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MATHEUS COUTINHO COSTA FERREIRA

**INTENCIONALIDADE NA COMUNICAÇÃO ANIMAL:
REVISÃO DE EVIDÊNCIAS EM VOCALIZAÇÕES DE
CONTATO**

Alfenas-MG, fevereiro de 2018



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Dissertação apresentada como parte dos requisitos para obtenção do Título de Mestre em Ciências Ambientais pela Universidade Federal de Alfenas/UNIFAL-MG.

Orientador: Rogério Grassetto Teixeira da Cunha
Co-orientador: Thibaud Gruber



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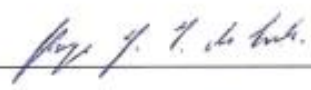
MATHEUS COUTINHO COSTA FERREIRA

“Intencionalidade na Comunicação Animal: revisão de evidências em vocalizações de contato”

A Banca julgadora, abaixo assinada, aprova a Dissertação apresentada como parte dos requisitos para a obtenção do título de Mestre em Ciências Ambientais pela Universidade Federal de Alfenas. Área de Concentração: Ciências Ambientais.

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Dedico esse trabalho a minha tia
Lúcia, a July, e a Loren, que
sempre estimularam meu fascínio
e amor pela vida animal.

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RESUMO

A presença de intencionalidade na comunicação animal é um tema controverso. A existência de um sistema de chamados e respostas de vocalizações de contato em momentos nos quais há indivíduos separados de seu grupo é questionada. Argumenta-se que os chamados refletem apenas o estado mental do animal que vocaliza, demonstrando seu medo, por exemplo, e não intenção de informar outros animais. Há na literatura vários trabalhos sobre chamados de contato, com diferentes espécies de vertebrados. Alguns desses trabalhos trazem evidências que podem ser utilizadas para se analisar duas hipóteses alternativas sobre intencionalidade na comunicação acústica: os chamados são um comportamento totalmente mecânico (intencionalidade de ordem zero) ou refletem a intenção do animal que vocaliza em se reunir com outros indivíduos do grupo (intencionalidade de primeira ordem)? As informações que podem ser usadas como evidências são: se indivíduos vocalizam independentemente de estarem isolados de seu grupo, se animais de maior ranking hierárquico, parentes, afiliados ou de um mesmo grupo recebem mais respostas, e se as vocalizações têm indícios de elaboração e persistência quando um animal não recebe respostas. Fizemos uma revisão sistemática da literatura relativa a vocalizações de contato em vertebrados, com objetivo de testar indiretamente as duas hipóteses por meio das predições acima. Encontramos 4 artigos apoiando apenas a hipótese de intencionalidade de ordem zero, 49 artigos apoiando a hipótese de intencionalidade de primeira ordem, e 11 artigos que apoiavam ambas. Apenas a ausência de preferência por responder certos tipos de indivíduos apoiou a hipótese de explicação mais simples. Por outro lado, até evidências não previstas previamente apoiaram a hipótese de intencionalidade de primeira ordem. Nossos resultados mostraram como a intencionalidade pode estar presente em chamados de contato, além da importância dessas vocalizações em descobertas sobre intencionalidade na comunicação acústica.

Palavras-chave: Intencionalidade. Comunicação acústica. Chamados de contato.

ABSTRACT

The occurrence of intentionality in animal communication remains controversial. Some authors argue that animal vocalizations only reflect the emotional state of the caller, displaying for example their fear rather than an intention to inform others. A particular context of interest is contact calls where the existence of a call-and-answer system, especially when individuals are away from the group, is questioned. In this review, we analyze 64 publications on contact calls in the literature in 35 vertebrate species reviewing evidence for intentional calling. In particular, we evaluate their findings in regards to two alternative hypotheses about intentionality in acoustic communication: calling is a mechanistic behavior (zero-order intentionality) or it reflects the animal's intention to reunite with others from its group (first-order intentionality). The criteria we use to test these hypotheses are: whether individuals vocalize despite being isolated from its group; whether calls elicits answers in receivers; whether calls from certain categories of emitters (like kin and higher rank individuals) elicits more answers; and whether the calls are goal directed – used until individuals are reunited. We found 4 papers supporting only the zero-order intentionality hypothesis, 49 supporting only the first-order intentionality hypothesis and 11 supporting both. Only the absence of preferences for categories of emitters supported the zero-order intentionality hypothesis. On the other hand, even unpredicted evidence could be found supporting first-order intentionality. Our results show that at least first-order intentionality is widespread in contact calls across vertebrates, suggesting that this type of vocalization can provide meaningful avenues of research to understand the evolution of intentionality in acoustic communication.

Key words: Intentionality. Acoustic communication. Contact call.

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1 INTRODUÇÃO

A comunicação entre indivíduos dá-se pela transmissão de sinais, que partem de um emissor, com propósito de influenciar o comportamento de um possível receptor, que deverá ter um sistema sensorial sensível e poderá apresentar mudanças comportamentais em resposta ao estímulo (SEMPLE; HIGHAM, 2013).

A troca de sinais entre animais se faz necessária em diversos contextos, seja para a identificação de um indivíduo ou elemento, delimitação territorial, proteção, forrageio, vida social e defesa própria, entre outros (TOMECEK, 2009). Uma das formas de comunicação que evoluiu em vários grupos de animais, tanto vertebrados quanto invertebrados, é a acústica (HOLZMANN; AGOSTINI; DI BITETTI, 2012). Como as demais modalidades, essa forma possui vantagens e desvantagens sobre as outras formas de comunicação (ENDLER, 1993). O som se espalha mais rapidamente pelo ambiente que compostos químicos (DA CUNHA; BYRNE, 2009), sendo conduzido por todas direções ao redor do emissor, e ainda contornando obstáculos (TOMECEK, 2009). Consegue-se usá-lo em locais sem luz (KANWAL et al., 1994) e debaixo d'água (BASS; CLARK, 2002), podendo ser um sinal de maior alcance em relação a sinais elétricos, táteis e olfativos (FARMER, 2011). Seus parâmetros físicos, como amplitude e frequência, podem ser modificados, o que pode gerar um bom potencial de codificação (ENDLER, 1993). Apesar de tais benefícios, ambientes com muitos sons podem causar interferência em chamados e tornar a comunicação acústica inoperante (SLABBEKOORN; RIPMEESTER, 2008). Além disso, os chamados podem atrair predadores (IBÁÑEZ-ÁLAMO; ARCO; SOLER, 2012) e aumentar índices de parasitismo (TOMÁS; SOLER, 2016).

No âmbito da comunicação acústica, existem vocalizações com diversas funções aparentes, por exemplo: manter contato, advertir a presença de predadores e ameaças, demarcar territórios e atrair parceiros sexuais (TOMECEK, 2009). Dentre as categorias funcionais, um tipo de chamado bastante ubíquo em espécies sociais é o das vocalizações de contato. Classificamos desta forma as vocalizações com função de manter contato ou coesão entre os membros de um grupo (CHENEY; SEYFARTH; PALOMBIT, 1996). Essa denominação compreende chamados usados em diversas situações, como comunicação entre animais que se distanciaram do bando (para se alimentar, por exemplo) e também para reintegrar algum indivíduo isolado. Alguns

autores as nomeiam de chamados de isolamento (MISHIMA et al., 2015) ou de coesão (MUMM; URRUTIA; KNÖRNSCHILD, 2014). São vocalizações utilizadas tanto por indivíduos que se afastaram, quanto por aqueles que chamam “em resposta”, indicando a localização do bando (DA CUNHA; BYRNE, 2013). Além de indicar a localização do animal, o chamado em si pode possuir informações adicionais, como sobre a identidade de coespecíficos num bando (TIBBETTS; DALE, 2007), assim como sobre o sexo e idade dos indivíduos (FISCHER et al., 2002).

Este tipo de vocalização foi encontrado em diversas espécies de mamíferos e aves sociais, como *Alouatta caraya* (DA CUNHA; BYRNE, 2009) e *Saguinus fuscicollis* (BRADLEY; MCCLUNG, 2015) (Primata); *Antrozous pallidus* (Chiroptera) (ARNOLD; WILKINSON, 2011); *Delphinapterus leucas* (Cetacea) (MISHIMA et al., 2015); *Pomatostomus ruficeps* (Passeriformes) (CRANE et al., 2015).

Muitos desses trabalhos trazem evidências de uma modulação dos chamados, dependente principalmente de fatores como: qual indivíduo inicialmente vocaliza (para as respostas dos chamados de contato) (SNOWDON; HODUN, 1985; ARNOLD; WILKINSON, 2011), a composição dos receptores (se o indivíduo é do mesmo grupo, seu nível de afiliação, grau de parentesco e nível hierárquico), e a persistência no chamado até seu objetivo ser atingido (DIGWEED; FEDIGAN; RENDALL, 2007, SCHEL et al., 2013; TOWNSEND et al., 2016).

Tais características relacionam-se potencialmente a um aspecto da comunicação acústica bem discutido na literatura: a intencionalidade (BYRNE, 2000; RENDALL; CHENEY; SEYFARTH, 2000; SEYFARTH; CHENEY, 2003; DA CUNHA; BYRNE, 2009; TOWNSEND et al., 2016; SIEVERS et al., 2017). Um chamado gerado com intenção não é apenas produzido instintivamente ou de forma mecânica, mas sim com objetivo de modificar o comportamento de outro indivíduo (SCHEL et al., 2013).

Porém, intencionalidade não é um conceito com definição trivial. Para auxiliar na análise de fenômenos que possam envolver intencionalidade, Daniel Dennett (1983; 1987) propôs uma escala de intencionalidade na comunicação animal que possui ao menos três níveis. O de ordem zero é aquele que envolve um comportamento completamente mecânico, que não há relação com o estado mental do animal, onde, por exemplo, um animal vocalizaria ao ver um predador, como forma de reflexo. O nível de primeira ordem abrange um comportamento proposital, com um objetivo (por exemplo, um animal usa uma vocalização para deixar alerta outros indivíduos em relação a um predador, mas sem ter noção do estado mental destes).

No nível de segunda ordem, o comportamento apresentado leva em consideração o estado da mente do próprio animal e de outros com os quais esteja interagindo (por exemplo, um animal vocaliza em resposta a um chamado por acreditar que o emissor esteja perdido).

Aplicando-se estes conceitos de graus de intencionalidade aos chamados de contato, podemos nos perguntar se eles seriam apenas um mecanismo fisiológico ativado pelo ambiente (nível de ordem zero), isto é, disparados apenas pelo próprio isolamento do emissor (DA CUNHA; BYRNE, 2009). Ou eles seriam um comportamento intencional, apresentado com o propósito de se reunir com outros do grupo, ou seja, possuiriam um nível de ordem um (DA CUNHA; BYRNE, 2009)? A primeira hipótese prevê que o animal só usa o chamado se estiver separado do grupo, e apenas receberá resposta de outros animais que também estejam isolados; ou seja, a resposta é ativada mecanicamente pelo fato de estar desacompanhado (DA CUNHA; BYRNE, 2009).

No segundo caso, o previsto é que o animal responda o chamado de contato estando ou não separado do grupo, e que tanto o emissor quanto o receptor da mensagem a usem com o propósito de se reunir a outros membros, independente do estado de mente dos outros indivíduos; podendo-se ainda esperar uma chance maior de resposta dependendo de categorias dos emissores, como os de maior nível hierárquico (como visto em RAMOS-FERNÁNDEZ, 2005), e com maior grau de afiliação com este indivíduo (DA CUNHA; BYRNE, 2009).

Um comportamento de nível de segunda ordem (animais vocalizando com o intuito de modificar o estado de informação/conhecimento de outros) é criticado por alguns autores, já que isso requereria conhecimento do estado mental de outros indivíduos (PREMACK, WOODRUFF, 1978). Portanto, seria necessário aos animais não humanos a percepção de que a mente de cada indivíduo é diferente de sua própria, e as evidências já encontradas são consideradas por alguns cientistas como insuficientes (VAN DER VAART; HEMELRIJK, 2014). No contexto de chamados de contato, seria como se um animal vocalizasse com o intuito de informar a localização do bando a um indivíduo, por saber que ele está isolado.

Em primatas não humanos, níveis intencionais de primeira ordem já foram detectados na comunicação gestual, como no chimpanzé (*Pan troglodytes*) (ROBERTS; ROBERTS; VICK, 2014), no bonobo (*Pan paniscus*) (DEMURU; FERRARI; PALAGI, 2014) e no gorila (*Gorilla gorilla*) (GENTY et al., 2009). Até mesmo

em chamados de alerta, na primeira espécie citada (SCHEL et al., 2013), evidenciou-se sinais de intencionalidade.

Na literatura há diversos trabalhos envolvendo chamados de contato, e muitos, apesar de não testarem previsões diretamente ligadas à intencionalidade, podem trazer evidências que apoiam ou refutam as hipóteses acima (vocalização com intencionalidade de grau zero ou grau um). Nosso objetivo é realizar uma revisão sistemática da literatura sobre vocalizações de contato, quantificando aqueles trabalhos que apoiam ou rejeitam estas hipóteses.

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2 ARTIGO

I call when I want to: intentionality in contact calls across vertebrates

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Abstract

The occurrence of intentionality in animal communication remains controversial. Some authors argue that animal vocalizations only reflect the emotional state of the caller, displaying for example their fear rather than an intention to inform others. A particular context of interest is contact calls where the existence of a call-and-answer system, especially when individuals are away from the group, is questioned. In this review, we analyze 64 publications on contact calls in the literature in 35 vertebrate species reviewing evidence for intentional calling. In particular, we evaluate their findings in regards to two alternative hypotheses about intentionality in acoustic communication: calling is a mechanistic behavior (zero-order intentionality) or it reflects the animal's intention to reunite with others from its group (first-order intentionality). The criteria we use to test these hypotheses are: whether individuals vocalize despite being isolated from its group; whether calls elicits answers in receivers; whether calls from certain categories of emitters (like kin and higher rank individuals) elicits more answers; and whether the calls are goal directed – used until individuals are reunited. We found 4 papers supporting only the zero-order intentionality hypothesis, 49 supporting only the first-order intentionality hypothesis and 11 supporting both. Only the absence of preferences for categories of emitters supported the zero-order intentionality hypothesis. On the other hand, even unpredicted evidence could be found supporting first-order intentionality. Our results show that at least first-order intentionality is widespread in contact calls across vertebrates, suggesting that this type of vocalization can provide meaningful avenues of research to understand the evolution of intentionality in acoustic communication.

Key-words: Intentionality. Acoustic communication. Contact call.

INTRODUCTION

Acoustic communication is widespread among animal species, and can be used in the multiple scenarios, such as social interactions, territorial defense and individual identification, among others (Holzmann et al. 2012). The acoustic signal is advantageous because its physical parameters can be modulated, generating several channels for communication (Endler 1993). Besides that, it can be used in darkness (Kanwal et al. 1994) and underwater (Bass and Clark 2002), having a greater range than electric, tactile and olfactory signals (Farmer 2011). These advantages make acoustic signals very convenient for a recurrent issue of social animals: distancing and isolation of individuals from their mates or group. Vocalizations used in this context, which help a group to be cohesive and individuals to regain or keep contact with one another, are generally labeled contact calls (Cheney et al. 1996). These vocalizations have also been known as isolations calls (Mishima et al. 2015) or cohesion calls (Mumm et al. 2014). They are used by individuals that have moved away from the group, as well as by those that call back as an apparent answer to a first call, indicating their location by doing so (da Cunha and Byrne 2013). Besides this information, calls can also inform about an individual's identity (Tibbetts and Dale 2007), age, sex (Fischer et al. 2002) or hierarchical rank (Digweed et al. 2007).

In the literature on contact calls, papers demonstrate variation in the calling and answering behavior of given species for various reasons. For example, specific individuals receive more answers than others after calling (e.g. dominant males - Digweed et al. 2007; affiliated individuals – Kulahci et al. 2015). Also, consecutive calls following a call that failed to elicit answers from conspecifics have acoustic characteristics, which increased their detectability (Koda 2004).

This capacity for modulating vocalizations is potentially related to a cognitive issue which presence in animal vocalizations is still discussed in the literature: intentionality (Byrne 2000; Rendall et al. 2000; Seyfarth and Cheney 2003; da Cunha and Byrne 2009; Gruber and Zuberbühler 2013; Schel et al. 2013; Townsend et al. 2016; Sievers et al. 2017). An intentional call is produced with the aim to change another individual's behavior or mental state (Schel et al. 2013). Therefore, it is not produced in a mechanic way, nor vocalized instinctively. Intentionality is a key characteristic factor of human communication: we communicate to persuade, alert,

share information (van der Vaart and Hemelrijk 2014). As the evolutionary origin of human language and how it became so distinctive from that of other animals is still in debate, the comparison of characteristics of our communication with other species has received interest from multiple areas, such as linguistic, psychology, biology and neuroscience (Hauser et al. 2002). In order to help analyzing events that may involve intentionality, the philosopher Daniel Dennett (1983; 1987) proposed an intentionality scale in cognitive ethology that have at least three degrees. The zero-order is the one representing a mechanistic behavior, one that does not relate to the individual's mental state, e.g. the animal would vocalize when isolated from its group merely as a reflex of its internal, emotional state. The first-order degree covers a purposeful behavior, one that is goal-directed. For example, an animal vocalizes as an answer to a contact call with the intention to reunite with the first caller, but without any attribution of mental state to that individual. In other words, the animal signaller does not intend to let the other individual know where it is, it just wants to reunite with the other individual. Note that, at this stage, whether the animal is in a particular emotional status does not prevent the call from being potentially intentional (Gruber and Grandjean 2017). Finally, in the second-order degree, the animal considers its mental state and those of the ones with whom it is interacting (e.g. an animal vocalizes as an answer to a contact call because it believes the first caller is lost or isolated). Evidences on non-human animals attributing mental states to other individuals are still unconvincing (van der Vaart and Hemelrijk 2014, but see Krupenye et al. 2016), therefore, the presence of second-order intentionality is little supported (see discussion in Schel et al. 2013). Recently, Townsend et al. (2016) have provided operative criteria to isolate intentionality of at least the first-order in animal communicative behavior. The criteria, adapting to the context of contact calls (usually with at least an animal in isolation), are as follow: calling behavior is goal-directed, with cues of selective use of the signal; there is an audience effect when calling; there is manipulation of attentional state of the receiver.

Applying the concept of intentionality degrees and using the criteria put forwards by Townsend et al. (2016) to contact calls, in the present review, we test whether contact calls across vertebrate are mechanically and physiologically triggered by the environment (zero-order), that is whether animals call indistinctively when they are isolated (da Cunha and Byrne 2009); or whether contact calling is intentional, with the goal to reunite with others from the group, as a first-order production (da Cunha and

Byrne 2009)? The first hypothesis predicts that an animal would only call when separated from its group, and would only receive answers from equally isolated individuals. That is, the answer is mechanically “activated” by the anxiety/stress of being separated from others (da Cunha and Byrne 2009). The second hypothesis predicts that animals may answer when isolated or not, with possible asymmetries on answers rates (depending on first caller hierarchical rank, affiliation levels and kin – in other words, important individuals to the answering animal) (da Cunha and Byrne 2009). Audience specificity, while not necessary, has thus been seen as evidence for intentional production (Townsend et al. 2016). As in this case the behavior represents an intention to reunite, we would also expect that calling continues or become more elaborated until the reunion happens – as a goal-directed behavior (Schel et al. 2013; Townsend et al. 2016). It is also expected that this signal elicits changes in receivers behavior in a consistent and repeatable way (Townsend et al. 2016), evoking vocal answers and approaches, since this is necessary to complete the objective of contact calling.

Contact calls have elicited much interest in the literature. Despite the potential to test intentionality hypotheses on contact calls, this wasn't explicitly done yet. The data contained by some of the papers, while not explicitly testing predictions related to the intentionality hypotheses above, may bring evidence that help support or reject them (vocalizations of zero or first-order intentionality). Thus, our objective in this paper is to systematically review the literature on contact calls, looking for evidence that support or reject the presence of intentional production in contact calls across the widest range possible of species.

METHODS

To compile data about contact calls, in July 2017 we systematically reviewed the literature using the JSTOR, NCBI – PubMed and Web of Science™ search engine using the following expression: "contact call*" or "contact vocal*" or "cohesion call*" or "cohesion vocal*" or "isolation call*" or "isolation vocal*".

We included in the analysis only articles that had data on contact calls (in the context of isolation and/or risk of becoming separated from the group) of one or more

vertebrate taxa, and which showed results that could be unambiguously related to one or more of the predictions from either hypothesis under test (Table 1). Townsend et al. 2016 also proposes as criterion for intentionality the “manipulation of attentional state of the receiver”, which we thought that could happen (in the context of isolation) as a high note at the start of a call, but no papers brought this information. Thus, this criterion was excluded from the analysis.

Table 1. Predictions searched in articles that could support zero or first-order intentionality hypotheses.

Zero-order intentionality	First-order intentionality
Emission of contact calls are made only by isolated individuals;	Calls are emitted both when an animal is isolated or with other individuals;
When answering a call, an animal response behavior is the same to all individuals;	Answering call rate is altered when initial calling animal ranking is higher, when individuals have an affiliative and/or kin relation, and if they belong to the same group;
Calling behavior is automatic or habitual, and can't be related to an objective of the emitter.	Calling behavior persists or intensifies until individuals answer or reunite (goal directed).

We also checked the reference list of the selected articles to add other papers that were not found by the search engine and might also bring evidence to test the hypotheses. We decided not to include articles dealing with vocalizations between mothers and infants because of potentially confounding issues. In particular, infants are known to commonly use the same vocalization labeled as contact calls for adults in other contexts besides being away from the group core or their mother (e.g. Gros-Louis 2002; da Cunha and Byrne 2013). We also excluded contact calls labeled as such but that were related to affiliative interactions or close contact interactions, such as grooming (e.g. Sakura 1989; Masataka 1988). In our search, we did not include abstracts of conference presentations, or similar kinds of literature, given the limited nature of the information provided.

After the initial screening, for each remaining article we registered any result that matched one or more of the predictions of either hypothesis. We also recorded the studied taxa, research area(s), number of groups and individuals involved, along with their age and sex (when available), and if they were wild, free-ranging or captive (see Online Supplementary Material). We also recorded the data collection methodology

(observations, experiments or both), sampling effort and context involving the vocalizations (e.g. foraging, resting, travelling, etc).

The main reasons for excluding papers were: they didn't bring relevant data to answer any of the hypotheses of this study; they only tested isolated individuals, so we couldn't verify if animals with their group or other individual would answer; they were habituation-dishabituation tests; researchers measured answers as approaches, looks or body movements, and not as vocal answers; they only analyzed acoustic differences between different calls and from different categories of individuals; the contact calls studied were not used in an isolation or contact context; and studies included infants' vocalizations in their tests or only measured infants' answers.

RESULTS

Our search resulted in 2046 articles (without duplicates). From this initial list, we selected 176 (8,6%), which could have potential data to test the intentionality hypotheses, based on the information in the abstract. We added a further 49 papers that the search engine did not find, and which were retrieved from the references in the selected articles, leading to a total of 225 articles analyzed. Evaluating them, we could select 64 articles (spanning 35 species) with reliable information to test the hypotheses (Table 2).

When considering all criteria together (no papers analyzed all criteria at once), we found 49 papers supporting only first-order intentionality, 4 supporting only zero-order intentionality, and 11 supporting both hypotheses. When a paper was considered bringing evidence for both hypotheses, this means that they supported the zero-order hypothesis by some criteria, and the first-order intentionality hypothesis by other criteria.

We only found evidence supporting zero-order intentionality when analyzing the criterion of asymmetries on vocal answers. Evaluating this criterion alone we found 26 papers supporting only first-order intentionality, 8 supporting only zero-order intentionality, and 7 supporting both hypotheses (23 papers did not show results of asymmetries on vocal answers) (Figure 1 categories 3-7).

Table 2. (continued)

Author	Species	Intentionality criteria						
		GD	ID	AS-HR	AS-K	AS-G	AS-A	AS-O
Primata								
Teixidor & Byrne 1999	<i>Ateles geoffroyi</i>	■	■	■	■	■	■	■
Chen et al. 2009	<i>Callithrix jacchus</i>	■	■	■	■	■	■	■ c
Choi et al. 2015	<i>Callithrix jacchus</i>	■	■	■	■	■	■	■
Miller & Wang 2006	<i>Callithrix jacchus</i>	■	■	■	■	■	■	■
Yamaguchi et al. 2010	<i>Callithrix jacchus</i>	■	■	■	■	■	■	■
Snowdon & Hodun 1981	<i>Cebuella pygmaea</i>	■	■	■	■	■	■	■
Snowdon & Pola 1978	<i>Cebuella pygmaea</i>	■	■	■	■	■	■	■
Snowdon & Cleveland 1980	<i>Cebuella pygmaea</i>	■	■	■	■	■	■	■
Snowdon & Cleveland 1984	<i>Cebuella pygmaea</i>	■	■	■	■	■	■	■
Digweed et al. 2007	<i>Cebus capucinus</i>	■	■	■	■	■	■	■
Lemasson et al. 2010	<i>Cercopithecus campbelli</i>	■	■	■	■	■	■	■ c
Nakagawa 1992	<i>Erythrocebus patas</i>	■	■	■	■	■	■	■
Salmi & Doran-Sheehy 2014	<i>Gorilla gorilla gorilla</i>	■	■	■	■	■	■	■ d
Kulahci et al. 2015	<i>Lemur catta</i>	■	■	■	■	■	■	■
Oda 1996	<i>Lemur catta</i>	■	■	■	■	■	■	■
Sugiura 2007a	<i>Macaca fuscata</i>	■	■	■	■	■	■	■ e
Sugiura 2007b	<i>Macaca fuscata</i>	■	■	■	■	■	■	■ e
Sugiura et al. 2013	<i>Macaca fuscata</i>	■	■	■	■	■	■	■
Suzuki & Sugiura 2011	<i>Macaca fuscata</i>	■	■	■	■	■	■	■
Koda 2004	<i>Macaca fuscata</i>	■	■	■	■	■	■	■

Table 2. (continued)

Author	Species	Intentionality criteria						
		GD	ID	AS-HR	AS-K	AS-G	AS-A	AS-O
Primata								
Mitani 1986	<i>Macaca fuscata</i>	■	■	■	■	■	■	■
Lemasson et al. 2016	<i>Macaca fuscata</i>	■	■	■	■	■	■	■
Lemasson et al. 2013	<i>Macaca fuscata</i>	■	■	■	■	■	■	■ ^c
Mitani & Nishida 1993	<i>Pan troglodytes</i>	■	■	■	■	■	■	■
Cheney et al. 1996	<i>Papio cynocephalus ursinus</i>	■	■	■	■	■	■	■
Rendall et al. 2000	<i>Papio cynocephalus ursinus</i>	■	■	■	■	■	■	■
Fischer et al. 2001	<i>Papio cynocephalus ursinus</i>	■	■	■	■	■	■	■
Byrne 1981	<i>Papio papio</i>	■	■	■	■	■	■	■
Snowdon & Hodun 1985	<i>Saguinus mystax</i>	■	■	■	■	■	■	■
Jordan et al. 2004	<i>Saguinus oedipus</i>	■	■	■	■	■	■	■
Soltis et al. 2002	<i>Saimiri sciureus</i>	■	■	■	■	■	■	■
Masataka & Symmes 1986	<i>Saimiri sciureus</i>	■	■	■	■	■	■	■
Boinsk & Mitchell 1992	<i>Saimiri sciureus</i>	■	■	■	■	■	■	■
Proboscidea								
Leighty et al. 2008a	<i>Loxodonta africana</i>	■	■	■	■	■	■	■
Soltis et al. 2005	<i>Loxodonta africana</i>	■	■	■	■	■	■	■
McComb et al. 2003	<i>Loxodonta africana</i>	■	■	■	■	■	■	■
McComb et al. 2000	<i>Loxodonta africana</i>	■	■	■	■	■	■	■
Leighty et al. 2008b	<i>Loxodonta africana</i>	■	■	■	■	■	■	■

Table 2. (continued)

Author	Species	Intentionality criteria						
		GD	ID	AS-HR	AS-K	AS-G	AS-A	AS-O
Psittaciformes								
Vehrencamp et al. 2003	<i>Aratinga canicularis</i>	Shaded	Black	Shaded	Shaded	Black	Shaded	Shaded
Balsby et al. 2012	<i>Aratinga canicularis</i>	Shaded	Black	Shaded	Shaded	Shaded	Shaded	Shaded
Balsby & Adams 2011	<i>Aratinga canicularis</i>	Shaded	Shaded	Shaded	Shaded	Shaded	Black	Shaded
Balsby & Bradbury 2009	<i>Aratinga canicularis</i>	Shaded	Black	Shaded	Shaded	Shaded	Shaded	Shaded
Buhrman-Deever et al. 2008	<i>Aratinga pertinax</i>	Shaded	Black	Shaded	Shaded	Shaded	Black	Shaded
Saunders 1983	<i>Calyptorhynchus funereus latirostris</i>	Shaded	Shaded	Shaded	Shaded	Shaded	Black	Shaded
Scarl & Bradbury 2009	<i>Eolophus roseicapillus</i>	Shaded	Black	Shaded	Shaded	Shaded	Shaded	Shaded
Wanker et al. 1998	<i>Forpus conspicillatus</i>	Shaded	Shaded	Shaded	Black	Gray	Black	Shaded
Wanker et al. 2005	<i>Forpus conspicillatus</i>	Shaded	Shaded	Shaded	Shaded	Shaded	Shaded	Black ^f
Berg et al. 2011	<i>Forpus passerinus</i>	Shaded	Shaded	Shaded	Shaded	Shaded	Black	Shaded
Ali et al. 1993	<i>Melopsittacus undulatus</i>	Shaded	Shaded	Shaded	Shaded	Shaded	Black	Shaded
Hobson et al. 2015	<i>Myiopsitta monachus</i>	Shaded	Shaded	Shaded	Shaded	Shaded	Black	Shaded
Ribot et al. 2013	<i>Platycercus elegans</i>	Shaded	Black	Shaded	Shaded	Shaded	Shaded	Shaded

GD: presence of goal-directedness on signal emission; ID: dependence on isolation degree; AS: asymmetry on answers; HR: more answers to higher ranking individuals; K: more answers to kin; G: more answers to individuals from the same group; A: more answers to affiliated individuals; O: other kinds of asymmetries, specified by the following letters:

^a more answers to same ecomorph; ^b selectivity on ignoring calls; ^c more answers to older individuals; ^d more answers to lower rank individuals; ^e more answers to closer individuals; ^f more answers to playbacks of individuals that had previous interaction.

Gray area: support zero-order intentionality hypothesis; Black area: support first-order intentionality hypothesis; Shaded area: no available evidence to evaluate the hypotheses.

We also analyzed each criterion separately (Figure 1). However, besides the kinds of asymmetries on vocal answers that we had originally included in our predictions, we found new ones (Figure 1 category 7): individuals answering more to others of their same ecomorph (Sewall & Hahn 2009); individuals answering more when older conspecifics were calling (Chen et al. 2009; Lemasson et al. 2010); individuals answering more playbacks of those animals that they had a previous interaction (Wanker et al. 2005); higher rank animals answering more to lower ranking ones (Salmi and Doran-Sheehy 2014); more answers received by those at a closer distance (up to 10 meters) (Sugiura 2007a; Sugiura 2007b); and even a selectivity on “ignoring” calls that weren’t aimed to that specific individual (Masataka 1986).

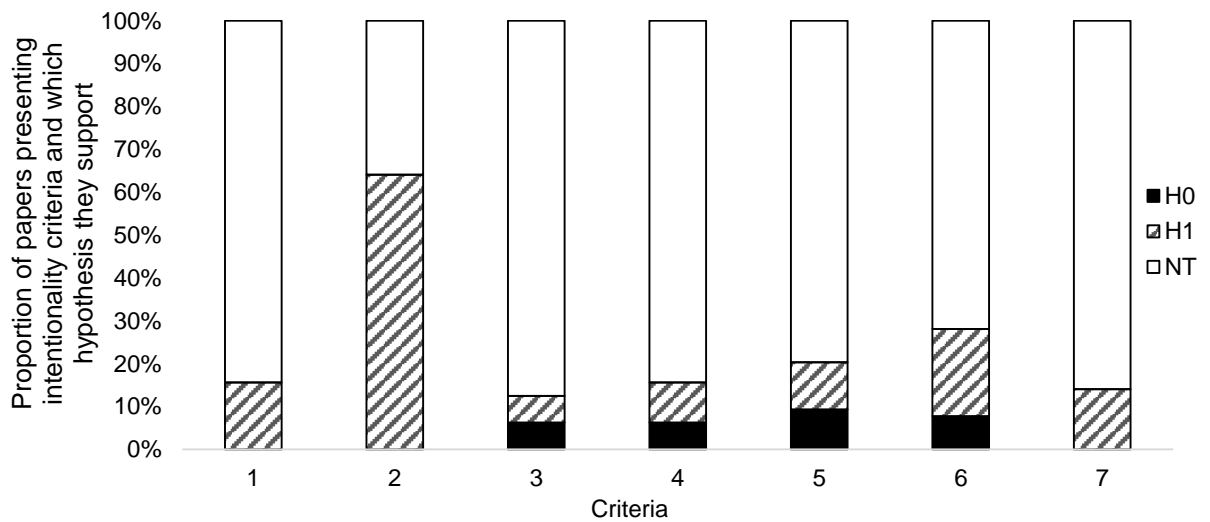


Fig. 1 Proportion of papers supporting the zero (H0) and first-order intentionality (H1) hypotheses, and those with no available evidence to evaluate the hypotheses (NT), according to the following criteria (after Townsend 2016): 1) goal directedness; 2) dependence on isolation degree; 3) more answers to higher rank individuals; 4) more answers to same kin; 5) more answers to individuals from the same group; 6) more answers to affiliated individuals; 7) other kinds of asymmetries on vocal answers cited above.

As evidences of goal-directedness in signal emission we could find: call persistence (Salmi & Doran-Sheehy 2014); increased call duration when farther from the group (Digweed et al. 2007; Koda 2004; Masataka & Symmes 1986; Snowdon & Hodun 1981; Sugiura 2007b), higher frequency modulation range when farther from the group (Koda 2004; Sugiura 2007b; Snowdon & Hodun 1981); calls with shorter duration, higher pitch and stronger frequency modulation from isolated individuals (Oda 1996); smaller subgroups of individuals showed increased call rate when

compared to larger ones (Boinsk & Mitchell 1992); vocal answers with higher amplitude to simulated distant calls when compared to simulated closer calls (Choi et al. 2015); increased duration and frequency in calls when test individuals did not receive answers (Yamaguchi et al. 2010).

The criterion we found most often in the analyzed papers (41 out of 64, 64,06%) was the occurrence of vocal answers according to the degree of isolation of an individual (calling only when isolated or in the presence of others as well). In all of them researchers found that individuals vocally answered contact calls independently of being isolated or not. By this criterion alone, we only found support for the first-order intentionality hypothesis. The other criteria had much more scarce information.

With respect to the taxa presented in compiled results, Primata was the most studied order, and Anseriformes, Cetacea and Gruiformes were the least studied (Table 2). Proportionally (considering the number of evaluated papers), Proboscidea was the order that showed more behaviors supporting first-order intentionality, and Psittaciformes, the one that showed more behaviors predicted by the zero-order intentionality hypothesis (Figure 2). Nonetheless, all taxonomic groups exhibited more evidence supporting the first-order than the zero-order intentionality hypothesis.

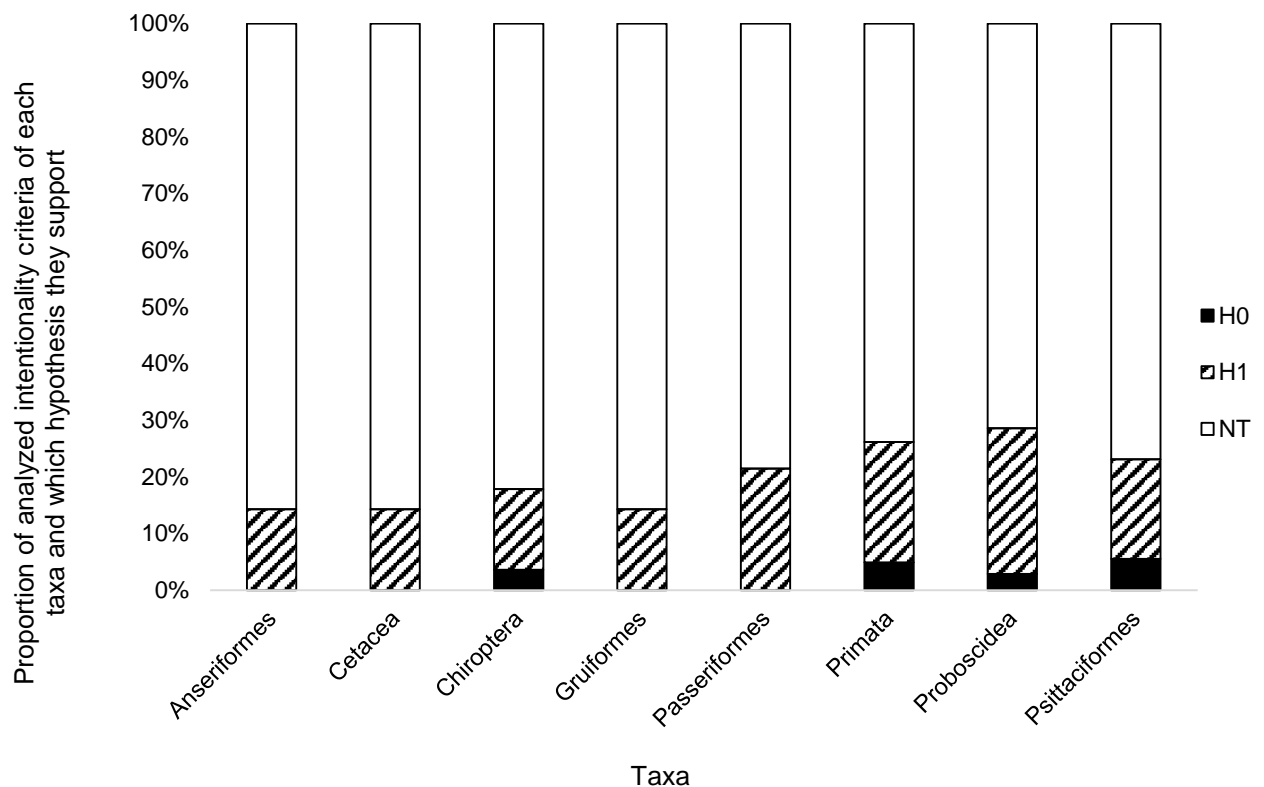


Fig. 2 Proportion of analyzed intentionality criteria of each taxa supporting the zero (H0) and first-order intentionality (H1) hypotheses, and those with no available evidence to evaluate the hypotheses (NT), according to the taxa studied.

DISCUSSION

Contact calls have been studied in many different species, and our review shows that they are not limited to giving an individual's location. With this analysis of the literature on contact calls, along with patterns and behaviors of animals that were described in the articles, we could find many evidences that support first-order intentionality hypothesis. In contrast, only a few papers brought information that does not allow us to reject the alternative hypothesis, that contact calling is a behavior with zero-order intentionality. As the researcher's primary goal for data collection weren't designed to specifically test the intentionality hypotheses, a high number of criteria could not be tested because the information that allowed us to test some predictions were not available. Nevertheless, across the criteria that we could test, evidence supporting first-order intentionality were more common. The only criterion supporting a zero-order intentionality was the absence of preferences on answers to first emitters.

Although this preference to answer specific classes of individuals has become standard for identifying intentional communication (Townsend et al. 2016), it was not present in Dennett's original discussion of intentional vocal production. Indeed, audience specificity is not necessary for intentional behavior to occur (although its presence is a positive indication of first or higher order intentionality).

We have also detected contrasting results for some species, with some behaviors following predictions for zero-order and others for first-order intentionality. For example, *Aratinga pertinax*, in Buhrman-Deever et al. 2008, showed evidences for first-order intentionality because calls elicited answers, which happened independently of a responder being isolated and with preferences for vocalizing back to social partners; but also, for zero-order intentionality because there was no difference on vocal answer rate to group members when compared to strangers. How can we better understand divergent results for the same species?

Regarding asymmetries on vocal answers (the criterion that we found more instances supporting zero-order intentionality hypothesis), we need first to consider what is "necessary" for an individual to selectively answer calls from different categories of emitters. The first requirement is the presence of distinct acoustic cues in the signals of different individuals or groups. Specific measures in a call [for example, the frequencies of energy bands as detected in *Ateles geoffroyi* (Masataka 1986)] can

make this signal individually distinctive. Variation in calls can also appear from a group or place to another [as seen in *Aratinga canicularis* (Vehrencamp et al. 2003)]. Even inside the same group, call structure may be able to inform the social rank of an individual (Digweed et al. 2007). Nonetheless, it is reasonable to think that not all species have acoustic cues for all possible classes of emitters (kin, partner, dominant, etc.), and that these call measures may appear depending on selective pressures of each taxon. For example, roosting bats *Thyroptera tricolor* didn't preferably answer calls from their social group (Chaverri et al. 2012). Previous acoustic analysis of their calls suggests weak group signatures, but strong individual signatures (Gillam and Chaverri 2012), so we could predict that they can better distinguish animal A from B, than if the signal came from an animal from group X or Y. Nevertheless, if the signal does not sound distinct, we cannot expect preferences on answers to animals from two different groups.

Besides verifying different signatures on calls, it is important to know if individuals are sensitive to them, a characteristic that varies between species, and possibly suffers selective pressures to develop. For example, spectacled parrotlets (*Forpus conspicillatus*), selectively answer their offspring, siblings and mates (which are important to their social and reproductive success), but not group members (Wanker et al. 1998). So, when choosing a taxon to study selectivity of answers, researchers must take into account its natural history, social behavior and reproductive strategies, in order to propose predictions that make "biological sense". Thus, strictly speaking, in order to appropriately test both alternative hypotheses by the criterion of audience specificity, we need to know if there are signatures of some kind and if individuals can perceive them. Otherwise, we reduce possibilities of testing the first-order intentionality hypothesis.

Furthermore, there are also methodological issues, which may interfere with the results. In particular, several studies were carried out in captivity (for examples, see Leighty et al. 2008b; Soltis et al. 2002; Janik and Sletten 1998), and we may not know if characteristics of this environment are modifying individual answers to others and to playbacks. Limited space (very different from the broad areas in which contact calls usually happen), stress from confinement, individuals from different groups or places in the same enclosure, are factors that may generate answers out of the context. Another possible source of unnatural responses is expectancy violation. In the context of playback experiments, this situation happens when a call from an individual is played

back to its group, but that individual is not removed from the experiment at that moment (Crane et al. 2015). Tests for this effect have shown different answers from animals when compared a controlled situation (removing the stimulus source) with an uncontrolled one (Townsend et al. 2012) – individuals looked more and showed more vigilance under the second condition. Thus, if we do not control for this possibility, test animals may answer more to playbacks than in natural situations.

Applying Dennett's approach of evaluating intentionality, Schel et al. (2013), Townsend et al. (2016) and Sievers et al. (2017) have suggested that first-order intentionality hypothesis can be tested through the fulfillment of a few operative criterion, like the ones used for this research. The last approach avoids considering the attribution of mental states by emitters and receivers (Townsend et al. 2016), something that seems to be unhelpful for intentionality studies for two reasons: first, human children find difficulties in communication with higher intentionality orders, and even adults do not speak considering mental states all the time – this view brings human and animal communication to a more likely framework. Second, a purpose of studying animal communication is to better comprehend evolutionary precursors of human language, and not to try to put them both at the same complexity level – this may hinder biological and psychological comparisons between human and animal communication. Therefore, applying operative criterion analysis to evaluate the presence of intentionality in communication, can bring advantages to a better understanding of intentionality in animal communication.

Dennett (1983) established his approach on the Gricean framework of human communication (where the signaler emits a signal intending to cause a response on the receiver, together with the aim that this receiver recognizes his intention). Such approach, when applied to animal communication, is fruitless (Townsend et al. 2016; Sievers et al. 2017). High cognitive abilities of emitters and receivers were required to fit the model (which can be at least a fourth-order in Dennett's scale), and up this point, still couldn't be shown in non-human animals. The so called neo-Gricean framework, without requirement of theory of mind to characterize a signal as intentional, proposes the flexibility of emitters and receivers to produce signals as a reference of intentionality (Sievers et al. 2017). Such flexibility could be found in some articles we revised, e.g. calls getting more elaborated when not answered at a first time.

As a topic still in intense debate, intentionality in animal communication needs studies from multiple areas. In this review, we showed that contact calling displays

evidences of volitional initiation and modulation of acoustic parameters of calls, which makes this vocalization a good model to study intentional production. Interestingly, because these calls are also produced by respondents, they also offer insights on intentional replies, and altogether on intentional communication in animals (Sievers et al. 2017). If future studies find support to first-order intentionality in contact calls, it may be also indicated to develop protocols to test evidence for second-order intentionality (e.g. Crockford et al. 2012). As such, contact calls, as signals largely influenced by social relations, may constitute useful tools to better comprehend the evolution of intentionality, an important attribute to human communication.

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