



Attractive males are less than adequate dads in a multimodal signalling passerine



Pedro Diniz^{a, *}, Desirée M. Ramos^{b, 1}, Regina H. Macedo^{c, 2}

^a Programa de Pós Graduação em Ecologia, Universidade de Brasília, Brasília, Brazil

^b Programa de Pós Graduação em Botânica, Universidade de Brasília, Brasília, Brazil

^c Laboratório de Comportamento Animal, Universidade de Brasília, Brasília, Brazil

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Parental attractiveness influences paternal and maternal efforts in a wide range of animals that exhibit biparental care. However, we still lack an understanding concerning the direction of the covariance between attractiveness and parental effort, perhaps because studies typically consider only one or a subset of multiple attractiveness signals. In this study we investigated predictions of four hypotheses about the relationship between attractiveness traits (plumage coloration, song and leap display traits) and parental effort (feeding rates) in a wild population of the blue-black grassquit, *Volatinia jacarina*, a Neotropical sexually dichromatic bird with biparental care. Paternal effort was negatively correlated with male blue-black coloration (UV chroma) and maternal effort was positively correlated with male provisioning rate. Thus, more attractive males relative to the UV chroma are worse fathers relative to less attractive males in this trait. However, female provisioning rate was positively correlated with another male attractive trait: the blue-black plumage coverage. The song, leap display and other features of male coloration were not associated with either male or female parental effort. Taken together, these results support the parental–mating trade-off hypothesis for paternal behaviour, which predicts that attractive males should invest less in current offspring in order to acquire extrapair matings. Also, our results partially support the positive differential allocation hypothesis: although females invested highly in offspring of males with more blue-black plumage coverage, they did not compensate for the low investment of males with UV-shifted blue-black plumage. We highlight the need for future studies to consider multiple sexual traits in order to investigate the relationship between attractiveness and parental investment.

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According to life history theory, parental investment is influenced by trade-offs between the reproductive value of current offspring and the survival and reproductive prospects of a parental individual (Trivers, 1972). In taxa with biparental care, parental attractiveness is an important component that is associated with reproductive value of current offspring (Burley, 1986; Sheldon, 2000). Individual attractiveness may also influence and define the reproductive strategies of both mating partners (Alonso-Alvarez et al., 2012; Osorno et al., 2006; Senar, Figuerola, & Pascual, 2002). However, studies disagree about how parents should allocate their investment in the offspring relative to their own and their

partner's attractiveness (Harris & Uller, 2009; Horváthová, Nakagawa, & Uller, 2012; Kokko, 1998), which has led to a confusing and diverse array of hypotheses.

There are three hypotheses that attempt to explain covariation between self-attractiveness and parental investment in socially monogamous taxa (Table 1): (1) the good parent hypothesis; (2) the parental–mating trade-off hypothesis; and (3) the positive differential allocation hypothesis. The good parent hypothesis predicts that an individual's attractiveness should reliably and positively indicate parental effort (Hoelzer, 1989). In this case, the trade-off between parental and mating efforts may be reduced (Kokko, 1998; Stiver & Alonzo, 2009). On the other hand, the parental–mating trade-off hypothesis predicts that an individual's attractiveness (usually the male's) should be negatively correlated with its parental effort, because the benefits derived from parental care do not compensate the costs of losing extrapair mating opportunities (Magrath & Komdeur, 2003; Schwagmeyer, Parker,

* Correspondence: P. Diniz, Departamento de Zoologia, Instituto de Ciências Biológicas, Universidade de Brasília, Brasília, 70919-970, Brazil.

E-mail address: pdadiniz@gmail.com (P. Diniz).

¹ E-mail address: desibio@gmail.com (D. M. Ramos).

² E-mail address: rhmacedo@unb.br (R. H. Macedo).

Mock, & Schwabl, 2012; Stiver & Alonzo, 2009). This prediction is also made by the third explanation, the positive differential allocation hypothesis, but in this case an attractive individual reduces its parental effort because its mate is willing to compensate for it (see below; Burley, 1986).

An individual's attractiveness should also influence its partner's investment in the social parents' offspring (e.g. Mahr, Griggio, Granatiero, & Hoi, 2012). In socially monogamous taxa, there are two hypotheses that suggest how an individual should invest in offspring depending on the partner's attractiveness, leading to opposing predictions (Table 1): (1) the positive differential allocation hypothesis (Burley, 1986; Ratikainen & Kokko, 2009; Sheldon, 2000); and (2) the negative differential allocation hypothesis (Ratikainen & Kokko, 2009; alternatively known as the reproductive compensation hypothesis; Gowaty, 2008). According to the positive differential allocation hypothesis, male attractiveness indicates male quality and is heritable. Therefore, this hypothesis predicts that male attractiveness should positively affect the female's parental effort, because females gain a higher fitness per unit of parental care by investing in offspring sired by high-quality males (Sheldon, 2000). In addition, higher maternal effort could compensate for the possibly lower paternal effort strategy of highly attractive males (Ratikainen & Kokko, 2009). Finally, according to the negative differential allocation hypothesis, ecological and social circumstances may not allow all females to mate with preferred or more attractive males. Offspring from nonpreferred or less attractive males would have low viability and females would compensate for that in terms of parental effort. Therefore, this hypothesis predicts a negative covariation between male attractiveness and maternal effort (Gowaty, 2008).

There is only mixed support for the parental–mating trade-off and the positive differential allocation hypotheses; in addition, few general patterns have emerged, perhaps because it appears that the associations between parental attractiveness and parental effort are species specific (Mazuc, Chastel, & Sorci, 2003; Rutstein, Gilbert, & Tomkins, 2005). Furthermore, recent observational and experimental studies point to patterns that are not predicted by any of the hypotheses mentioned above, such as differences between populations in the covariance patterns between parental effort and parental attractiveness (Limbourg, Mateman, & Lessells, 2013; Mahr et al., 2012), differences between sexes in the same population (Limbourg et al., 2013), or patterns that depend on which male sexual signals are considered (Galeotti et al., 2006). The latter category, for example, is illustrated by female freshwater crayfish (*Austropotamobius italicus*) that lay a few large eggs when paired with small-sized, large-clawed males and lay numerous but smaller eggs when paired with large-sized, small-clawed males (Galeotti et al., 2006).

Few studies have examined the covariation between parental investment and individual attractiveness in the context of multiple

sexual signals. Different secondary sexual traits may convey different, redundant or emergent messages to the same or to different receivers (Bro-Jørgensen, 2010; Hebets & Papaj, 2004). Moreover, different signals in multiple sexual signalling systems may: (1) have different functions or propagation efficiency according to social and environmental contexts (Bro-Jørgensen, 2010), and (2) convey different information about individual quality (Bro-Jørgensen & Dabelsteen, 2008; Freeman-Gallant et al., 2009), including parental quality (Pizzolon et al., 2011). In addition, multiple signals may have greater importance in mate choice and mating success than only one or a subset of multiple signals (Pizzolon et al., 2011; Taylor, Buchanan, & Doherty, 2007). Because most biparental bird species have multimodal sexual traits (Hebets & Papaj, 2004), understanding their adaptive functions and plasticity may generate reliable predictions concerning the covariation between parental effort and parental attractiveness.

Here, we investigated whether multimodal sexual signals of male blue-black grassquits, *Volatinia jacarina* (Aves: Thraupidae), a Neotropical socially monogamous species with biparental care, predict paternal and maternal effort in social pairs. We sampled visual (plumage coloration and leap display) and acoustic (song) parameters of male sexual traits, and measured provisioning rates by males and females during the nestling period. We used grassquit social pairs to test predictions of the four hypotheses that suggest explanations for possible relationships between male attractiveness and parental effort (see Table 1). In relation to paternal care, we tested for a positive (good parent hypothesis) or negative (parental–mating trade-off hypothesis and positive differential allocation hypothesis) covariation between male attractiveness and paternal effort. In relation to maternal care, we tested for a positive (positive differential allocation hypothesis) or negative (negative differential allocation hypothesis) covariation between male attractiveness and maternal effort.

METHODS

Study Species

The blue-black grassquit is an ideal model for studies involving multiple sexual sensory modalities and parental care. Blue-black grassquits exhibit sexual dichromatism: females have dull brown plumage while males acquire an iridescent blue-black plumage with a white underwing patch during the breeding season. Males vary in expression of the blue-black plumage coverage and their spectral characteristics (Maia, Caetano, Bão, & Macedo, 2009). Males perform an acrobatic display expressed in a vertical flight (leap display), with body rotation, high-speed wing beats and exhibition of white underwing patches (Macedo, Manica, & Dias, 2012). They also have a stereotyped and short song, which is coupled with leap displays (i.e. complete displays) but that can also

Table 1
Hypotheses and predictions regarding the relationship between parental effort and male attractiveness

Hypotheses	Authors	Covariation between male attractiveness and parental effort		Corroborating evidence
		Paternal	Maternal	
Good parent	1	+		7, 8, 9
Parental–mating trade-off	2	–		10, 11
Positive differential allocation	3, 4	–	+	12, 13, 14
Negative differential allocation	4, 5, 6		–	15, 16

Symbols indicate positive (+) or negative (–) covariations.

¹Hoelzer (1989); ²Magrath and Komdeur (2003); ³Burley (1986); ⁴Sheldon (2000); ⁵Ratikainen and Kokko (2009); ⁶Gowaty (2008); ⁷Germain, Reudink, Marra, and Ratcliffe (2010); ⁸Linville, Breitwisch, and Schilling (1998); ⁹Siefferman and Hill (2003); ¹⁰Mitchell, Dunn, Whittingham, and Freeman-Gallant (2007); ¹¹Sanz (2001); ¹²Maguire and Safran (2010); ¹³Alonso-Alvarez et al. (2012); ¹⁴Osorno et al. (2006); ¹⁵Bluhm and Gowaty (2004); ¹⁶Gowaty, Drickamer, and Schmid-Holmes (2003).

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