PRODUCTION AND PERCEPTION OF DEFENSIVE CALLS IN COMMON RAVENS

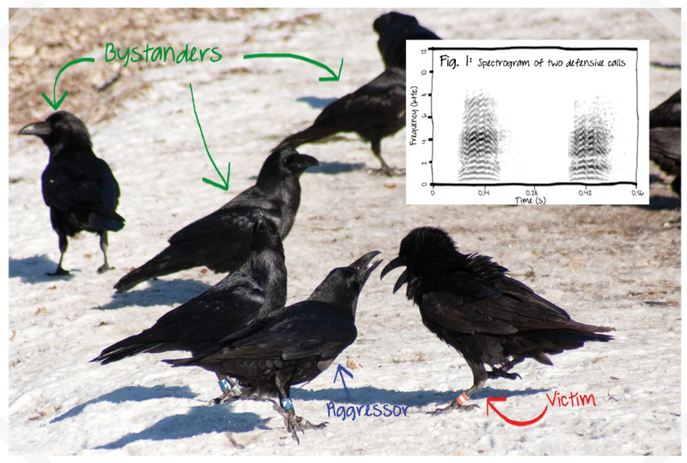
Georgine Szipl[1,2], Eva Ringler[1,3], Michela Spreafico[1,2], Thomas Bugnyar[1,2]

[1]University of Vienna, Austria; [2]Core Facility Konrad-Lorenz Research Station, Austria; [3]University of Veterinary Medicine Vienna, Austria

Introduction

Common ravens (Corvus corax) are opportunistic scavengers and gather at large ephemeral food sources [1], where they engage in agonistic interactions of varying intensity with conspecifics [2]. The intensity of an attack can be divided into attacks with and without contact aggression: during **fights** and **forced retreats**, the aggressor attacks the victim with its beaks and claws, while the victim either fights back, or retreats; during approach-retreat interactions ('**retreats**') and **submissive displays**, the victim is displaced without physical aggression. During all types of aggression, the victims may utter defensive calls (Fig. 1). Ravens have a large vocal repertoire [3,4], and while some call types are well-studied (e.g. food-associated calls: [5-8]; territorial calls: [9,10]), defensive calls have not been investigated in detail, yet. They have been described as highly variable in duration, and are uttered as single calls or sequences of several calls when retreating from dominant conspecifics at the feeding sites [11].

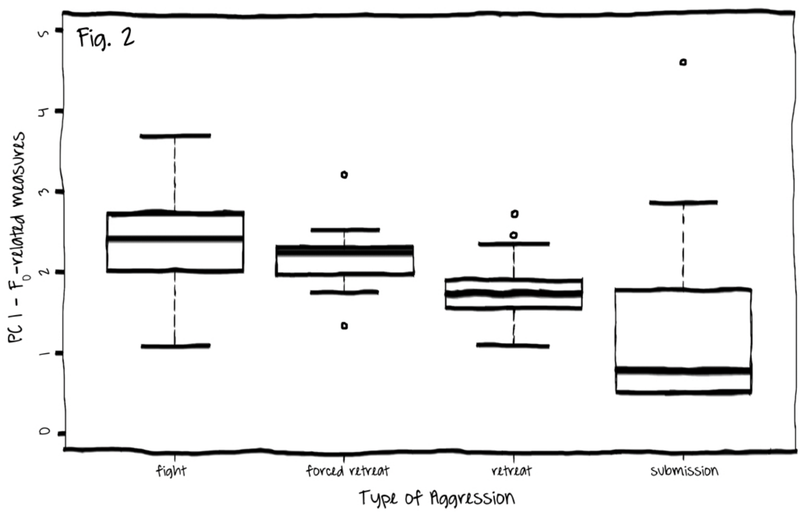
The underlying emotions of victims during attacks are expected to be low in valence and high in arousal, however, the level of arousal may vary with the intensity of the aggression, and therefore should be detectable in the acoustic structure of defensive calls [12,13]. Importantly, as communication usually occurs in a network of several animals in signalling and receiving range of each other [14], investigations should take into account whether listeners are able to infer the emotional state of the caller.

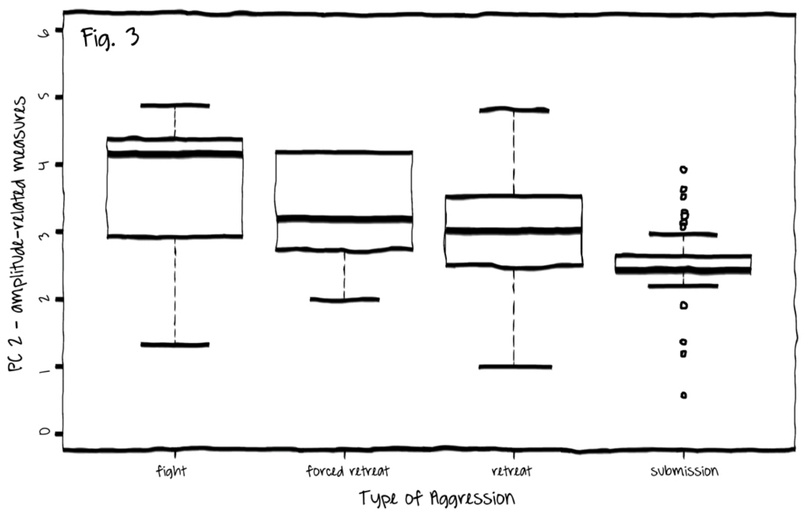


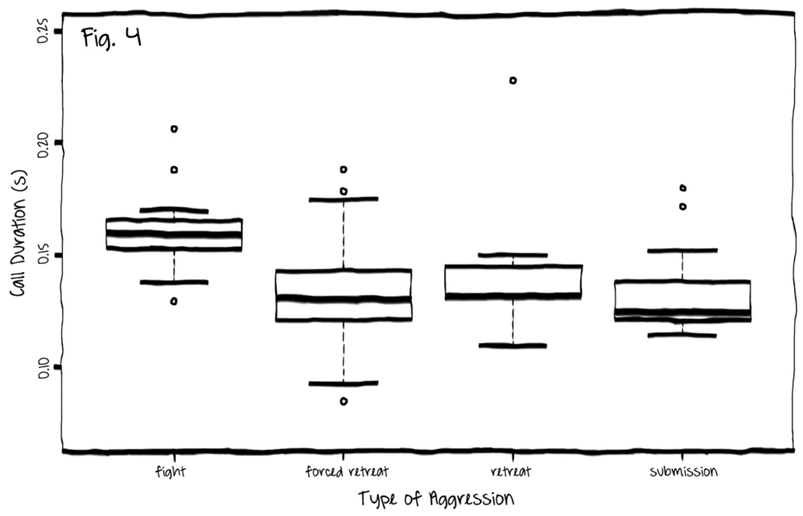
A The Senders' Perspective

Methods: SSS defensive calls were recorded during agonistic interactions in free-ranging ravens foraging at the Cumberland Game Park in Grünau im Almtal, Upper Austria. Calls were analysed in Praat [15], measuring call duration (s), harmonicity (dB), amplitude measures: mean (Hz), minimum (Hz), relative time of minimum (%), maximum (Hz), relative time of maximum (%), amplitude variation over time (Hz/s); measures of the fundamental frequency (F_0): mean (Hz), minimum (Hz), relative time of minimum (%), maximum (Hz), relative time of maximum (%), range (Hz), start (Hz), end (Hz), and sum of variation (sum of all F_0 changes); jitter; tonality (relative duration of tonal parts; %); mean formants 1-3 (Hz); and formant dispersion (Hz). The amount of acoustic parameters was reduced with a Principle Component Analysis (PCA) to four Principal Components (PCs): PC1 grouped measures related to F_0, PC2 combined amplitude-related measures, PC3 contained formant-related measures and PC4 grouped the variables tonality and jitter. Call duration did not group with other parameters and was analysed separately.

Results: Victims produced calls that varied in measures related to F_0 (Fig. 2), amplitude (Fig. 3), and call duration (Fig. 4) as a function of the intensity of the attack: calls were longer and showed higher F_0- and amplitude-related measures when the attack was severe, and decreased as the aggression became less severe. PC3 and PC4 did not show significant variation.



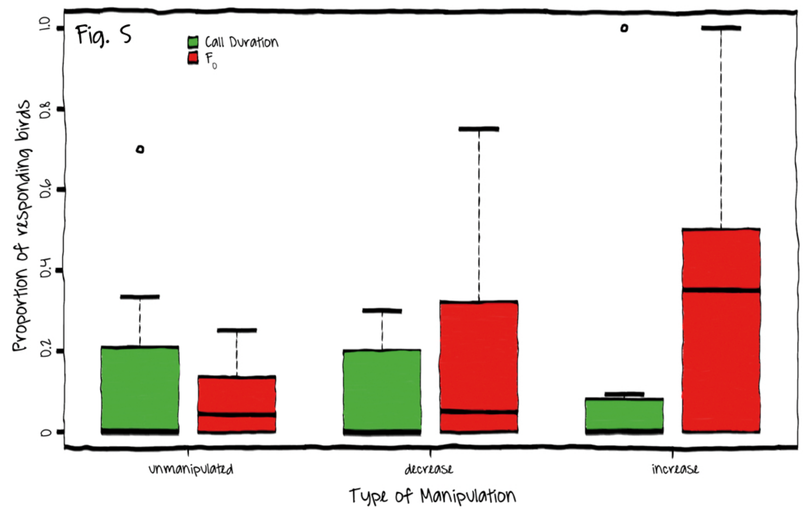




B The Receivers' Perspective

Methods: To test whether ravens responded to arousal-based call variations, defensive calls were manipulated in duration (50% longer or 50% shorter) and F_0 (shifted up or down by 100 Hz). We conducted 16 playback sessions in a group of foraging wild ravens: 8 sessions to test responses to duration manipulations, and 8 sessions to test responses to F_0 manipulations. In each session, we played three calls: the original, unmanipulated defensive call, and two calls either manipulated in duration or in F_0 in randomized order. Responses were videotaped and the number of birds present and the number of birds responding by turning towards the speaker was scored.

Results: Higher proportions of responses were found when F_0 was increased compared to unmanipulated calls and calls with lower F_0, the latter two categories showing no differences in the proportions of responses. Proportions of responses did not differ for call duration (Fig. 5).



Discussion

PC1 was found to increase with the intensity of the aggression, which indicates that arousal could have influenced variations in F_0. The same was found for PC2, which combined amplitude-related measures of ravens' defensive calls. These results are in line with literature reporting an arousal-based increase in F_0 and amplitude in mammals (reviewed in [16]), and birds [17]. Likewise, with increased arousal, call duration was reported to increase in some mammals [16], which was also the case for defensive calls in ravens. However, ravens only payed attention to an increase in F_0. To bystanders, the highly variable call duration does not seem to be a reliable cue to victims' distress.

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