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Variations in killer whale food-associated calls produced during different prey behavioural contexts

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ABSTRACT

Killer whales produce herding calls to increase herring school density but previous studies suggested that these calls were made only when feeding upon spawning herring. Herring schools less densely when spawning compared to overwintering; therefore, producing herding calls may be advantageous only when feeding upon less dense spawning schools. To investigate if herding calls were produced across different prey behavioural contexts and whether structural variants occurred and correlated with prey behaviour, this study recorded killer whales when feeding upon spawning and overwintering herring. Herding calls were produced by whales feeding on both spawning and overwintering herring, however, calls recorded during overwintering had significantly different duration and peak frequency to those recorded during spawning. Calls recorded in herring overwintering grounds were more variable and sometimes included nonlinear phenomena. Thus, herding calls were not produced exclusively when feeding upon spawning herring, likely because the call increases feeding efficiency regardless of herring school density or behaviour. Variations in herding call structure were observed between prey behavioural contexts and did not appear to be adapted to prey characteristics. Herding call structural variants may be more likely a result of individual or group variation rather than a reflection of properties of the food source.

1. Introduction

Food-associated acoustic signalling is common amongst birds and mammals and may provide selective advantages to signallers. For example, it can provide information to related individuals about the location of food (Von Frisch, 1967), attract conspecifics to increase the signaller's food intake (Brown et al., 1991), decrease predation risk (Elgar, 1986), defend resources against competitors (Bugnyar et al., 2001; Acevedo-Gutiérrez and Stienessen, 2004) or repel conspecifics to regulate spacing between individuals, which increases foraging efficiency (Boinsky and Campbell, 1996; Gros-Louis, 2004). Although food-associated signalling is common, it lacks a unifying function (Clay et al., 2012). Variations in food-associated calls most often occur in the rate at which calls are produced and may reflect signaller motivational state and potentially information about the quantity, quality or divisibility of resources (e.g. Elgar, 1986; Bugnyar et al., 2001). Changes in call structure or type occur less often and may convey information about caller sex or identity (Gros-Louis, 2006), motivational state or properties of the food source (Benz et al., 1992; Benz, 1993; Evans and Marler, 1994; Slocombe and Zuberbühler, 2006; Clay and Zuberbühler, 2009; Kalan et al., 2015).

Most food-associated signals studied to date are used for intra-specific communication (see review by Clay et al., 2012). Between-trophic-level environmental signalling is often by prey to repel predators (e.g. aposematic signalling) or by organisms benefiting from attracting receivers (e.g. recruitment of pollinators to flowers). However, there are few known examples of call production directed at prey (Bradbury and Vehrencamp, 1998). Cetaceans are a unique species group in which food-associated calling is thought to function primarily in prey manipulation, although attraction of conspecifics may be a by-product (Janik, 2000). Known food-associated calls include bottlenose dolphin bray calls (*Tursiops truncatus*; Janik, 2000), humpback whale feeding calls (*Megaptera novaeangliae*; Jurasz and Jurasz, 1979; D'Vincent et al., 1985; Cerchio and Dahlheim, 2001; Sharpe, 2001) and killer whale 'herding' calls (Simon et al., 2006). The acoustic structure of these signals and specifically their frequency appears optimal to affect prey behaviour rather than for communication between conspecifics,

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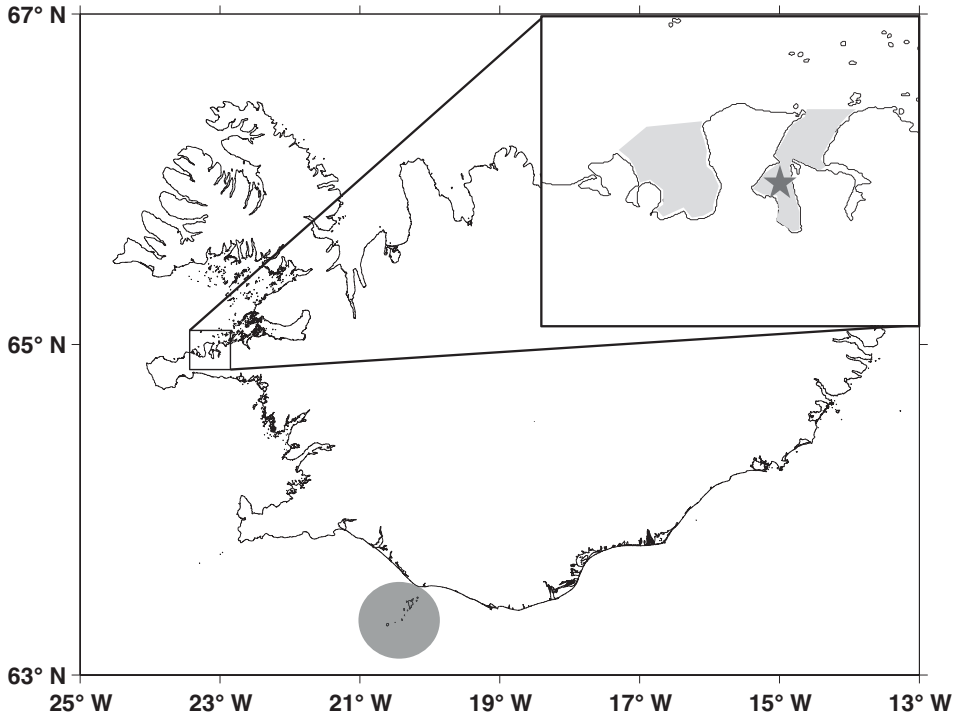

Fig. 1. Map of Iceland showing the approximate location of the herring spawning grounds (dark grey, SW Iceland) and overwintering grounds (light grey, W Iceland) where recordings were collected. The overwintering grounds are shown in detail to illustrate the inner part of Kolgrafafjörður, where the EAR was deployed in 2014 (star).

particularly in the case of bottlenose dolphins and killer whales. If these signals are indeed used specifically to affect prey, variations in acoustic structure might be expected to relate to prey behaviour, rather than conveying information to other conspecifics. However, the existence and factors behind variations in cetacean food-associated calls are still poorly understood due to the logistical difficulties in studying these animals in their natural environment. To date, only the variations in humpback whale feeding calls have been investigated (Cerchio and Dahlheim, 2001). These calls may convey individual identity information or have actively mismatched fundamental frequency when calls are simultaneously produced, to maximise effects on prey (Cerchio and Dahlheim, 2001).

Killer whales feeding upon herring (*Clupea harengus*) schools encircle and herd their prey into tight schools before hitting it with their tail fluke ('tail slap'; Similä and Ugarte, 1993), producing a characteristic broadband multi-pulsed sound (Simon et al., 2005). Tail slaps thus, provide an acoustic cue for feeding attempts. In some feeding events, killer whales produce the feeding-specific herding call just before a tail slap (Simon et al., 2006). The low sound frequency of the herding call falls outside the optimal hearing sensitivity of killer whales (Hall and Johnson, 1972; Szymanski et al., 1999) but within the range of frequencies where herring hearing is most sensitive (Enger, 1967; Mann et al., 2005). This makes the call well suited to manipulate prey behaviour (Simon et al., 2006). The call is presumably used to herd herring schools further before a tail slap to increase feeding efficiency (Simon et al., 2006).

However, the herding call is not consistently produced in all feeding events (Simon et al., 2006). To date, herding calls have only been recorded from killer whales feeding upon herring in Iceland and Shetland during the herring spawning and pre-spawning seasons, respectively (Simon et al., 2006; Deecke et al., 2011). Despite extensive studies on the vocal behaviour of herring-eating killer whales in herring overwintering grounds in Norway, herding calls or other feeding-specific calls were never recorded in that area (Strager, 1993; Van Opzeeland et al., 2005; Simon et al., 2006; Shapiro, 2008). Similarly, a small sample of acoustic recordings of killer whales feeding upon overwintering herring in Iceland did not include calls resembling herding calls (Moore et al., 1988). These contrasting observations suggest that herding call production may be seasonal, related to prey behaviour, or a behaviour that is not widespread amongst herring-eating killer whales (i.e. it is population or group-specific). Herring changes its behaviour dramatically between overwintering and spawning (Nøttestad et al., 1996, 2004). During overwintering large aggregations of herring can be found in relatively small areas (Nøttestad et al., 2004). In contrast, school densities during spawning are lower, school sizes are smaller and herring distribution tends to be more dispersed (Nøttestad et al., 1996). Thus, the production of herding calls may be an additional means for killer whales to deal with the decreased density of spawning herring schools by helping herd the herring further.

In this study, a large dataset of acoustic recordings was collected from feeding killer whales with their herring prey in two distinct, seasonal behavioural contexts: overwintering and spawning. Since herring behaviour is clearly different between these phases, acoustic signals directed at prey may reflect such differences in behaviour. Due to the smaller school sizes and more dispersed distribution of herring during spawning, if herding calls are produced exclusively to deal with small herring schools, killer whales may be expected to produce herding calls only when feeding upon spawning herring. Herding herring further during overwintering may simply be unnecessary, justifying the absence of herding calls in recordings of killer whales feeding upon overwintering herring. To test this hypothesis, acoustic recordings collected during the spawning and overwintering phases were inspected for the occurrence of herding calls. Recorded calls were then characterised and variations in herding call production and acoustic structure were discussed in the context of potential variation in prey characteristics or social drivers.