All in the Family: Bottlenose Dolphin Kin Recognition Using Signature Whistles

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Abstract

Kin recognition aids in preventing incest as well as determining which conspecifics to compete with and which to give aid to. There are various kinds of kin recognition, and some of which have been shown to be more cognitively demanding. Kin recognition based on familiarity is cognitively demanding as it requires organisms to learn and remember certain characteristics of their kin in order to reach the level of individual recognition. To determine if dolphins use this cognitively demanding form of kin recognition, we scored the video and audio recordings from a playback study (Bruck 2013) based on behavior and acoustic responses. We found that a dolphin's response is predicted by its degree of relatedness to the dolphin whose whistle is being played. This study is the first to provide evidence that Bottlenose Dolphins (*Tursiops truncates*) perform kin recognition based on familiarity and are able to recognize individuals.

Introduction

Kin Recognition

Kin recognition has been seen in various organisms and is beneficial in preventing incest as well as determining which conspecifics to compete with and which to give aid to (Hamilton 1964). Mateo and Johnston (2000) discussed that both vertebrates as well as invertebrates recognize unfamiliar kin based on a degree of relatedness. This discernment is made through self-referent phenotype matching (or the "armpit effect") in which an animal collects information on their own traits as well as those of familiar kin and uses the memory as a comparison (Oxford University Press). The most common modality for self-referent phenotype matching is odor, where animals identify each another by their scent, and then use the chemical cues as a source of comparison (Mateo & Johnston 2000). In the 1996 study of vocal recognition of individuals and kin in free-ranging rhesus monkeys (Rendall et al. 1996), rhesus monkeys had significantly faster and longer responses to the playback of vocalizations of kin than to those of non-kin. These rhesus monkeys may identify kin using familiarity, but the rhesus monkeys vocalizations tend to be similar to those of their kin. So, they may simply identify similarities in their vocalizations and their kin's' vocalizations. As a mechanism, self-referent phenotype matching has a low cognitive demand, as it requires no long-term memories; and organisms merely carry a referent cue set on their body wherever they go. There are other mechanisms of kin recognition that require memory and individual recognition. Kin recognition based on familiarity, for example, is cognitively more demanding as it requires organisms to learn and remember certain characteristics of their kin in order to reach this level of individual recognition (Sayigh et al. 1999). Kin recognition based on familiarity is essential for animals that cannot use phenotype matching as a mechanism of kin recognition. For example, dolphins possess signature whistles used for identifying individuals, which are not coded for by genetics. It was seen in the Sayigh,

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Tyack, Wells, Scott, & Irvine 1995 study that female calves have a tendency to produce whistles that are very different from that of their mothers in order to avoid confusion between the two in their social group, but male calves are more likely to produce whistles that have similarities to that of their mother (Sayigh et. al. 1995). Therefore, it is unlikely that they use phenotype referencing because the whistles are innovative signals that are learned and show specific differences in structure within kin on purpose to prevent confusion amongst the social pods. One of the purposes of this study is to determine if dolphins are able to recognize the calls of kin as distinct from non-kin (i.e. familiarity and learned whistle association as a mechanism of kin-recognition)

Social Structure

Bottlenose dolphins have shown complex fission-fusion social patterns characterized by variations in social partners overtime (Connor et. al. 1992). Their complex social structure is evident in Shark Bay, Western Australia, which is the most studied social alliance amongst dolphins (Connor et. al. 2001). The males in Shark Bay form couples and trios to maintain consortships with females. In addition, they form another male alliance to attack other groups of males in an effort to get mates (Connor et. al. 2001). This 'super-alliance' is composed of "stable alliances" and "labile alliances" (Connor et. al. 2001). The stables alliances may last for 14 or more years. Often, these stable alliances are formed between male dolphins in order to collaborate in times of need (Conner et. al. 2001). The intertwining of all of the ever-changing alliances within the 'super-alliance' creates a diverse and complex social system amongst the bottlenose dolphins.

Communication

Bottlenose dolphins use a form of vocal communication known as whistles. David and Melba C. Caldwell (1965) were the first to document that dolphin's possess individualized signature whistles given most frequently during periods of separation. Whistles are a narrow-band vocalization with frequency contours ranging between 9.3 to 27.3 kHz (Esch et al. 2009, López 2011). At a young age, Bottlenose dolphins develop a distinctive whistle to identify them (Janik et al, 2006). Whistles allow dolphins to communicate to one another helping to maintain group cohesion and coordination (Esch et al. 2009). Signature whistles crystallize in the first year of life and are stable for 12 or more years (Sayigh et al. 1990). Dolphins are able to distinguish familiar from unfamiliar callers, and they possess multi-decade long social recognition of these whistles (Bruck 2013). It is unclear the degree to which dolphins are able to recognize the calls of familiar animals as being synonymous with the caller or whether certain individual calls are more meaningful to receivers (i.e. the calls of close kin). The second purpose of this study is to demonstrate that dolphins respond differentially to kin as a class of whistles independent of amount of time together, sex or age of the caller (indicating that signature whistles do function similarly to human names)

Methods

The study utilized 26 males and 30 females aged 5 months to 47 years from six different zoos/aquaria affiliated with The Atlantic Bottlenose Dolphin Breeding Consortium: Brookfield Zoo, Indianapolis Zoo, Minnesota Zoo, Disney's Animal Programs and Environmental Initiatives, Dolphin Quest, and the Texas State Aquarium. IACUC approval was obtained from each facility. Additionally, 20 more

historical signature whistles were obtained from recordings maintained at the Woods Hole Oceanographic Institution. When possible, dolphins were recorded using two SS03-10 Sea Phone hydrophones placed at least 3 m apart. For multi-point recordings both hydrophones were connected to a PreSonus® AudioBox™ two channel input device. The stereo recordings assisted with identifying the correct caller. A playback design was used to assess familiarity. Calls were triggered after respondent swam past speaker (head within 1 m). Dolphins (respondents) were presented with both kin and non-kin familiar signatures played through a Lubell Labs® LL9816 underwater speaker. Responses were videotaped and blindly scored for number of times the animal looked at the playback speaker, approached the playback speaker (within 1 m) as well as the duration of the approach and look behaviors. Acoustic data were also taken measuring the number of reply whistles and the number and duration of echolocation bouts (events separated by 1 s). Combined these represent the seven response variables used for our principal component analysis.

The seven dependent measurements were combined into principal components (PC1 and PC2) that explained about 80% of the variation. All seven variables loaded equally onto PC1, making this a measure of overall response strength. In PC2, the behavioral measures of approach and looks loaded negatively, while the acoustic measures loaded positively, meaning that positive values of this variable indicate the dolphin is more willing to call and less willing to approach and vice versa. We ran linear mixed models with dolphin ID and zoo as random effects and degree of association (factoring in both time together and time apart), age, sex and kin as fixed effects.

Results

Dolphins respond more to the signature whistles of kin than to the whistles of non-kin ($z = 3.904$, $p < .001$, figure 1). In fact, dolphins increased their magnitude of response to playbacks in proportion to their coefficient of relatedness to the caller ($z = 4.078$, $p < .0001$, figure 2). Dolphins do not respond more to callers based on familiarity. Degree of association did not influence the level of response ($z = 2.152$, $p = .146$). Age

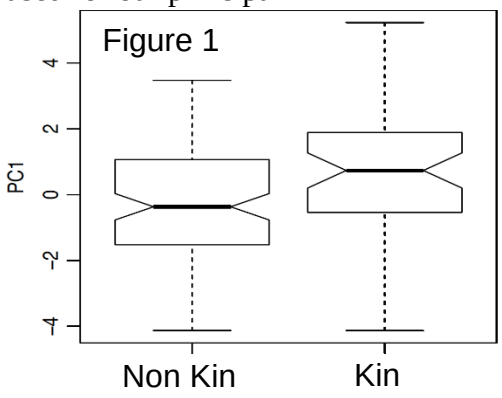

Figure 1. Strength of overall response to playbacks for kin and non-kin callers (p , .001). PC1 was a measure of equal weighting between seven dependent measurements including: duration of time respondent was looking, duration of time respondent is within 1 m of playback speaker, number of times respondent looked, number of times respondent approached the speaker within 1 m, number of echolocation bouts (events separated by 1 s), amount of time spent echolocating and number of reply whistles.

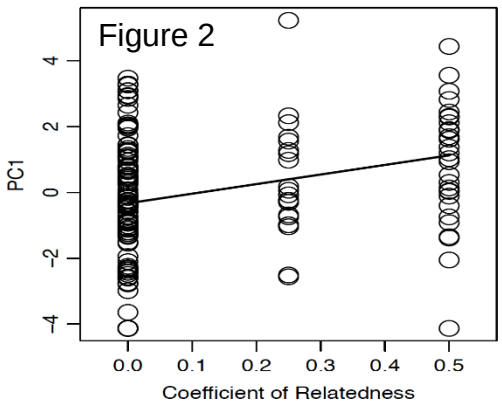

Figure 2. Strength of overall response to playbacks in relation to the coefficient of relatedness between the caller and respondent ($p < .0001$).

(z = .575, p = .571) and sex (z = 2.359, p = .080) overall were not strongly significant factors. However, PC2 indicates that males are less likely to respond to the calls of females by vocalizing, but are more likely to approach or look at them (z = 4.282, *p < .01, figure 3).

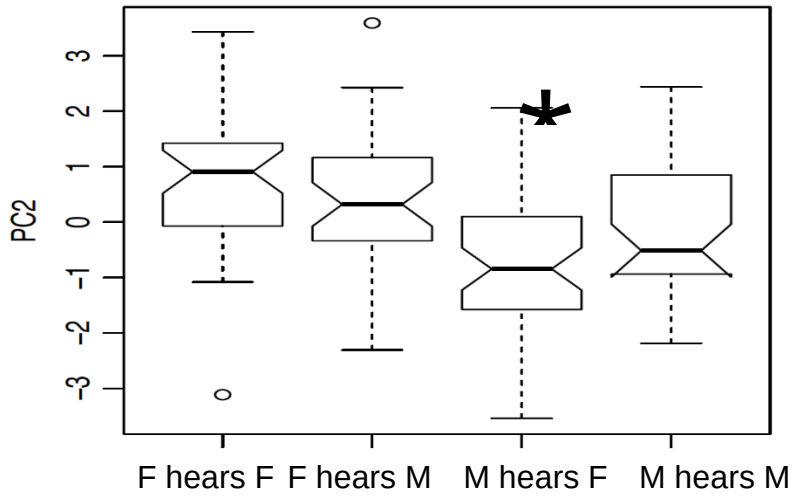

Figure 3. Sex differences in dolphin responses to familiar playbacks. Only males hearing females is significant (p < .01). PC2 was a measure that negatively loaded dependent measurements including: duration of time respondent was looking, duration of time respondent is within 1 m of playback speaker, number of times respondent looked and number of times respondent approached the speaker within 1 m- but positively loaded number of echolocation bouts (events separated by 1 s), amount of time spent echolocating and number of reply whistles.

Discussion

When presented with a series of familiar whistles dolphins were able to discriminate kin from non-kin. This provided evidence that kin recognition mechanisms in dolphins are based on familiarity in much the same way human kin recognition works, as signature whistles are innovated and learned (Janik 1999). This type of recognition differs from the kin recognition used by belding's ground squirrels that use the armpit effect to differentiate between kin (Mateo & Johnston 2000). Also, organisms like fur seals use voice to determine who is kin because the calls of the kin have certain characteristics in their voice that are more familiar, leading to a higher response (Charrier Mathevon & Jouventin 2003). In this case of fur seals, the fur seals are responding based off of the familiarity with the call and not with due to individual kin recognition. All of these are far less impressive than what dolphins are doing because dolphins are associating individuals with arbitrary signals. This study provides the first evidence that dolphins us language like representation giving us an insight into the dolphin's mind and understanding that they perceive individuals. Because degree of association was not significant, differential responding according to coefficient of relatedness indicated that dolphins were perceiving the caller when hearing a playback and not just responding to the familiarity of the signal. Age of both the calling and responding dolphins was not a factor in the strength of the animals' responses to playbacks, indicating that kin recognition develops early. This was in keeping with research that shows that young dolphins first learn to produce their mother's signature whistle before any other vocalization (Tyack and Sayigh 1997). The only sex difference observed related to how males responded to the sound of females (related and unrelated). Interestingly, they chose not to respond to female calls with vocalizations of their own, but with approach and look behaviors. This may have implications for mating behavior.

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