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Come dine with me: food-associated social signalling in wild bottlenose dolphins (*Tursiops truncatus*)

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Abstract

The occurrence of food-related signaling is prolific in the animal kingdom with some food-associated vocalizations considered functionally referential. Food calls can, however, vary greatly in the type of information they convey. Thus, there are a multitude of purposes for which food calls are used, including social recruitment, caller spacing, the indication of type, quantity, quality, divisibility of food and/or the caller's hunger level and even as tools to manipulate prey behaviour. Yet little work has focused on the social aspect of food calling in animals. We investigated the association of social signals in wild bottlenose dolphins with foraging behaviour where context specific food-associated calls are commonly produced. Our data showed that specific social signals were significantly correlated with food call production and these calls rarely occurred in the absence of food calls. We suggest that animals are sharing additional information on the food patch itself with their social affiliates.

Keywords: food calls, bottlenose dolphin, signature whistles, vocal learning, call matching.

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Introduction

Food calls are found throughout the animal kingdom when animals are trying to attract others to

a foraging site (Clay et al. 2012). In many cases, these vocalizations function in attracting related

animals to increase the caller's inclusive fitness. Animals may also call to attract non-related

partners, which may help enhance the caller's social standing (Slocombe et al. 2010).

Alternatively, the presence of others may increase the caller's food intake by helping to herd

prey (Brown et al. 1991) or protecting against predators (Radford and Ridley 2007) or competing

conspecifics (Heinrich 1988). Animals may also communicate more detailed information such as

the type, quality or quantity of food available (Clay et al. 2012). Thus much interest has been

placed on understanding how food-related signaling benefits the caller. Yet little focus has been

placed on the other types of social signals that may accompany the production of food-associated

calls.

In cetaceans, for example, food-associated vocalizations have been described for several species

in the wild, including killer whales (*Orcinus orca*, Ugarte et al. 2006; Deecke et al. 2011),

humpback whales (*Megaptera novaeangliae*, Stimpert et al. 2011; Parks et al. 2014), and

bottlenose dolphins (Janik 2000a). While these calls may be used to attract conspecifics, reports

suggest that their primary function may be one of manipulating prey to facilitate capture (Janik

2000a). While this is an interesting possibility, there is so far no experimental confirmation. One

study looked at the effect of high, mid and low frequency dolphin clicks on fish behaviour but

found no effect (Benoit-Bird et al. 2006). Many of these food-related burst-pulsed calls,

however, are stimulus specific and therefore particular calls may have evolved to modify the

behaviour of particular prey species. If food associated calls do play a role in facilitating prey

capture in wild animals then the attraction of conspecifics may be a by-product that does not

52   actually benefit the caller. However, animals may use other social calls concurrently with food-

53   associated vocalizations in order to share information on the food patch.

54   Ridgway et al. (2014) reported calls in a food context in captive bottlenose dolphins and beluga

55   whales that were structurally different from other dolphin food calls, such as the bray call (Janik

56   2000a). Ridgway et al. (2014) believed these calls signalled the emotional state of the animal

57   where by an animal is anticipating a food reward. Thus, these calls should not be specific to a

58   food context and would therefore not qualify as food calls (Clay et al. 2012). Interpreting calls in

59   training contexts can be difficult and further work on wild animals is required to explore the

60   distinction between such calls.

61   To investigate the possibility of added communication through other social calls when food calls

62   are given, we investigated the association of whistle interactions with bray calls in bottlenose

63   dolphins. Bray calls have a frequency spectrum that makes them suitable for manipulating prey,

64   but also for attracting conspecifics to the foraging location (Janik 2000a). We investigated

65   whether there was a correlation between food calling and a certain sign of social interaction, the

66   matching of whistles between different animals (Janik 2000b).

67   **Materials and Methods**

68   During May to September 2010, we collected acoustic recordings from the dolphins that frequent

69   St. Andrews Bay, Scotland. These animals are members of a resident population of

70   approximately 195 bottlenose dolphins that range between the Moray Firth and the Firth of Forth

71   (Cheney et al. 2013). To identify foraging, we looked for the presence of food-related bray calls

72   in our acoustic recordings. Animals produce bray calls at depth (20m-30m) (Hastie et al. 2006)

73 and often return to the surface visibly chasing and foraging on large fish (Janik 2000a; Hastie et

74 al. 2006). We then explored if whistle matching occurred in close proximity to bray calls.

75 Group follows were conducted from a 6-m boat at Beaufort sea state three or less and animals

76 were photographed with a Canon Digital 30D SLR camera with a Sigma 100-300mm, F4 zoom

77 lens. Acoustic recordings were taken using two HTI-96 MIN hydrophones (frequency response:

78 0.002 to 30 kHz ±1 dB) towed at 2-m depth and a Toshiba Satellite Pro Laptop with an Edirol

79 UA-25 sound card (sampling rate: 96 kHz, 16 bit).

80 We analysed acoustic recordings by screening the spectrographic displays (FFT length 1024,

81 87.5% overlap, Hanning window) in Adobe Audition v2.0 (Adobe Systems) by eye for

82 occurrences of low-frequency bray calls and frequency modulated whistles. Those recording

83 segments where engine noise exceeded 2 kHz were discarded from the analysis. Bray calls are

84 highly distinctive and were identified by detecting their two-part structure consisting of a long,

85 low frequency (peak at less than 2 kHz) pulsed sound followed by a short down-sweep (Janik

86 2000a). Each bray call is 500 to 600 milliseconds in length (dos Santos et al. 1995; Janik 2000a)

87 and can be recorded from over a km from the calling animal. Bray calls are usually produced in

88 bouts (Janik 2000a) and therefore a series of brays in close proximity was treated as one braying

89 event (Figure 1). Bray sequences can last up to 30 s (dos Santos et al. 1995). Frequency

90 modulated whistles were identified and could either be continuous in their frequency contour

91 pattern or could be multi-loop whistles. Multi-loop whistles were defined as a repeated

92 modulation pattern that could be separated by periods of stereotyped silence up to 250ms in

93 length (Esch et al. 2009). Whistles with periods of silence of less than 250ms but not overlapping

94 were treated as one whistle. A total of 23 hours and 51 minutes of recordings were inspected

95 spanning 18 days from June to August 2010, of which 12 hours and 08 minutes from 15 days

96   were of sufficient sound quality for further analysis. A total of 81 braying events were identified
97   in this recording time.

98   The simple two-element recording system used in this study meant we were unable to localise
99   whistles to individual animals. Instead we used overlapping whistle interactions as an indicator
100 of two animals communicating with each other. We focused on those overlaps in which both
101 animals were using the same whistle type, an indicator of animals addressing each other (Janik
102 2000b; King and Janik 2013; King et al. 2014).

103 An 'overlap match' was defined as two whistles of the same contour pattern (change of
104 frequency over time) where the end point of one whistle finished after the start of the other
105 whistle (Figure 2). All identified occurrences of overlap whistle matching were separately
106 checked and then agreed by both authors who have been shown to agree with classifications by
107 groups of independent observers (Janik 1999; Deecke and Janik 2006; Janik, King, Sayigh,
108 Wells 2013).

109 To be sure the overlapping of whistles was not merely a result of an increase in call rate, we also
110 looked at the occurrence of different whistle types that overlapped but did not match. An
111 'overlap no match' was defined as two whistles with different contour patterns where the end
112 point of one whistle finished after the start of the second whistle.

113 Permutation tests were performed to test whether overlap matching and bray calls occurred in
114 close temporal proximity above chance levels. The times between each 'overlap match' and the
115 nearest bray call (n=30) were shuffled with the times between each 'overlap no match' and the
116 nearest bray call (n=55). The random distribution was calculated from 10000 permutations under
117 the null hypothesis that there was no relationship between the timing of the 'overlap matches'

118   and bray call production. The observed test statistic (mean proximity between 'overlap matches'

119   and bray calls) was then compared with the random distribution. The observed difference in

120   mean proximity to bray calls between overlap matches and overlap non-matches was also

121   compared to a random distribution of differences in mean proximities between the two whistle

122   categories, which was calculated from 10000 permutations.

123   All analyses were performed in R (R project for statistical computing; GNU project).

124   **Results**

125   A total of 30 occurrences of overlap matching and 55 occurrences of overlap non-matching

126   events were identified from recordings made during 10 encounters across 9 days (Table 1).

127   Individual re-sightings of animals across the 10 encounters were relatively low (mean: 1.85,

128   range: 1-5) and group sizes were large (mean: 9.5 animals, range: 3-23); see Table 2. A total of

129   46 animals were identified plus 4 calves. Of those, 69% were only sighted in one or two

130   encounters, 22% in three encounters, and 9% in four or five encounters. No single animal was

131   found in all 10 encounters.

132   Overlap matches occurred in significantly closer temporal proximity to bray calls than whistles

133   that overlapped but did not match ($P < 0.0066$, permutation test, Table 1 and Figure 3). Under

134   the random distribution only 57% of whistles were expected to occur within 1 minute of a bray

135   call. However, 73% of observed overlap matches occurred within 1 minute of a bray call

136   whereas of those cases where whistles overlapped but did not match, only 49% occurred within 1

137   minute of a bray call. The randomization test showed that overlap matches and bray calls

138   occurred in tight temporal proximity with the mean proximity between overlap matches and bray

139   calls significantly smaller than expected by chance (permutation, $P < 0.0001$; Figure 4). In

140   contrast, the mean proximity between whistles that overlapped but did not match and bray calls

141   was significantly larger than expected by chance (permutation, $P < 0.0001$; Figure 4).

142   Thus the rapid matching of call-types was closely associated with bray call production and

143   appears to play a significant role in bottlenose dolphin foraging behaviour while the animals

144   decrease rapid, non-matching interactions during foraging.

145   The majority (60%) of whistles used in overlap matching events were variations of one particular

146   whistle pattern (type A; Figure 2 & Table 2), with a second whistle pattern (type D) produced in

147   20% of events (Figure 5 & Table 2).

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150   **Discussion**

151   We have shown that bottlenose dolphins repeatedly produce specific social signals, overlap

152   matches, alongside food-associated calls and that they rarely produce these signals independently

153   of the food call. In addition, they appear to decrease the production of overlapped non-matched

154   calls when foraging. This suggests that there is a social aspect of food calling in animals that has

155   not previously been reported.

156   A few studies have reported matching exchanges (Janik 2000b; King et al. 2013) and

157   overlapping in dolphin whistles (Caldwell and Caldwell 1968; Nakahara and Miyazaki 2011).

158   Bottlenose dolphins use vocal learning to develop individually distinctive signature whistles that

159   allow for individual recognition (Janik and Sayigh 2013). In specific contexts, these are also

160   used in matching interactions (Janik and Slater 1998; King et al. 2013). In captive bottlenose

161   dolphins, signature whistle matching i.e. copying the signature whistle of an animal right after it

162   produced one, leads to further signature whistling (King et al. 2014). This does not occur when

163   using whistles of other types as a reply. Furthermore, the animals show no sign of aggression

164   when matched, suggesting that signature whistle matching is affiliative and helps to maintain

165   contact (King et al. 2013; King et al. 2014). In the wild, the matching of call types in quick

166   succession in coordinated foraging, as shown here, could facilitate the directing of signals to

167   particular individuals that share a large communication network (McGregor and Dabelsteen

168   1996; Janik 2005).

169   The production of food-related bray calls in dolphins has previously been correlated with

170   animals swimming quickly towards the caller's location, perhaps facilitating joining events

171   between individuals or groups of animals(Janik 2000a). Animals who wish to join may therefore

172   use overlap matching to signal their intention when approaching a caller. However, although

173   dolphins are known to increase whistle rates dramatically when groups join together, whistle

174   matching has not been observed during these joining events (Quick and Janik 2012). It is thus

175   unlikely that overlap matching facilitates group joins, but it may help coordination between

176   animals within a group when rapid reactions are needed.

177

178   An example for this type of rapid signaling can be found in the pied-babbler (*Turdoides bicolor*),

179   a species that uses a close call, called the 'chuck' to regulate spacing between foraging

180   competitors (Radford and Ridley 2008). Although not used aggressively, the close call did deter

181   conspecifics that attempted to share an individual's foraging patch, and was effective in

182   indicating the forager's current position. Pied-babblers increased chuck production rate when in

183   larger groups, and when neighbours were closer (Radford and Ridley 2008).

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185   Overlapping can occur in a chorus when animals compete over resources such as females

186   (Staicer et al. 1996) or aim at an acoustic dilution effect for predator avoidance (Gerhardt and

187   Huber 2002). We suggest a more interactive function here where overlapping of shared whistles

188   regulates the spacing of individuals during intensive feeding bouts where group sizes are large.

189   Such directed overlapping can be an aggressive signal in some species (e.g. manakins; Maynard

190   et al. 2012), and a sign of social bonding (e.g. chimpanzees; Fedurek et al. 2013) or social

191   cohesion (e.g. wolves; Mazzini et al. 2013) in others. Additional studies are needed to clarify the

192   function of overlapping during foraging in dolphins.

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194   As one may expect with vocal matching interactions, the number of whistles that occurred within

195   an overlap match was usually two, indicating only two animals were vocalizing. However, there

196   were two occasions where three matching whistles overlapped (Figure 2). Janik (2000b) also

197   found that matching interactions mostly involved two animals, where each produced a single

198   whistle. He used a randomisation test to show that the number of matching interactions was

199   significantly greater than expected if all animals were calling independently of each other (Janik

200   2000b). The fact that mainly pairs and sometimes trios of animals engaged in these relatively

201   isolated sharing events, makes them different from the production of food calls found in other

202   species (Clay et al. 2012). In the events we reported here, the bray call is the food call, and

203   whistles are used additionally to apparently coordinate behavior between pairs or trios of animals

204   within the larger foraging group.

205   Interestingly, the fact that only a small number of whistle types appear to be represented in this

206   dataset suggests that these calls may not be signature whistles. While we had re-sightings of

207   animals in encounters, our sample comprised a large number of animals. We therefore think that

208   these whistles may represent shared whistles, which are used by multiple animals in this very

209   specific context. If so, the matching of calls by bottlenose dolphins may go beyond the exchange

210   of signature whistles. However, since we cannot completely rule out that the whistles are not

211   signatures of specific animals, further investigation into whistle use during group foraging is

212   needed.

213   We do not know how many different individuals participated in these matching events. Whether

214   it was a small or large number of animals, our results show that overlap matching is closely

215   related to bray call production across multiple recordings. Further work is required to fully

216   understand the function of overlap matching, now that we have shown that there is a social

217   aspect to food calling. Future studies should investigate not only the use of the food call itself,

218   but the social signals that accompany those calls in order to give further insight into the cognitive

219   significance of food-associated vocalizations.

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221   **Acknowledgements**

227

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Table 1. The number of occurrences of the two whistle categories and their mean proximity to the nearest bray call.

| Whistle Category	# of occurrences	mean proximity to bray call (seconds)
overlap match	30	82 (range: 0.0001-627)
overlap no match	55	392 (range: 0.0001-3163)

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Table 2. The number of different recording days where overlap matching occurred, the number of overlap matches that were recorded, the group size at the time of recording, with the additional number of calves identified provided in parentheses, and the whistle type (frequency contour pattern).

Recording Day	# of overlap matches	Group Size	Whistle Type
1	1	7	A
2	1	3	B
3	1	4 (1)	A
4	3	3 (1)	BC
5	4	5	A
6	6	8	AD
7	5	18 (2)	AD
8	4	8	ABD
9.1	2	21 (2)	A
9.2	3	11 (1)	A

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335   **Figure 1.** Food-associated calls in wild bottlenose dolphins; example of a braying bout.
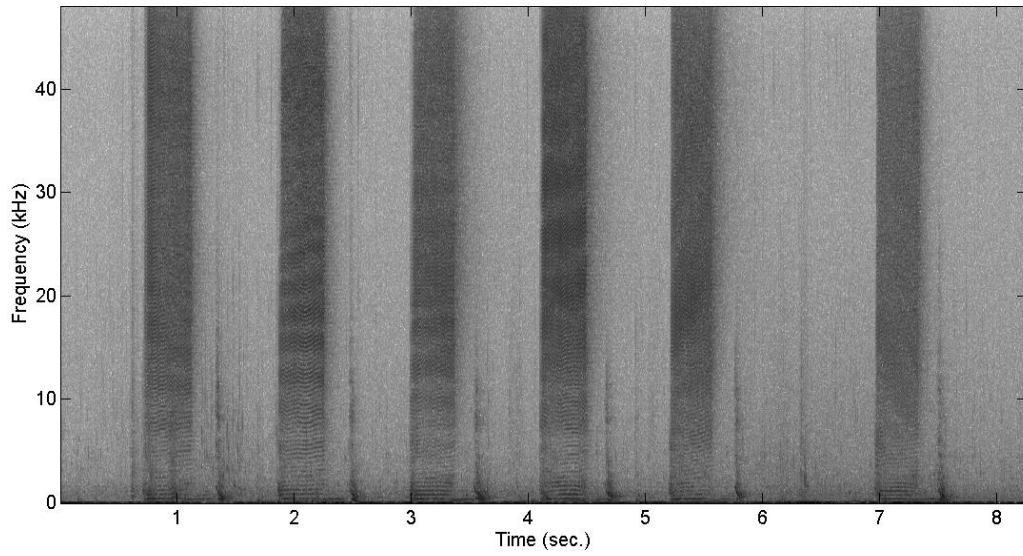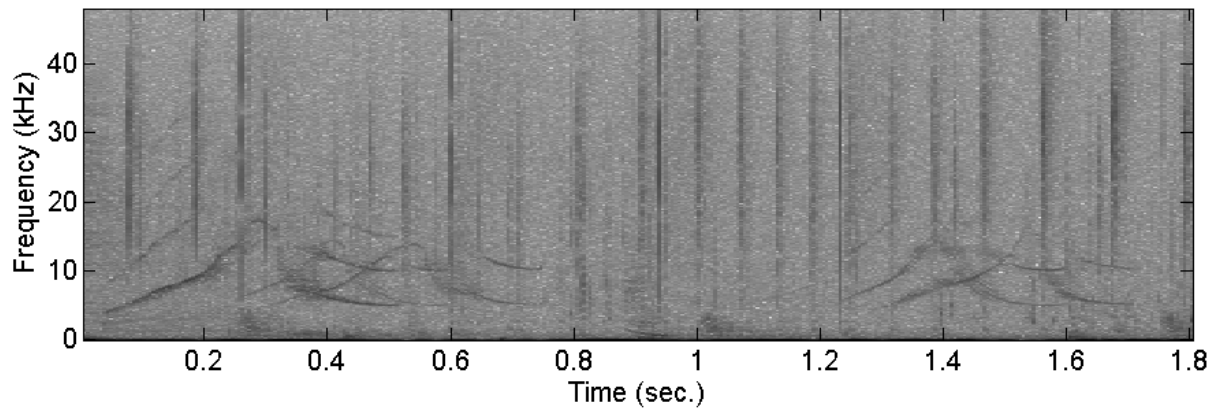

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345   **Figure 2.** Examples of two occurrences of a matching overlap, where three and then two

346   whistles of the same type (whistle type A) overlap in time. The end of the first whistle occurs

347   after the start of the second and third whistle.


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350   **Figure 3.** The distribution of proximities to the nearest bray call for the two whistle categories;

351   the median proximity to the nearest bray call is 13.5 seconds for overlap matches and 71 seconds

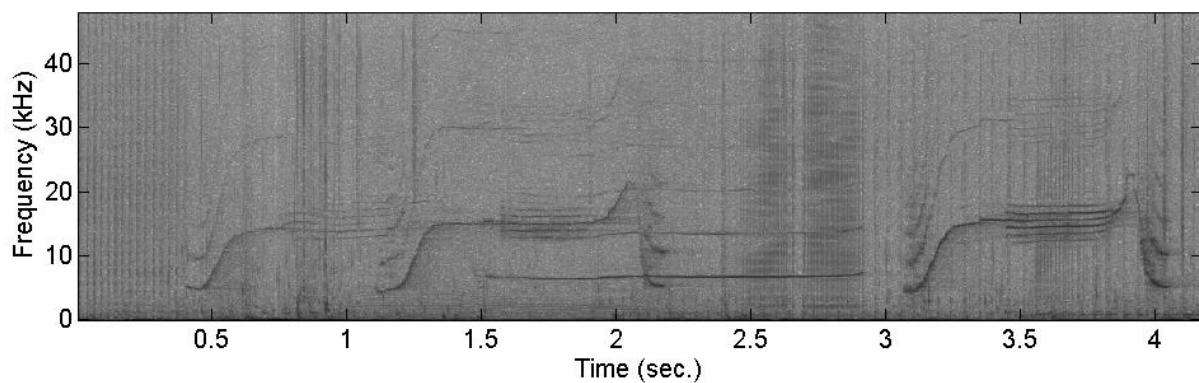352   for whistles that overlap but do not match.
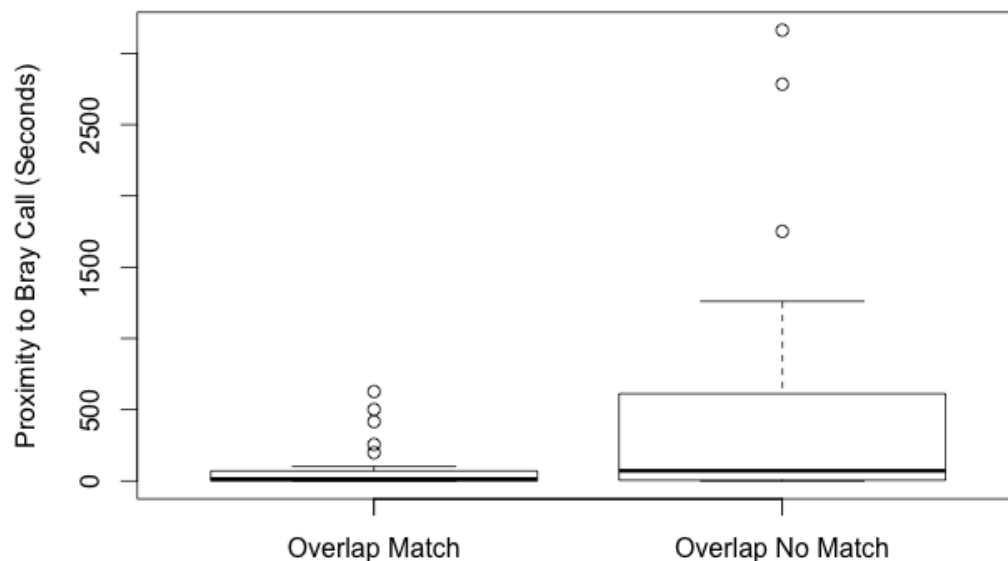
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355 **Figure 4**. Histograms of the expected mean proximities, based on 10 000 randomisations, of

356 each whistle category to the nearest bray call (seconds), the dotted line indicates the observed

357 mean proximity.
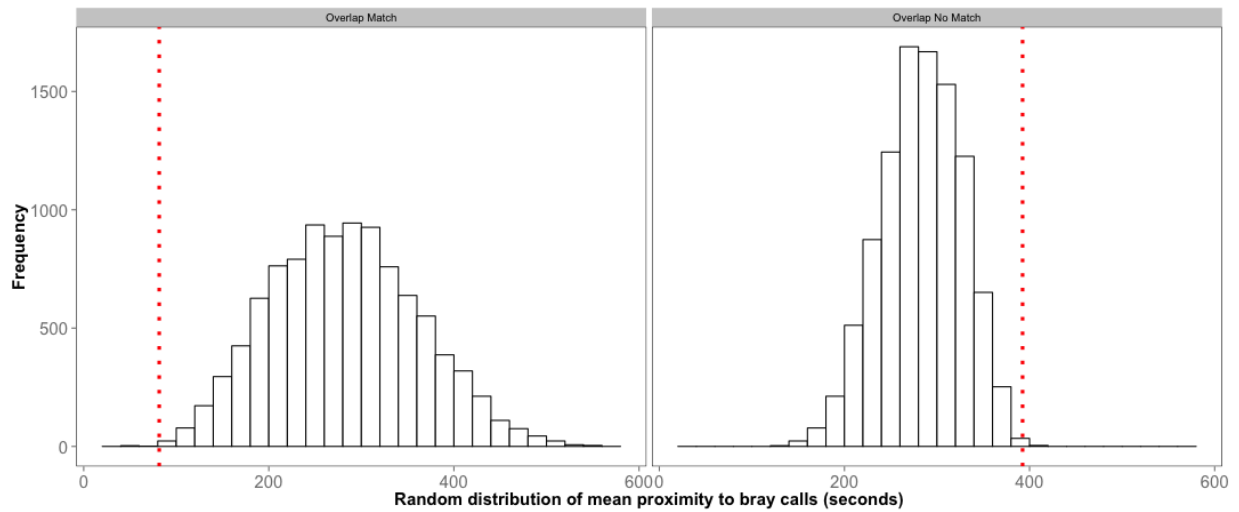
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360 **Figure 5.** Example of overlap matching, where two whistles of the same type (whistle type D)

361 overlap in time. The end of the first whistle occurs after the start of the second whistle. A third

362 whistle (type D) follows later.

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