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Exclusion in the field: wild brown skuas find hidden food in the absence of visual information

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Abstract

Inferential reasoning by exclusion allows responding adaptively to various environmental stimuli when confronted with inconsistent or partial information. In the experimental context, this mechanism allows selecting correctly between an empty option and a potentially rewarded one. Recently, the increasing reports of this capacity in phylogenetically distant species have led to the assumption that reasoning by exclusion is the result of convergent evolution. Within one largely unstudied avian order, i.e. the Charadriiformes, brown skuas (*Catharacta antarctica* ssp *lonnbergi*) are highly flexible and opportunistic predators. Behavioural flexibility, along with specific aspects of skuas' feeding ecology, may act as influencing factors in their ability to show exclusion performance. Our study aims to test whether skuas are able to make choice by exclusion in a visual two-way object-choice task. Twenty-six wild birds were presented with two opaque cups, one covering a food reward. Three conditions were used: 'full information' (showing the content of both cups), 'exclusion' (showing the content of the empty cup), and 'control' (not showing any content). Skuas preferentially selected the rewarded cup in the full information and exclusion condition. The use of olfactory cues was excluded by results in the control condition. Our study highlights the cognitive potential of this predatory seabird and opens new investigations for testing further its cognition in the wild.

Keywords: avian cognition · Charadriiformes · cups task · exclusion performance · inferential reasoning

Introduction

The capacity of nonhuman animals to choose via exclusion has recently received considerable interest (e.g. Paxton et al. 2018; Nawroth et al. 2014; Petit et al. 2015; Subias et al. 2019). This cognitive mechanism, which refers to ‘the ability to understand that if there are only two possibilities and if it is not A, it must be B’ (O’Hara et al. 2016), is typically explored through the use of a two-way object-choice paradigm i.e. the *cups task* (Call 2004; Mikolasch et al. 2012; Pepperberg et al. 2013; Plotnik et al. 2014; Subias et al. 2019). In the visual version of this test, a food reward is hidden underneath one of two identical opaque cups (Darmaillacq et al. 2018). In the crucial phase, the experimenter lifts the empty cup only. The subject is able to choose via exclusion if it excludes the presented empty cup and selects the potentially rewarded, non-lifted one.

Successful performance on this task can be achieved through the use of low- and/or high-level cognitive strategies (Call 2004; Penn and Povinelli 2007; Watanabe and Huber 2006). Subjects may solve the task by learning to *avoid* the empty cup, without acquiring any knowledge about the other rewarded container (i.e. low-level strategy). Other individuals, however, may be able of *inferring* the logical presence of the food under the non-lifted container (i.e. high-level strategy). Although both mechanisms are not mutually exclusive, e.g. one subject can follow a mixed strategy (e.g. Jelbert et al. 2015), choosing by avoiding the incorrect option is less cognitively challenging than inferential reasoning *per se* (Mikolasch et al. 2012), and may be present in more individuals.

The ability to choose by exclusion has been found in various animals such as elephants (Plotnick et al. 2014), dogs (Aust et al. 2008; Erdőhegyi et al. 2007), goats (Nawroth et al. 2014), or non-human primates (Hill et al. 2011; Sabbatini et al. 2008; Schmitt et al. 2009). In birds, mainly in Corvids and Parrots, some species pass the cups task (e.g. carrion crows *Corvus corone*, Mikolasch et al. 2012; Clark’s nutcracker, *Nucifraga Columbiana*, Tornick

and Gibson 2013; red-tailed black cockatoo *Calyptorhynchus banksii*, Subias et al. 2019), whereas others demonstrate marked difficulties (e.g. Eurasian Jays, *Garrulus glandarius*, Shaw et al. 2013; jackdaws, *Corvus monedula*, Schloegl 2011; keas, *Nestor notabilis*, Schloegl et al. 2009, but see O'Hara et al. 2016).

Whilst some researchers have supported hypotheses about ecological factors promoting the emergence of exclusion in specific animal orders (e.g., 'the adapted intelligence hypothesis' in food-caching corvids e.g. Mikolasch et al. 2012; Schloegl et al. 2009; Schloegl 2011, but see Shaw et al. 2013; 'social complexity' in primates e.g. Petit et al. 2015), others have proposed this ability to be a fundamental cognitive capacity ('general intelligence'; Pepperberg et al. 2013), or, lately, to be of higher importance in flexible foraging species (Nawroth et al. 2014).

A good way to further understand the possible drivers favouring the emergence and evolution of exclusion is to expand the spectrum of species studied with this paradigm in species possessing traits associated with this ability (Marsh et al. 2015; Mikolasch et al. 2011; Schloegl et al. 2009). Moreover, experiments with free-living animal populations are crucial to understand how exclusion performance – and cognitive processes more generally – operates under natural conditions (Byrne and Bates 2011; Cauchoix et al. 2017; Völter and Call 2017).

However, as testing individuals in the wild is often prohibitively challenging (Shaw et al. 2015), we still lack studies about the use of exclusion in wild individuals. For instance, species can show high neophobia (preventing their willingness to participate in the task), be non-territorial (struggling with locating individuals when several trials need to be administrated), or live in groups (making difficult their isolation from conspecifics; Shaw et al. 2015). To our knowledge, only two captive exclusion experiments have been conducted

with wild birds brought into captivity (New Caledonian crows, *Corvus moneduloides*: Jelbert et al. 2015; Clark's nutcrackers: Tornick and Gibson 2013).

This study aims to assess exclusion performance in a new avian model: the wild brown skua (*Catharacta antarctica* ssp *lonnbergi*). This large gull-like seabird frequents Antarctic Peninsula and Subantarctic islands of Atlantic, Indian and Pacific Oceans (Carneiro et al. 2014, 2015; Furness et al. 2018). Skuas are top marine predators that display a wide range of feeding techniques i.e. aerial and terrestrial hunting, cannibalism, fishing, kleptoparasitism, and scavenging (Moncorps et al. 1998; Mougeot et al. 1998; Schreiber and Burger 2002). When spatial or seasonal fluctuations in prey availability occur, these birds exhibit high degree of flexibility by adjusting their movements and switching to different resources (Burton 1968; Carneiro et al. 2015). Moreover, skuas can be locally highly selective in their prey intakes and show preferences for hunting specific seabird species (e.g. blue petrel, *Halobaena caerulea*), while others seem to be avoided (e.g. diving petrels, *Pelecanoides urinatrix*; Mougeot et al. 1998). Both previous characteristics, behavioural flexibility and selectivity, have been suggested as explanatory factors for exclusion skills in animals (Nawroth et al. 2014). Indeed, some highly flexible species may show higher aversion to losses through the avoidance of the empty container (Nawroth et al. 2014).

Regarding one species' feeding ecology may also provide significant insights on the occurrence of exclusion performance under natural conditions (Völter and Call 2017). In the Kerguelen archipelago, some populations (e.g. skuas at Cape Ratmanoff) predate and scavenge mainly on king penguin chicks and eggs (*Aptenodytes patagonicus*; Furness 1987). In this environment, a penguin egg covered by its incubating parent's fold of skin is often hardly visible (FB, JCC, AN: personal observations). In this context, being able to locate prey without directly perceiving it could be highly adaptive for skuas, which may have favoured the appearance of exclusion performance in the wild (Marsh and Levendoski 2015).

Noteworthy, similarly to other birds endemic to isolated islands (e.g. kea, *Nestor notabilis*, Gadjon et al. 2006; wild robin, *Petroica longipes*, Garland et al. 2014), the skua is highly explorative and shows very low neophobia (Furness et al. 2018). It is also highly territorial during the breeding season, forming breeding pairs and establishing a territory that is fiercely defended against conspecific intruders or potential predators (Hahn and Peter 2003; Trivelpiece et al. 1980). Such aspects of this species' feeding ecology, along with complex foraging flexibility and territoriality, make the skua a promising model for exclusion experiments in the field (Gadjon et al. 2006).

In this study, we aimed to assess whether wild brown skuas were capable to use exclusion to find hidden food in a visual two-way object choice task. According to the species' feeding ecology, we predict skuas to be able to solve the task.

Methods

Study population

Between Feb 2010 – and Mar 2012, 26 wild brown skuas were tested at Cape Ratmanoff, Courbet Peninsula, Kerguelen Island (48°25'-50°00'S; 68°27'-70°35'E). All birds had a minimum age of 1 year (i.e. colour pattern, uniformity, distinct wing flashes of the body plumage, Furness et al. 2018). Eighteen subjects were individually identified based on leg bands coloured by Darvik®, 2 based on temporary coloured dye sprays (Porcimark®, Langeskov, Denmark, 22 Feb 2010 – 3 Mar 2010), and 6 based on specific aspects of their appearance (i.e. body plumage, presence/absence of scars on the feet' webbing, 2 Mar 2012 – 10 Mar 2012). In both field seasons, trials were performed between 7 a.m. and 5 p.m. and each subject was tested separately (a second experimenter prevented conspecifics from entering the test area, by approaching and making the intruders leave within approximately 5 meters radius of the setup). Prior to the current study, no skua had ever been tested in any exclusion task.

Experimental setup and Materials

Two identical opaque plastic cups (13 cm in height and 11 cm in diameter) with a piece of string forming a loop on the top (braided sisal cord, 3 mm in diameter and 6 cm in length) were set up on the ground, 25 cm apart (Fig. 1). Both cups and string loops were coated with fish flesh to avoid birds to use any smell-related clue. Depending on the procedure (see below), two (training phase) or one container (test phase) held a motivating food reward (a fresh fish piece of *Salmo trutta*, ca. 3 g). At the onset of each trial during all 3 conditions, an opaque blind (a flat wooden board, 30 x 40 cm) was placed vertically between the subject and the cups (3 cm before the containers) to prevent subjects from seeing under which cup the experimenter hid the food reward.

< Fig. 1 about here >

Procedure

Familiarization phase.

The free-ranging 26 subjects were initially familiarized with the experimental apparatus. When a skua was sufficiently close to the apparatus (≤ 1 meter), the experimenter showed two food rewards and placed one under each cup. Skuas were then allowed to touch the cups. Once a subject successfully retrieved the rewards by lifting the cups (4 times within 2 min), we considered that it was familiarized with the apparatus.

Test phase.

Three conditions were presented to all birds in the following order: full information, exclusion, and control. In all conditions, the position of the reward was pseudo-randomized and balanced equally on the left/right side in each condition (i.e. Control: left = 93/right = 94; Exclusion: left = 255/right = 263; Full information: left = 124/right = 126). The subject's choice was considered as correct when the bird lifted the cup and retrieved the reward. The order in which birds participated every day was randomly assigned through the subjects'

voluntary participation. If a bird left the test area during the test and did not return within 1 minute, the trial was performed again from the beginning later in the day. During the whole procedure, the experimenter stayed approximately 0.5 m behind the cups, looking straight ahead.

Full information condition. In this condition, we wanted the birds to learn that they would have to make a choice. For that purpose, one reward was hidden under one cup by the experimenter behind the blind. Then, the experimenter removed the blind and both cups were simultaneously lifted so the subject could locate visually which cup contained the food. After 3 sec, both containers were put down in same places and the skua could choose between one of them (see S1 in supplementary material). If the subject lifted the rewarded cup, it was allowed to consume the food. Conversely, if the subject chose the unrewarded cup, the experimenter stopped the trial to prevent the bird from obtaining the food. Each subject received 10 trials in total (60 sec each, max. 10 per day, between 10 sec-1 min apart).

Exclusion condition. Same procedure as in *Full information condition* was followed, except that after baiting, only the empty cup was lifted while the experimenter simultaneously touched the rewarded cup (see S1 in supplementary material). This was made to prevent the reliance on enhancement effects (e.g. the tendency to choose the cup that is manipulated last, Mikolasch et al. 2012; Nawroth et al. 2014). Each subject received 20 trials in total (60 sec each, max. 20 per day, between 10 sec-1 min apart).

Control condition. We assessed whether the subjects' choices were influenced by the use of olfactory or any other uncontrolled cues. Here, one cup still contained the reward, but subjects had no information about food position i.e. the experimenter did not lift the cups but touched them simultaneously. Each subject received 10 trials in total (60 sec each, max. 10 per day, between 10sec-1 min apart).

Analysis

All trials were coded live. When the weather allowed (no strong winds, nor flying sand), we also recorded trials using a video camera mounted on a tripod. Inter-observer reliability was not calculated as the subjects' choice in each trial was unambiguous (binary response: success or failure). We modelled birds' success probability at trials as a random variable following a binomial distribution. To compare birds' performance depending on test condition and to assess the possible effects of lateralization and learning, the probability to find the reward was modelled as a function of test condition (full information, exclusion, control), position of the food (right/left), and trial number (or ID_trial), in a generalized linear mixed-effects model (GLMM). To account for individual differences in probability to pass the test, we set individual identity as a random effect with a Gaussian distribution in the error structure of the model. We implemented generalized linear mixed-effects model trees (Fokkema et al. 2019) to identify relevant clusters and effects. The algorithm finds subgroups (or terminal nodes) that differ in their success rate, while taking into account the nested structure of the dataset (individuals). The algorithm evaluates the stability of model parameters (i.e. stability of the intercept coefficient) at each node. The node becomes terminal (stable) if $p > 0.05$ for all splitting variable of the model.

As position of the food (right or left cup) was not available for all testing sequences, we implemented two trees. Model tree I was based on a reduced dataset with only individuals for whom we had full information on the position of food (left/right) within the 3 conditions ($n = 19$). This first model was implemented with test condition and food position effects in interaction. Model tree II was implemented on the complete dataset including all the individuals ($N = 26$). We back transformed coefficients from the logit scale to get success probabilities on the response scale. We refer to these transformed coefficients as probability of success (P_s). P_s is reported with 95% confidence intervals. All the analyses were carried

out with R version 3.6 (R Core Team, 2019), and glmer package (Fokkema et al. 2019) was used to perform the analysis.

Results

Model tree I: test conditions and food position

With the model accounting for food position, we identified a difference in success probability between each of the 3 experimental conditions (control, exclusion and full information), as well as an effect of food position on success during control tests. Results are shown in Fig. 2.

< Fig. 2 about here >

There was a difference in performance between the control condition and the exclusion/full information condition ($p < 0.001$; Node 1). Food position had an effect on success probability but only within the control condition ($p = 0.023$; Node 2): birds' success probability was $P_s = 0.43$ [95% IC: 0.32 – 0.54] when food was on the left (Node 3), and $P_s = 0.62$ [95% IC: 0.47 – 0.75] when the reward was located on the right (Node 4). Thus, there was a mean side bias towards the right container during this condition. At the individual scale, we could detect birds 100% lateralized (Left side: $N = 1$, right side: $N = 3$). Skuas were on average more successful in the full information condition ($P_s = 0.74$ [95% IC: 0.63 – 0.83]) than in the exclusion condition ($P_s = 0.64$ [95% IC: 0.53 – 0.74]) ($p = 0.024$; Node 5).

Model tree II: test conditions and learning

With the model accounting for trial number (complete dataset), we identified a difference between each of the 3 experimental conditions (control, exclusion and full information), as well as an effect of trial number (ID_trial) during exclusion tests. Results are shown in Fig. 3.

< Fig. 3 about here >

There was a difference in performance between the control condition and the exclusion/full information condition ($p < 0.001$; Node 1). Mean success probability during the control condition (Node 2) was $P_s = 0.51$ [95% IC: 0.43 – 0.59]. The model tree procedure identified

a difference between the exclusion and full information condition ($p = 0.021$; Node 3). During the exclusion condition, there was a difference between the first 12 trials and the last 8 trials ($p = 0.021$; Node 4), with an average success probability $P_s = 0.58$ [95% IC: 0.49 – 0.67] during the first 12 trials (Node 5), and an average success probability $P_s = 0.71$ [95% IC: 0.62 – 0.79] during the last 8 trials (Node 6). Thus, there was a learning effect emerging over the course of the exclusion condition. During the full information condition (Node 7), mean success probability was $P_s = 0.72$ [95% IC: 0.64 – 0.80].

Discussion

Overall, our results demonstrate that free-living skuas are capable of showing exclusion performance. Subjects succeeded above the level expected by chance in the full information and exclusion conditions, and their performances confirm that they did not use olfactory cues (smell of the hidden food reward) in the control condition. This experiment is the first to reveal exclusion skills in Charadriiformes within a natural setting.

When no information was available (control condition), most birds failed in locating the baited cup above chance. This result is not surprising when we refer to the species' biological and behavioural features. Skuas possess small olfactory bulbs and display no reaction when faced to striking odour changes of a same food item (Furness et al. 2018). Noteworthy, a mean side bias emerged over trials in the control condition with a mean preference to select the right cup in tested individuals. At the individual level, four subjects chose constantly the same side (three skuas selected the right one, one the left one). This behaviour is not uncommon when subjects are confronted with two-way object-choice tasks (e.g. Danel et al. 2018; Gagne et al. 2012; Ketchaisri et al. 2019), and represents a useful strategy when environmental stimuli are unpredictable, such as in our control condition (Jacobs and Osvath 2015; Ketchaisri et al. 2019; Plotnik et al. 2013; Tebbich et al. 2007). In contrast, skuas were able to derive relevant information from the full information and exclusion conditions

without displaying any side bias, probably because both conditions were predictable.

Similarly to other avian species (e.g., African grey parrots, Mikolasch et al. 2011, Pepperberg et al. 2013, Schloegl et al. 2012; carrion crows, Mikolasch et al. 2012; Clark's nutcrackers, Tornick and Gibson 2013; Eurasian jays, Shaw et al. 2013; jackdaws, Schloegl et al. 2011; keas, Schloegl et al. 2009; ravens, Schloegl et al. 2009; red-tailed black cockatoos, Subias et al. 2019), skuas chose significantly more the rewarded cup over the unrewarded one in the full information condition (success probability $P_s = 0.72$ [95% IC: 0.64 – 0.80]). Our results indicate that this species was able to rely on direct visual information for solving the task. We also suggest that skuas showed spontaneous object permanence (Piaget 1954), i.e. the understanding that hidden objects do not cease to exist (Pepperberg et al. 2013), as they successfully selected the opaque container covering the food reward.

Crucially, this species was also able to use indirect information (i.e. the view of the empty cup) to choose substantially more the baited cup over the unbaited one in the critical exclusion condition (success probability $P_s = 0.64$ [95% IC: 0.53 – 0.74]). Unlike other captive avian species (e.g., Schloegl et al. 2009), skuas in this experiment did not require extensive training and all birds were naive to experimental testing. In this case, the subjects may not have had the time to learn the causal cues (low-level explanation i.e. avoidance of the empty cup) required to solve the task (Nawroth et al. 2014; Shaw et al. 2013; Schloegl 2011; Schloegl et al. 2009). Moreover, exclusion performance might not normally require elementary associative learning when a limited number of tests is proposed (Darmaillacq et al. 2018; Shaw et al. 2013). However, we found a progressive amelioration in subjects' performance over trials within the exclusion condition. We therefore cannot rule out the possibility that subjects have used a non-costly cognitive strategy through the avoidance of the empty cup in the following trials (Call 2006; Paukner et al. 2009; Mikolasch et al. 2012;

Schmitt and Fischer 2009). Only a further study with proper controls will clarify the use of low-level strategies in this species (e.g. see the different tests used in Call 2006 and in Mikolasch et al. 2011, with the procedure pioneered by Premack and Premack 1994; or the follow-up conditions of the modified *tubes task* employed by Jelbert et al. 2015). Future experiments may also assess whether wild skuas still show success when they are confronted with an increased number of containers, such as in the 3-cups object choice task (Grether and Maslow 1937). This version may provide contrasting results and is considered more complex than the binary cups task (Marsh et al. 2015).

At first glance, our results support the adaptive specialisation hypothesis (De Kort and Clayton 2006), which suggests that cognitive abilities may vary depending on specific aspects of one species' feeding ecology. Referring to this assumption, Nawroth et al. (2014) recently found a link between highly selective feeding behaviour and exclusion performance in small ruminants. Although it would be tempting to propose similar mechanisms operating in our model species, only a comparative approach may reveal the potential role behavioural flexibility plays in exclusion. For instance, further experiments may test exclusion performance in skuas' genetically related species that possess different feeding ecologies, e.g. specialist predators such as long-tailed skuas (*Stercorarius longicaudus*, Sitter et al. 2011).

Naturally, predatory animals might be highly attentive and sensitive to the sound emitted by their preys (Grant and Samways 2015; Rice 1982; Schmitt and Fischer 2009). Although vision seems to play a significant role in skuas' ecology, this species relies also on acoustic information during foraging (Furness 1987). For instance, on Mayès Island, Kerguelen archipelago, acoustic information helps specialized skuas in finding burrow-nesting birds at night (Mougeot and Bretagnolle 2000). Thus, in order to determine potential variations in levels of exclusion performance across sensory modalities, further experiments should assess skuas' capacity to locate hidden food when given acoustic information.

In conclusion, wild brown skuas are capable of showing exclusion performance in the visual domain. Although the role ecological traits play in the emergence of exclusion performance must be the object of further research, our results corroborate the hypothesis that this capacity has emerged in distantly related taxa through convergent evolution (O'Hara et al. 2015). Skuas possess life history and ecological traits that are commonly linked to enhanced cognition (Morand-Ferron et al. 2007; Ricklefs 2004) e.g. late sexual and physical maturity, longevity, high innovation rate, kleptoparasitism, and generalism (Chester 1993; Furness et al. 2020; Spear et al. 1999). However, to date, we are aware of only one previous experimental cognitive work showing the capacity of skuas to recognize human faces (Lee et al. 2016). Research is needed to explore further the cognitive abilities of this promising new model system. We also hope this study will encourage future field comparative work on this capacity across taxonomic groups, so as to enhance our current view of the distribution of exclusion skills in avian phylogeny.

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Figure captions

Fig. 1 Schematic representation of the conditions and the experimental setup for a typical exclusion test trial. **(a)** The ‘full information’, ‘exclusion’, and ‘control’ conditions are presented from left to right, respectively **(b)** Two identical opaque cups are simultaneously showed on a wooden platform. In the sketch, the reward is located under the *right* cup. The subject is watching a human experimenter lifting the empty left cup. To solve the task, the skua must exclude the left cup (low-level explanation) and/or infer that the right cup covers the reward (high-level explanation), by raising this container accordingly.

Fig. 2 Model tree I: test conditions and food position. The Tree shows skuas’ estimated mean success probabilities in each of the terminal nodes during the different test conditions, including the potential effect of food position during the control condition. The black bars show 95% confidence intervals associated with estimated means. Dots show the observed performance of each individual during the different tests between 0 and 1 (0 to 100% success), dots’ colour include transparency so that darker dots show that multiple individuals performed with the same success rate.

Fig. 3 Model tree II: test conditions and learning. The Tree shows skuas’ estimated mean success probabilities in each of the terminal nodes during the different test conditions, including the potential effect of learning through trial number (ID_trial) during the exclusion condition. The black bars show the 95% confidence intervals associated with estimated means. Dots show the observed performance of each individual during the different tests between 0 and 1 (0 to 100% success), dots’ colour include transparency so that darker dots show that multiple individuals performed with the same success rate.

503 **Electronic supplementary material**

504 **S1.** Video of test trial examples in the full information and the exclusion conditions,
505 respectively.

Fig. 2

Fig. 3