| | PARECER | | ASSINATURA |
|---|---|---|---|
| **Pedro Ivo Simões (INPA/CPEC)** | **(X) Aprovado** | **( ) Reprovado** | |
| **Jansen A. S. Zuanon (INPA/CPBA)** | **(X) Aprovado** | **( ) Reprovado** | |
| **Cíntia C. Frische (UFAM)** | **(X) Aprovado** | **( ) Reprovado** | |
| **Carlos A. Quesada (INPA/CPEC)** | **( ) Aprovado** | **( ) Reprovado** | |
| **Leandro de Sousa (INPA/CPEN)** | **( ) Aprovado** | **( ) Reprovado** | |

Manaus(AM), 25 de abril de 2011

OBS:

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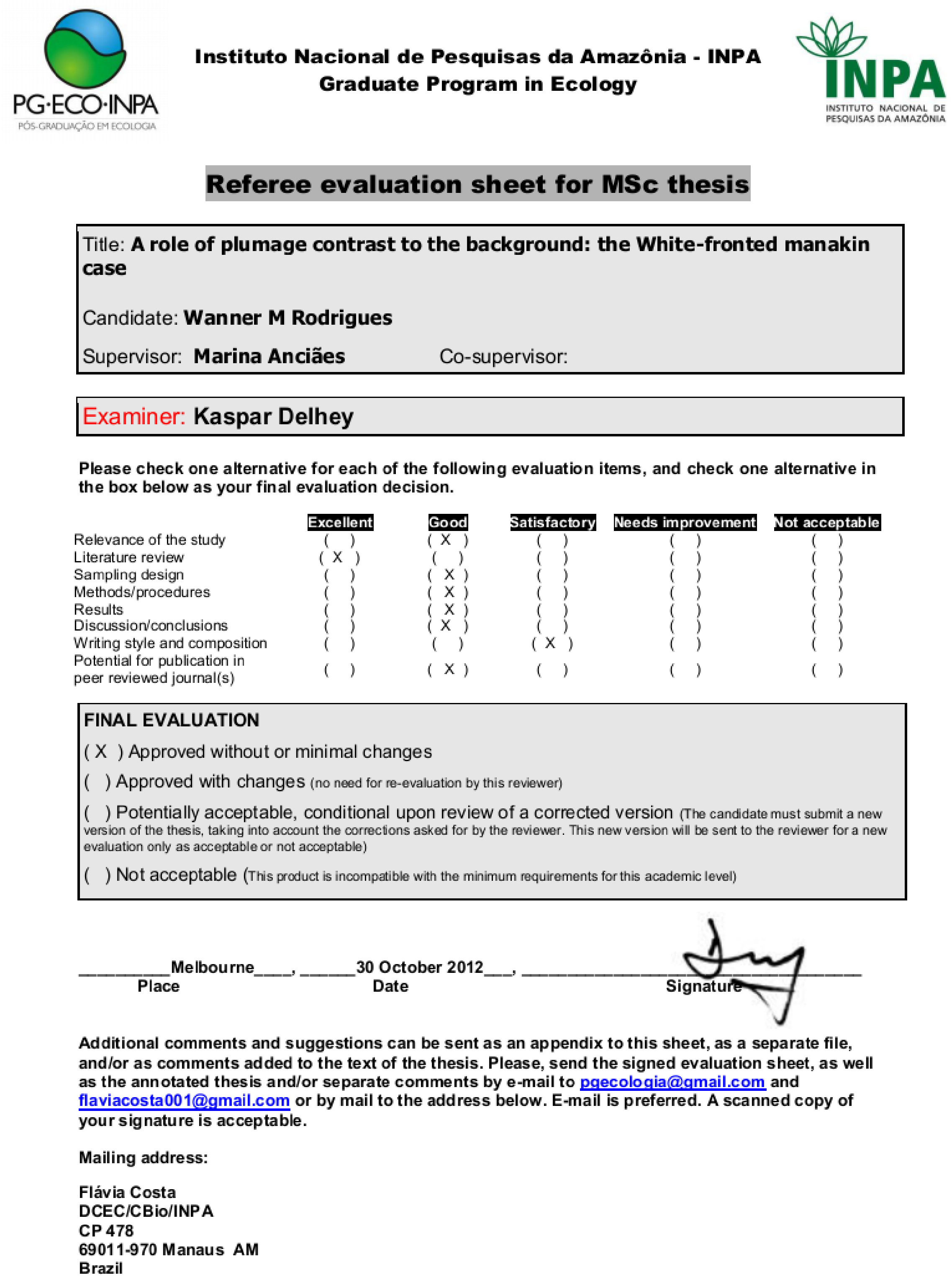
# APÊNDICE B – AVALIAÇÃO FINAL – KASPAR DEL HEY



**Instituto Nacional de Pesquisas da Amazônia - INPA**
**Graduate Program in Ecology**

## Referee evaluation sheet for MSc thesis

Title: **A role of plumage contrast to the background: the White-fronted manakin case**

Candidate: **Wanner M Rodrigues**

Supervisor: **Marina Anciães** Co-supervisor:

Examiner: **Kaspar Delhey**

**Please check one alternative for each of the following evaluation items, and check one alternative in the box below as your final evaluation decision.**

| | Excellent | Good | Satisfactory | Needs improvement | Not acceptable |
|---|---|---|---|---|---|
| Relevance of the study | ( ) | ( X ) | ( ) | ( ) | ( ) |
| Literature review | ( X ) | ( ) | ( ) | ( ) | ( ) |
| Sampling design | ( ) | ( X ) | ( ) | ( ) | ( ) |
| Methods/procedures | ( ) | ( X ) | ( ) | ( ) | ( ) |
| Results | ( ) | ( X ) | ( ) | ( ) | ( ) |
| Discussion/conclusions | ( ) | ( X ) | ( ) | ( ) | ( ) |
| Writing style and composition | ( ) | ( ) | ( X ) | ( ) | ( ) |
| Potential for publication in peer reviewed journal(s) | ( ) | ( X ) | ( ) | ( ) | ( ) |

FINAL EVALUATION

( X ) Approved without or minimal changes

( ) Approved with changes (no need for re-evaluation by this reviewer)

( ) Potentially acceptable, conditional upon review of a corrected version (The candidate must submit a new version of the thesis, taking into account the corrections asked for by the reviewer. This new version will be sent to the reviewer for a new evaluation only as acceptable or not acceptable)

( ) Not acceptable (This product is incompatible with the minimum requirements for this academic level)

**_________Melbourne____, ______30 October 2012___, __________________________________**
**Place Date Signature**

**Additional comments and suggestions can be sent as an appendix to this sheet, as a separate file, and/or as comments added to the text of the thesis. Please, send the signed evaluation sheet, as well as the annotated thesis and/or separate comments by e-mail to pgecologia@gmail.com and flaviacosta001@gmail.com or by mail to the address below. E-mail is preferred. A scanned copy of your signature is acceptable.**

**Mailing address:**

**Flávia Costa**
**DCEC/CBio/INPA**
**CP 478**
**69011-970 Manaus AM**
**Brazil**

# APÊNDICE C – AVALIAÇÃO – THOMAS PIKE

**Instituto Nacional de Pesquisas da Amazônia - INPA**
**Graduate Program in Ecology**

## Referee evaluation sheet for MSc thesis

Title: **A role of plumage contrast to the background: the White-fronted manakin case**

Candidate: **Wanner M Rodrigues**

Supervisor: **Marina Anciães** Co-supervisor:

Examiner: **Thomas Pike**

**Please check one alternative for each of the following evaluation items, and check one alternative in the box below as your final evaluation decision.**

| | Excellent | Good | Satisfactory | Needs improvement | Not acceptable |
|---|---|---|---|---|---|
| Relevance of the study | ( x ) | ( ) | ( ) | ( ) | ( ) |
| Literature review | ( ) | ( x ) | ( ) | ( ) | ( ) |
| Sampling design | ( x ) | ( ) | ( ) | ( ) | ( ) |
| Methods/procedures | ( ) | ( ) | ( x ) | ( ) | ( ) |
| Results | ( ) | ( ) | ( x ) | ( ) | ( ) |
| Discussion/conclusions | ( ) | ( x ) | ( ) | ( ) | ( ) |
| Writing style and composition | ( x ) | ( ) | ( ) | ( ) | ( ) |
| Potential for publication in peer reviewed journal(s) | ( ) | ( x ) | ( ) | ( ) | ( ) |

**FINAL EVALUATION**

( ) Approved without or minimal changes

( x) Approved with changes (no need for re-evaluation by this reviewer)

( ) Potentially acceptable, conditional upon review of a corrected version (The candidate must submit a new version of the thesis, taking into account the corrections asked for by the reviewer. This new version will be sent to the reviewer for a new evaluation only as acceptable or not acceptable)

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**_University of Lincoln, UK___, __24/10/2012_________, ____Thomas Pike (by email)______**
**Place Date Signature**

**Additional comments and suggestions can be sent as an appendix to this sheet, as a separate file, and/or as comments added to the text of the thesis. Please, send the signed evaluation sheet, as well as the annotated thesis and/or separate comments by e-mail to pgecologia@gmail.com and flaviacosta001@gmail.com or by mail to the address below. E-mail is preferred. A scanned copy of your signature is acceptable.**

**Mailing address:**

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**DCEC/CBio/INPA**
**CP 478**
**69011-970 Manaus AM**
**Brazil**

# APÊNDICE D – AVALIAÇÃO – RICHARD PRUM

**Instituto Nacional de Pesquisas da Amazônia - INPA**
**Graduate Program in Ecology**

## Referee evaluation sheet for MSc thesis

Title: A role of plumage contrast to the background: the White-fronted manakin in Central Amazon

Candidate: **Wanner Medeiros**

Supervisor: **Marina Anciães** Co-supervisor: **-----**

Examiner: **Richard Prum**

**Please check one alternative for each of the following evaluation items, and check one alternative in the box below as your final evaluation decision.**

| | Excellent | Good | Satisfactory | Needs improvement | Not acceptable |
|---|---|---|---|---|---|
| Relevance of the study | ( ) | ( X ) | ( ) | ( ) | ( ) |
| Literature review | ( ) | ( X ) | ( ) | ( ) | ( ) |
| Sampling design | ( ) | ( X ) | ( ) | ( ) | ( ) |
| Methods/procedures | ( ) | ( X ) | ( ) | ( ) | ( ) |
| Results | ( ) | ( ) | ( X ) | ( ) | ( ) |
| Discussion/conclusions | ( ) | ( ) | ( X ) | ( ) | ( ) |
| Writing style and composition | ( ) | ( ) | ( ) | ( X ) | ( ) |
| Potential for publication in peer reviewed journal(s) | ( ) | ( X ) | ( ) | ( ) | ( ) |

**FINAL EVALUATION**

( ) Approved without or minimal changes

( X ) Approved with changes (no need for re-evaluation by this reviewer)

( ) Potentially acceptable, conditional upon review of a corrected version (The candidate must submit a new version of the thesis, taking into account the corrections asked for by the reviewer. This new version will be sent to the reviewer for a new evaluation only as acceptable or not acceptable)

( ) Not acceptable (This product is incompatible with the minimum requirements for this academic level)

| | | |
|---|---|---|
| **New Haven,** | **30 October 2012** | |
| **Place** | **Date** | **Signature** |

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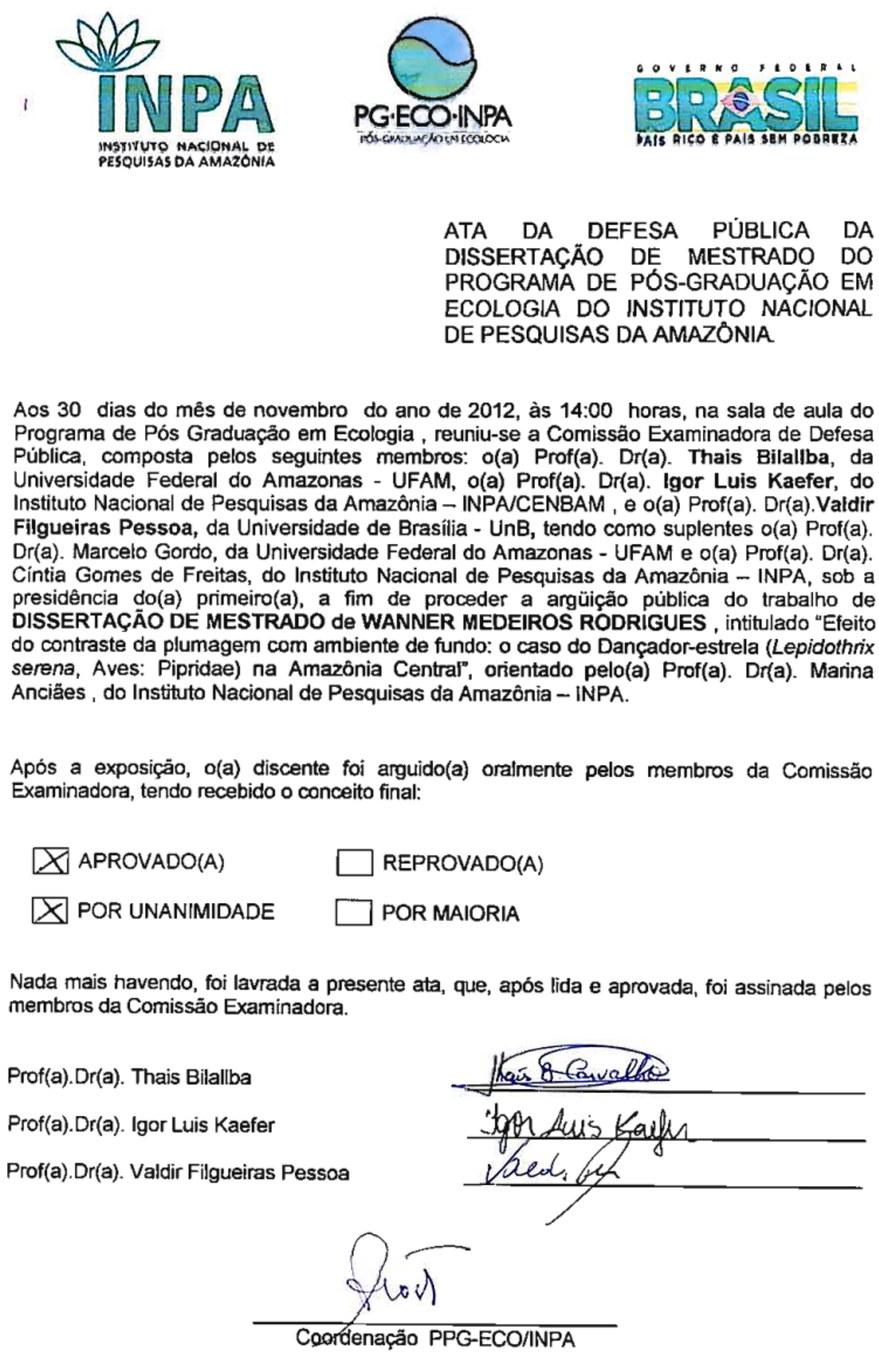
**Mailing address:**

**Flavia Costa**
**DCEC/CPEC/INPA**
**CP 478**
**69011-970 Manaus AM**
**Brazil**

# APÊNDICE E – ATA DA DEFESA PRESENCIAL



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PAÍS RICO É PAÍS SEM POBREZA

ATA DA DEFESA PÚBLICA DA DISSERTAÇÃO DE MESTRADO DO PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA DO INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA

Aos 30 dias do mês de novembro do ano de 2012, às 14:00 horas, na sala de aula do Programa de Pós Graduação em Ecologia , reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: o(a) Prof(a). Dr(a). **Thais Bilallba**, da Universidade Federal do Amazonas - UFAM, o(a) Prof(a). Dr(a). **Igor Luis Kaefer**, do Instituto Nacional de Pesquisas da Amazônia – INPA/CENBAM , e o(a) Prof(a). Dr(a).**Valdir Filgueiras Pessoa**, da Universidade de Brasília - UnB, tendo como suplentes o(a) Prof(a). Dr(a). Marcelo Gordo, da Universidade Federal do Amazonas - UFAM e o(a) Prof(a). Dr(a). Cíntia Gomes de Freitas, do Instituto Nacional de Pesquisas da Amazônia – INPA, sob a presidência do(a) primeiro(a), a fim de proceder a argüição pública do trabalho de **DISSERTAÇÃO DE MESTRADO de WANNER MEDEIROS RODRIGUES** , intitulado "Efeito do contraste da plumagem com ambiente de fundo: o caso do Dançador-estrela (*Lepidothrix serena*, Aves: Pipridae) na Amazônia Central", orientado pelo(a) Prof(a). Dr(a). Marina Anciães , do Instituto Nacional de Pesquisas da Amazônia – INPA.

Após a exposição, o(a) discente foi arguido(a) oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

☒ APROVADO(A) ☐ REPROVADO(A)

☒ POR UNANIMIDADE ☐ POR MAIORIA

Nada mais havendo, foi lavrada a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora.

Prof(a).Dr(a). Thais Bilallba Thaís B. Carvalho

Prof(a).Dr(a). Igor Luis Kaefer Igor Luis Kaefer

Prof(a).Dr(a). Valdir Filgueiras Pessoa

Coordenação PPG-ECO/INPA