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Behavioural responses to olfactory cues in carrion crows

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ABSTRACT

Until recently, the use of olfactory signals in birds has been largely ignored, despite the fact that birds do possess a fully functioning olfactory system and have been shown to use odours in social and foraging tasks, predator detection and orientation. The present study investigates whether carrion crows (*Corvus corone corone*), a bird species living in complex social societies, respond behaviourally to olfactory cues of conspecifics. During our experiment, carrion crows were observed less often close to the conspecific scent compared to a control side. Because conspecific scent was extracted during handling, a stressful procedure for birds, we interpreted the general avoidance of the 'scent' side as disfavour against a stressed conspecific. However, males, unlike females, showed less avoidance towards the scent of a familiar individual compared to an unfamiliar one, which might reflect a stronger interest in the information conveyed and/or willingness to provide social support.

1. Introduction

In many group living mammals chemical communication, i.e. information transfer via scent, plays an important role in social contexts (reviewed in: Doty, 1986). However, until the present day the use of olfactory signals in birds has been largely ignored, despite the fact that birds do possess a fully functioning olfactory system (Bang, 1971; Roper, 1999; Steiger et al., 2008) and have individually distinctive body odours (Bonadonna et al., 2007; Karlsson et al., 2010; Mardon et al., 2010; Whittaker et al., 2010). These body odours are present in birds' plumage (Campagna et al., 2012; Hagelin and Jones, 2007) and produced in a variety of glands, e.g. uropygial gland and so-called sebo-keratocytes epidermal cells (Jacob and Zisweiler, 1982; Menon and Menon, 2000). Birds have been shown to be attracted to conspecifics scent (Hagelin et al., 2003; Whittaker et al., 2011), recognize conspecifics' sex (Amo et al., 2012; Whittaker et al., 2011) and their partner based on odour, which facilitates the detection of the own nest (Bonadonna and Bretagnolle, 2002; Bonadonna and Nevitt, 2004; Bonadonna, 2003; Caspers and Krause, 2011). Zebra finch fledglings (*Taeniopygia guttata*: Krause et al., 2012), Humboldt Penguins (*Spheniscus humboldti*: Coffin et al., 2011) and European storm petrels (*Hydrobates pelagicus:* Bonadonna and Sanz-Aguilar, 2012) recognize kin based on scent. Birds have shown to behaviourally respond to the scent of predators (Amo et al., 2008; Roth et al., 2008) and olfactory orientation is believed to play a significant role in bird migration (Schmidt-Koenig, 1987; Wallraff, 2004). During foraging, procellariiform seabirds are attracted from the smell of dimethyl sulphide (Nevitt and Bonadonna, 2005). Still, the occurrence of chemical communication is often neglected in bird studies, which may partly be due to the fact that birds do not engage in the obvious scent marking and sniffing behaviours that mammals perform (Johnson, 1973), but seem to rely more on vocal and visual displays.

The present study investigates olfactory communication in carrion crows (*Corvus corone corone*), a bird species that lives in a complex social system. In most European populations they form non-breeding flocks up to adulthood and afterwards split up in territorial breeding pairs (Baglione et al., 2002a). In contrast, in northern Spain carrion crows live in cooperatively breeding groups up to nine individuals, consisting of the breeding pair, retained offspring and male immigrants (Baglione et al., 2003). Within social groups, carrion crows, as well as other corvids, form valuable relationships characterized by high levels of social tolerance and cooperation (Bugnyar and Kotrschal, 2001; Chiarati et al., 2011; De Kort et al., 2006; Emery et al., 2007; Fraser and Bugnyar, 2011, 2010) but they also act competitively (Bugnyar and Heinrich, 2006, 2005; Chiarati et al., 2010). In order to be successful in complex social interactions, corvids are known to strongly rely on visual and acoustic cues (Boeckle et al., 2012; Bugnyar and Kotrschal, 2001;

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Bugnyar et al., 2001; Kondo et al., 2012; Scheid et al., 2007; Wascher et al., 2014). Although the olfactory system in blue jays (*Cyanocitta cristata*), has been suggested to be less developed compared to other bird species (Bang and Cobb, 1968), other two corvid species, the black-billed magpie (*Pica pica*) and the common raven (*Corvus corax*), have been shown to rely on odour in foraging tasks (Buitron and Nuechterlein, 1985; Harriman and Berger, 1986). Feeding ecology aside, the complex social system of carrion crows suggests that the use of olfactory cues could be beneficial, for example, to detect stressed conspecifics in the context of predator and conflict avoidance.

Here we investigate whether carrion crows respond to olfactory cues of conspecifics and if they preferentially orient towards odours of familiar or unfamiliar individuals. If carrion crows are able to perceive scent cues and behaviourally respond to them, we expect them to orient towards a preferred stimulus and to avoid a non-preferred one.

2. Methods

2.1. Ethics statement

All bird manipulations were authorized by Junta de Castilla y León (EP/LE/359/2009). An experienced animal caretaker has conducted experiments and none of the animals were harmed by the procedure. Focal individuals were housed in captivity both prior to, and after completion of the present study. Previous studies on crows have found no negative effect of capture and manipulation (Baglione et al., 2010, 2002b).

2.2. Study subjects and housing

The subjects of the present study were part of a group of 19 carrion crows housed in a large outdoor aviary in La Sobarriba, Spain (42° 37′ 23.4336″, −5° 27′ 3.1788″). Birds were kept in three separate groups, reflecting different forms of social organisations found in carrion crows in the wild. The 'flock' contained seven non-breeding juveniles (four females and three males), comprising three pairs of siblings (one pair of female siblings, one pair of male siblings, and one mixed pair of siblings), and one unrelated individual. All individuals in the flock hatched between April and May 2008 and were hand-raised in captivity. The other two groups represented cooperatively breeding families. One family was composed of a breeding pair, a one-year old male helper (likely their offspring), and their three juvenile offspring (two females and one male). The other family comprised a breeding pair and their four juvenile offspring (two females and two males). Adult birds and the helper were captured in their territory during the chick feeding period, when the offspring was approximately 15–20 days old in June 2008. Their parents and the helper subsequently raised the nestlings in captivity.

The aviary (30 m × 12 m × 6 m) was separated in four major compartments (12 m × 6 m × 3 m), and eight testing compartments in the middle (3 m × 3 m × 3 m). The three groups were visually but not acoustically separated from each other and from the testing compartments. The aviary was equipped with wooden perches, natural vegetation, rocks, leaves, and feeders, which provided *ad libitum* access to food pellets. An enriched diet consisting of meat, apple, pear, cheese, and eggs was provided during the weekdays. Water was available *ad libitum* for both drinking and bathing.

2.3. Experimental procedure

The present experiment was conducted in October 2009. In order to extract carrion crows' conspecifics scent, we followed the procedure described by (Bonadonna and Nevitt, 2004). The model carrion crows, i.e. the ones that provided the scent, were placed into a cotton bag and held immobilized for 10 min with the wing, head and tarsus consecutively and temporarily unbaged in order to simulate the measurement of body parts. The scented cotton bag was used in an experimental session within 12 min after the procedure. The experimenter handled control bags during the same time. Both control and experimental bags were always handled with gloves. Carrion crows never defecated inside the bag, so that scented and unscented bags were visually identical. Before each experimental session, the cage and the bags were washed with 90% methanol. The carrion crows used to create the scented cotton bag were either unfamiliar, free-living crows ($n = 5$) or kin of the focal individuals ($n = 11$) that were housed together. Note that, in this experiment, all familiar scents presented to focal carrion crows originated form related individuals. We aimed at replicating the natural social environment of carrion crows, which in this population live in extended families and form long lasting social bonds only with kin (Baglione et al., 2003), to investigate the use of olfactory cues in communication. Disentangling the effect of familiarity from kinship was beyond the scope of this study and will be addressed in future experiments. Free-living unfamiliar carrion crows were captured using baited walk-in traps, commonly used at the study site in order to mark crows for individualized behavioural observations in the wild (Baglione et al., 2002c). After completion of the experiment, these carrion crows were released in the exact place of its capture. To minimize arousal of our captive carrion crows, we limited the number of attempts for placing them inside the experimental cage (see below). Eventually, 15 focal individuals were tested: seven birds in both, the familiar and unfamiliar condition (three males, four females), four with familiar stimuli only (two males, two females), and another four (three males, one female) only with the unfamiliar stimuli (Table 1).

Table 1
Details on the individuals tested: sex (F = female, M = male), age (A = adult, J = juvenile), group (F1 = family 1, F2 = family 2, FL = flock), breeding status (B = breeder, NB = non-breeder) and condition in which the individual was tested (F = familiar model, NF = unfamiliar model, B = familiar and unfamiliar model).

Individual	Sex	Age	Group	Status	Condition
Castana	F	A	F1	B	
Fidel	M	A	F1	B	F
Horst	M	A	F1	NB	F
Piti	M	J	F1	NB	
Pumuki	F	J	F1	NB	
Sancho	F	J	F1	NB	
Artemisa	F	A	F2	B	B
Pelotudo	M	A	F2	B	B
Batman	M	J	F2	NB	B
Caqui	F	J	F2	NB	F
Cerca	M	J	F2	NB	NF
Robin	F	J	F2	NB	B
Donald	F	J	FL	NB	B
Flash	F	J	FL	NB	B
Juana	M	J	FL	NB	NF
Margherita	M	J	FL	NB	B
Mari	M	J	FL	NB	NF
Sigur	F	J	FL	NB	F
Sombra	F	J	FL	NB	NF

During the experiment, the focal individual was placed in a wire cage measuring 120 cm × 40 cm × 40 cm. The carrion crow was allowed 60 min to acclimate inside the cage. The acclimatisation period, was followed by a 'control session', in order to account for any preference towards a particular side of the cage independent from the presence of a conspecific scent. During this control session, two unscented bags were placed under the cage at each end. Afterwards, the bags were exchanged for new ones, one of them scented. The side of the scent bag was randomized. Both, control and experimental lasted 12 min and the behaviour of the focal individuals