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Responses of Wild Skuas (*Catharacta antarctica* ssp. *lonnbergi*) to Human Cues in Cooperative and Competitive Social Contexts

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Abstract

Many animals respond to and use social cues emitted by other species (e.g., head direction). This capacity, allowing to gain information during foraging, predator avoidance, or social interactions, can, however, be masked when a given species' ecology is not considered (e.g., when a competing social species needs to cooperate with a human on a cognitive task). We presented wild brown skuas (*Catharacta antarctica ssp. lonnbergi*) with two versions of an object-choice paradigm. In the cooperative version (experiment 1), one human experimenter provided a salient cue indicating which of two containers covered a food reward. The cues administered consisted of touching, looking at, pointing at, or pointing and looking at the container hiding food. In experiment 1, skuas could thus 'cooperate' with a human experimenter by using the cues provided to locate the rewarded container. In the competitive version (experiment 2), two human experimenters presented a platform with a visible food reward. In six experimental conditions, we varied experimenters' body orientation, head orientation, eye-gaze direction, face occlusion and mouth occlusion, as well as the platform's location, ensuring that in each case only one experimenter had visual access to the rewarded platform. Here, birds could 'compete' with the experimenters by robbing the human who does not see the food. Skuas failed to use human-given cues spontaneously in experiment 1, and took the reward regardless of whether the experimenter could see in experiment 2. Our results contrast with those on other native bird species that differ in their ecology and experience with humans.

Keywords: Charadriiformes, cups task, human cues, interspecific communication, skua

Responses of Wild Skuas to Human Cues in Cooperative and Competitive Social Contexts

All human societies are based on large-scale cooperation among individuals who need to communicate for common good (Fehr & Fischbacher, 2004). In doing so, a myriad of social cues often supports or replaces verbal exchange, including expressive facial expressions, gaze configurations, gestures, or postures. Many studies originating from the 1970s have shown that humans are particularly skilful in using social cues during communication (e.g., Eibl-Eibesfeldt, 1975), and making inferences about the internal states of others (e.g. during gaze cueing: Teufel et al., 2010). Over the last two decades, the study of social cues has also received considerable interest within the context of inter-species communication, notably because of its potential implications for the welfare of domesticated animals raised in livestock production systems (e.g., Nawroth et al., 2014).

A well-established way of studying human-animal communicative capacities is the object-choice paradigm (Ketchaisri et al., 2019). In the visual cooperative version of this test, a human experimenter indicates with a cue, for instance by gazing or pointing, which container out of two covers a food reward. So far, this paradigm has been administered to various animals with at least one individual showing positive results in birds (e.g., Giret et al., 2009; Schmidt et al., 2011; Tornick et al., 2010) cats (Miklósi et al., 2005), canids (e.g., Bhattacharjee et al., 2020; Smith & Litchfield, 2010; Udell et al., 2008), dolphins (Pack & Herman, 2004), elephants (Smet & Byrne, 2013, but see Ketchaisri et al., 2019; Plotnik et al., 2013), goats (Kaminski et al., 2005; Nawroth et al., 2020), horses (Proops & McComb, 2010), non-human primates (e.g. Barth et al., 2005; Neiworth et al., 2002), pinnipeds (Highfill et al., 2007; Scheumann & Call, 2004), or swine (e.g., Albiach-Serrano et al., 2012, Nawroth et al., 2016).

Different hypotheses have been developed to explain the capacity of animals to use human-given cues. Some animal species may have been selected artificially against fear and aggression and, probably indirectly, for improved responsiveness to human referential communication (the “domestication hypothesis” e.g., Hare et al., 2005; Nawroth et al., 2014). Another assumption postulates

the role of social organization in understanding human-given cues during object-choice tasks (Giret et al., 2009). The rationale is that living in complex and stable social groups may have strongly channelled the evolution of the capacity to read social cues, first among conspecifics, and subsequently in the company of humans.

However, due to specific social and ecological factors, certain species may be less sensitive to human-given cues when the task requires cooperating in order to find a food reward. Indeed, in some cases, poor performance has been related to the *context* of the task rather than to the subjects' inability to use human-given cues, challenging both previous predictions and making interpretations unclear (Davidson & Clayton, 2016; Garland et al., 2014). Chimpanzees (*Pan troglodytes*), for example, demonstrate weak social-cognitive skills in the cooperative object choice task (e.g., Call et al., 1998). However, this species is skilful in the competitive (or human-predator) aversion context (Hare & Tomasello, 2004), which aligns more with the frequent competition reported within social groups of chimpanzees.

In birds, few captive studies have administered the competitive version of the object-choice paradigm to date (jackdaws, *Corvus monedula*: von Bayern & Emery, 2009 and grey parrots: Peron et al., 2011). In the field, experiments are even rarer. The wild North Island robin (*Petroica longipes*, Māori name: toutouwai), for example, an insular species that is highly territorial (Armstrong et al., 2000) and relatively fearless toward people (MacKinlay & Shaw, 2019), responds aversively to the presence of human eyes in a choice task (Garland et al., 2014). Likewise, the urban herring gull (*Larus argentatus*), a bird genetically related to our study species, can respond to human eyes or gaze direction (Goumas et al., 2019). Importantly, robins and gulls inhabit areas with regular and heavy exposure to humans, which may play a role in the ability to use human cues in cooperative and competitive contexts. In view of these results, studies on wild animals should optimally combine both cooperative and competitive versions of the object-choice paradigm, in order to understand how context, ecology, and experience

with humans, shape social cognition.

Wild brown skuas (*Catharacta antarctica* ssp. *lonnbergi*) are well suited for such investigations. This opportunistic predatory bird frequents the Antarctic Peninsula, sub-Antarctic Islands of the Atlantic, and the Indian and Pacific Oceans (Furness et al., 2020). At our field site, île Verte (Kerguelen archipelago), no human presence was reported at least until the 1950s, the time at which a scientific station was established on the mainland ('Port-aux-Français'; Frenot et al., 2001). Nowadays, île Verte is annually visited by scientists, mostly during the austral summer (Oct-Dec). Contact with humans was rare on île Verte before 2019/2020, the breeding season in which the first preliminary avian cognitive studies started to be conducted on the island. Interestingly, skuas are fast learners (Danel et al., 2021; Danel et al., 2022), not neophobic toward humans or experimental apparatuses (Lee et al., 2016), and are highly motivated by food (Danel et al., 2021; Danel et al., 2022), which makes them useful models for field studies (Danel et al., 2021; Janmaat, 2019; Shaw et al., 2015). Moreover, this species is relatively solitary in its social organization, usually travelling and foraging individually at sea (Furness et al., 2020). During the breeding season, established breeding pairs defend a territory against conspecific intruders and non-breeding skuas usually join mixed-species flocks or congregate in 'clubs' at foraging sites (Carneiro et al., 2014; Furness et al., 2020). In these gatherings, skuas can be hostile (Burton, 1968) and competitive interactions have been reported when a food resource is present (S. Danel, personal observation). In view of these features, brown skuas represent an ideal model for exploring interspecific communication in different social contexts.

In experiment 1, wild skuas were required to locate a hidden food reward by spontaneously using simple and salient cues. Given this species' evolutionary isolation and lack of experience with humans, we expected skuas to fail in using human-given cues in experiment 1, the cooperative version of the object-choice paradigm (prediction 1). Furthermore, based on their rather asocial nature, we also predicted skuas to respond - avoid - human cues in experiment 2 (i.e. by choosing to take the food

reward on the platform of the experimenter that *cannot* see, the competitive version of the object-choice paradigm (prediction 2).

Methods

Subjects

Both experiments took place at île Verte, Kerguelen Islands (48°25'-50°00'S; 68°27'-70°35'E), during the austral summer (breeding season) of 2019/2020 (experiment 1) and of 2020/2021 (experiment 2). Eight skuas participated in experiment 1: six females (01A, 03A, 11A, 12A, 21A, Sourcil blanche) and two males (13A, Blond), and 14 skuas in experiment 2: eight females (01A, 03A, 06A, 11A, 12A, 21A, Boiteuse, Sourcil blanche) and six males (02A, 05A, 13A, 18A, 22A, 32A). During the first field season (2019/2020), in November skuas were captured at their territory during incubation with a noose attached to a modified long fishing rod (a method of catching that has been successfully used before without any adverse effects on wild seabirds: [Gosler, 2004](#)) and fitted with metal rings (from the Natural History Museum, Montpellier, France) and coloured and numbered plastic leg bands (Interrex-rings, Poland). Two birds (Sourcil blanche and Blond), which formed a sexual pair and set up a breeding territory after the capture period, were not caught but individually identified based on specific aspects of their appearance (white head and colour patterns). All birds had a minimum age of one year during experiment 1 (determined from colour pattern, uniformity, and distinct wing flashes of the body plumage: [Furness et al., 2020](#)). Sex was determined based on reversed sexual dimorphism (females are larger than males: [Catry et al., 1999](#)). Skuas were tested after two to four weeks from banding, during the chick-rearing period and separately on their territory. Usually, two sessions (one session: five trials, see below) were performed per day for each bird in experiment 1 (first session: between 8 and 11 a.m., second session: between 2 and 5 p.m.), and one session per day for each skua in experiment 2 (one unique session of six trials, see below).

The protocols were carried out in accordance with published guidelines of the Association for

the Study of Animal Behaviour (ASAB) and the Animal Behavior Society (ABS). All experimental manipulations cited and performed were approved by French Ethical Committee (n° 201707131540776 of 22/07/2017) after favourable recommendation of Comité d'Éthique pour l'Expérimentation Animale, Languedoc-Roussillon (CEEALR), C2EA n°36, and by the Ethical Committee of Réserve Naturelle des Terres Australes et Antarctiques Françaises (arrêté n° 2019–130 du 28/10/2019).

Experimental Setup and Materials

In experiment 1, the apparatus consisted of a portable horizontal white standard Foamex PVC foam board (60 cm in length, 40 cm in width), fixed on each side to one vertical folding platform (16 cm in height, 16 cm in length; Figure 1). The vertical platforms prevented the view of the testing procedure by nearby conspecifics. The containers were two opaque brown plastic bowls (12 cm in length, 5.5 cm in width) fixed to a mobile wood platform (45 cm in length, 15 cm in width) that could be moved by the experimenter towards/away from the test bird. An additional horizontal wood platform served as a visual barrier (49 cm in length, 20 cm in width) to prevent the subject from seeing the baiting of the container. Experiment 2 was a replication of the experiment conducted by [Garland et al. \(2014\)](#). In this experiment, two human experimenters were simultaneously present during trials, and each experimenter presented a wooden platform (35 cm in length x 25 cm in width) on which a food reward was placed. In two conditions (i.e., *Face occluded/chest occluded* and *Mouth occluded/eyes occluded*; Figure 1), each experimenter used one piece of opaque dark blue polar fleece fabric (20 cm in width, 20 cm in length). The food reward consisted of a fresh piece of trout (*Salmo trutta*, about 3 g), known to be of particularly high value to the birds ([Danel et al., 2021](#); [Danel et al., 2022](#)). The trout (an introduced alien in Kerguelen) was fished in Kerguelen Islands' rivers and streams and was frozen three to five weeks before the start of the experiments, to be unfrozen 2 h before the start of the experimental sessions.

< Insert Figure 1 about here >

Procedure

Habituation (experiment 1 & 2)

Skuas were first habituated to collect the reward from the containers (experiment 1) and from the platforms (experiment 2). In experiment 1, learning occurred by gradual shaping; that is, depending on the individual subject's learning speed, the upside-down containers covered the rewards increasingly more until the rewards were entirely hidden. Once the subjects were readily obtaining the reward from the containers, they could pass to the pre-test phase. Sometimes, skuas tried to get the reward from one container but had difficulties lifting it and indicated their choice by touching one container. In this case, the experimenter lifted the chosen container so the subject could access it regardless of its content (either rewarded or empty). In experiment 2, two human experimenters, who wore identical clothing, were present and simultaneously dropped one food reward from the same height onto their respective platform. Subjects had to take the visible food reward on both platforms at least three times in a row. As soon as subjects took the three rewards, they could pass to the test phase (no pre-test phase was necessary in experiment 2).

Each skua was tested separately on its territory, and the order in which subjects participated every day was randomly assigned through the birds' voluntary participation. During the whole procedure, the experimenter(s) remained still in a sitting position behind the apparatus/platforms, looking straight ahead with a neutral facial expression.

Pre test (experiment 1)

Skuas had to visually locate the container under which a food reward was placed. This was to ensure that the birds learned that only one container was rewarded. At the onset of each trial, an opaque blind (wooden board) was placed vertically between the subject and the containers to prevent the birds from seeing under which container the experimenter hid the food reward. Then, the experimenter removed the blind and lifted both containers simultaneously for 3 s. After the

experimenter put down the containers, subjects were allowed to select one of them. If a correct choice was made, the bird was allowed to eat the food. If the bird made an incorrect choice, the experimenter slid back the container from the platform (subjects did not receive any food), and a new trial started. The reward was positioned randomly in the left or right container, with the exception that the food was not located on the same side more than three times in a row within a session. Birds could proceed to the test phase if they reached at least seven out of eight correct trials in a row (experiment 1: trials lasted 30 s each, maximum 10 per day, between 30 s - 1 min apart).

Test (experiment 1)

Five experimental conditions were administered (Figure 1). In (1) *Touch*, as soon as the visual barrier was removed, the experimenter put her ipsilateral hand on the baited container for 3 s. After giving the cue, she pushed the platform forward and waited until the subject chose between the two containers. In the four other conditions, same procedure as in *Touch* was used except that in (2) *Head*, the experimenter brought her head close to the rewarded container (about 6 cm) and looked towards the rewarded container for 3 s; in (3) *Point*, the experimenter pointed the index finger vertically above the baited container for 3 s (with a maximum fingertip-to-container distance of 1 cm); in (4) *Point + Head*, the experimenter used simultaneously head and point cues towards the rewarded container for 3 s; finally, in (5) *Control*, the experimenter did not give any cue and pushed the platform towards the subject. This condition was designed to rule out the use of olfactory cues to solve the task.

Each subject received 16 sessions in total. Each session consisted of five trials, one of each experimental condition (one touch trial, one head trial, one point trial, one point + head trial, one control trial). The order of presentation of cues within one session varied randomly across days and each subject received maximum five sessions per day. If the bird did not appear to be attending to the presented cue (due to a lack of motivation or distraction), it received two training trials and again a test trial that directly followed the second training trial. In such training trials (identical to pre-test trials), the

experimenter presented simultaneously both containers, one hiding a food reward, without giving any cue, and then allowed the bird to choose one container.

Test (experiment 2)

For comparative purposes, we used the same experimental conditions (Figure 1) as in [Garland et al. \(2014\)](#). At the onset of each trial, both experimenters simultaneously dropped the food reward on their platform, and directly took their respective final position. In (1) *Body away/toward*, one experimenter looked forward (facing the skua and the food reward) while the other experimenter had the back turned; in (2) *Side away/ toward*, both experimenters had their chest turned to the side (when viewed from the bird's point of view). In this condition, one platform was located in front of, and thus within the view of one experimenter, while, for the second experimenter, the platform was located behind their back, and was thus not visible to the experimenter; in (3) *Head away/toward*, one experimenter looked forward while the other turned the head 180° away; in (4) *Eyes away/toward*, experimenters differed only in the direction of the eyes: one experimenter gazed forward, while the eyes of the second experimenter were directed 45° outward therefore away from the first experimenter; in (5) *Face occluded/chest occluded*, the chest (first experimenter) and the face (second experimenter) were hidden by a piece of fabric; finally, in (6) *Mouth occluded/eyes occluded*, the eyes (first experimenter) and the mouth (second experimenter) were hidden by a piece of fabric.

Each subject received one session in total. A session consisted of six trials, one of each experimental condition. The position of the experimenter was counterbalanced in each condition, and platforms and experimenters were located about 20 cm apart. Each skua was given 3 min to take the reward in each trial.

Data Analysis

All tests were video recorded. A second naïve observer (L. Rangheard; blind to the experimental condition during the watching of videos) coded a random 20% of video recordings in experiment 1 (20

out of 97 trial sessions in total) and in experiment 2 (16 out of 84 trial sessions in total). The Cohen's kappa coefficients of inter-observer reliability calculated were $\kappa = .96$ in experiment 1, and $\kappa = .98$ in experiment 2, which are considered high reliability.

Prediction 1: Skuas fail in using human-given cues in the cooperative context

We used a Generalised Linear Mixed Model (GLMM; function: `glmer`) using a Binomial error structure and a logit link to assess whether skuas were able to use human-given cues during the test phase. Our response variable (Test) corresponded to success or failure (1 or 0) in using human-given cues, and our explanatory variables included Condition (i.e., *Touch, Head, Point, Point + Head, and Control*), Side choice (left vs right), and Trial number (learning: 1 vs 2 vs ...16). We also used binomial tests to analyse performance in using human-given cues at the individual level (criterion: at least 13 correct trials out of 16 trials in total; $p < .05$).

Prediction 2: Skuas do not respond to human cues in the competitive context

We used a Generalised Linear Model (GLM; function: `glm`) using a Binomial error structure and a logit link to assess whether skuas were able to use human-given cues during the test phase. Our response variable (Test) corresponded to success or failure (1 or 0) in showing aversion to human cues, and our explanatory variable included Condition (i.e., *Body away/toward, Side away/ toward, Head away/ toward, Eyes away/ toward, Face occluded/chest occluded, and Mouth occluded/eyes occluded*). We also used binomial tests to analyse side bias at the individual level (criterion: at least 6 correct trials out of 6 trials in total; $p < .05$).

We used the packages *MuMIn* (Bartón 2020) for model selection and *lme4* (Bates et al. 2015) to perform the analyses. All the analyses were conducted in R Version 3.6 (R Core Team, 2019).

Results

Prediction 1: Skuas in the cooperative context

We carried out a GLMM analysis to assess whether skuas were able to use human-given cues during the test phase. The best-fitting model contained only Side choice (Akaike weight: 0.687; sum of weights: Side choice = 1.00, Trial number = 0.27, and Condition = 0.06) and confirmed our prediction. The analysis revealed the presence of a side bias in participants (-0.778 ± 0.188 , $z = 4.148$, $p < .001$; Table 1; see also percentages in Table 2). At the individual level, skuas were not capable of obtaining the reward more often than expected by chance (at least 13 correct trials out of 16 trials in total; Table 2). Furthermore, after a number of trials, two males (13A, Blond) and three females (11A, 12A, Sourcil blanche) no longer wanted to participate in the task (Table 2).

< Insert Table 1 and Table 2 about here >

Prediction 2: Skuas fail to use human-given cues in the competitive context

We used a GLM to evaluate whether subjects responded in an aversive way to human cues. Skuas avoided the cue of human experimenters only in the *Side away/toward* condition (2.484 ± 0.978 , $z = 2.738$, $p = 0.011$; Table 1), and took the reward on the platform of the experimenter that faced forward in *Body toward/away* (-2.592 ± 1.073 , $z = -2.417$, $p = 0.015$; Table 1). At the individual level, two subjects out of 14 chose to take the reward on the 'correct' platform (i.e., not within the view of the experimenter) in the condition *Body away/toward*, seven out of 11 in the condition *Side away/ toward*, four out of 13 in the condition *Head away/ toward*, four out of 12 in the condition *Eyes away/ toward*, and five out of 12 in the conditions *Face occluded/chest occluded* and *Mouth occluded/eyes occluded* (Table 2). One subject avoided human cues in all six conditions (21A), but this subject had a side bias towards the left side (at least 0 or 6 correct trials out of 6 trials in total; Table 2). Three skuas (05A, 06A, 32A) did not complete all conditions due to the sudden intrusion of their partner during the trial session. These three subjects were not available during the rest of our fieldwork either because the target individual (i) was incubating, (ii) left the area to defend territory, or (iii) was accompanied by its partner.

Discussion

Ours is the first study conducted on wild subjects that combines both cooperative and competitive social contexts in a single experimental paradigm to test the comprehension of human-given cues. In accordance with our predictions, skuas failed to use human-given cues above chance level in the cooperative context (experiment 1). Moreover, most subjects stopped participating in trials during the experiment probably due to repeated failures. Conversely, although birds did not respond to human cues in the competitive context (experiment 2), they were more inclined to complete all trials by taking the food on the rewarded platform.

One may argue that skuas declining to participate in experiment 1 may be attributable to a lack of cognitive skills, such as object permanence (the ability to represent hidden objects; [Piaget, 1954](#)). Skuas might indeed be more willing to participate if they see the food reward directly. However, although the experimenter had to increase the administration of training trials through the experiments, lack of motivation was evident neither during the training phase, nor during other cognitive tasks performed subsequently where the food reward was covered. The genetic proximity between gulls and skuas also lead us to preclude the explanation that skuas are unable to properly *see* human experimenters' cues due to limited vision.

Another potential explanation underlying skuas' results in experiment 1 may relate to the timing of our experiments, given that we administered the tests during the breeding season. Due to the significant physical effort associated with chick rearing, birds might be less prone to participate in cognitive experiments ([Ibañez et al., 2018](#)). However, as shown by other cognitive experiments carried out during the breeding season (e.g., [Danel et al., 2021](#); [Danel et al., 2022](#)), including experiment 2, skuas are in fact strongly motivated to get the food reward and to interact with a human experimenter. Thus, it seems more likely that, due to their inability to use the experimenter's cues and the resulting failures in obtaining rewards, skuas increasingly lost motivation.

Skuas' overall performance in experiment 2 did not indicate a particular sensitivity to human

eyes. Indeed, subjects did not show a preference for the reward closest to the human experimenter who could not see them in all but one condition (Table 1). Furthermore, at the individual level, only one bird avoided the knowledgeable competitor in all conditions and this subject had a side bias toward the left side (Table 2). The significant effect found in the *Side away/toward* condition (when skuas see experimenters' profiles) may tentatively suggest that this species is sensitive to human eyes. However, this assumption does not align with the significant effect found in the *Body away/toward* condition, where skuas chose preferentially the rewarded platform of the experimenter who faced toward them. Therefore, a more convincing interpretation is that skuas are unlikely to respond to human eyes, because they do not perceive them as a threat.

Variation in performance has been attributed to the use of different methods ([Barth et al., 2005](#); [Tornick et al., 2010](#)). In our experiment, birds watched the human experimenter fixate her gaze at the correct container for 3 s and in a fixed manner. Then, she stopped cueing and allowed the birds to make a choice. In jackdaws, the human experimenter alternated the direction of eye gaze between the correct location and the bird for 5 s ([von Bayern & Emery, 2009](#)). This latter species was unable to use eye gaze when the cue was shown without alternations (when eye gaze was fixed). The salience of the cues may thus vary depending on the procedure applied. Further tests are necessary in order to draw firm conclusions about the capacity of skuas to spontaneously use interspecific cues (e.g., by using non-fixed cues of longer durations).

Our finding in this competitive version of the object-choice paradigm is in stark contrast with another insular species that was tested using the same procedure, the wild North Island robin ([Garland et al., 2014](#)). Indeed, contrary to skuas, robins responded to human eyes by choosing the rewarded platform of the experimenter who could not see the reward in all but one condition. Although the two species differ in their responses to human eyes, robins did not seem to perceive human cues as truly aversive (or 'threatening'), which may be partly explained by their evolutionary isolation. Indeed,

similarly to wild robins, the experimenters had to quickly remove both platforms after a bird had completed a trial as skuas constantly tried to take the second reward. It was often necessary for experimenters to 'hurry' before the start of each trial, as skuas attempted to take the food reward before experimenters took their final position. Skuas were tame toward human experimenters (going very close to platforms and humans) who had to make the birds move backwards several times between trials (by raising themselves and extending their arms toward the bird). Thus, skuas and robins' responses do not necessarily reflect competitive abilities *per se*, but why do they differ in terms of using what the human experimenter can - or can not - see?

Although these two birds have in common evolutionary isolation, lack of anti-predator behaviour, absence of complex social lives, and aggressive and competitive nature, they differ in regard to other ecological traits, such as food-hoarding behaviour (first possibility; [Burns & Van Horik, 2007](#)) and exposure to humans (second possibility; [Garland et al., 2014](#)). Contrary to skuas, New Zealand robins cache food, thus reading conspecifics cues might be adaptive in social contexts to avoid pilfering attempts ([Burns & Van Horik, 2007](#); [Van Horik & Burns, 2007](#); [Burns, 2009](#)). The prediction based on such social intelligence, however, does not align with the results obtained in non food-caching birds that responded to human cues in a competitive context (e.g., grey parrots, [Péron et al., 2011](#); hageda ibises, *Bostrychia hagedash*: [Bateman & Fleming, 2011](#); sparrows, *Passer domesticus*: [Hampton, 1994](#); starlings, *Sturnus vulgaris*: [Carter et al., 2008](#)).

It is worth noting that the studied population of New Zealand robins (and most species studied so far) has had regular exposure to humans before and during testing ([Garland et al., 2014](#)). Indeed, robins were accustomed to visitors and staff walking through the sanctuary forest park they lived in and some subjects had previously participated in cognitive studies mediated by a human experimenter. Exposure to humans has been suggested to influence subjects' ability to respond to human cues. For instance, another wild bird that responded to human eyes or gaze direction in the competitive version

of the object-choice task, the herring gull, also had extensive exposure to humans (Goumas et al., 2019). Many members in this species breed and forage in urban areas and may therefore benefit from the use of subtle cues (head or gaze direction) in order to identify potentially dangerous humans. In the cooperative social context, a number of studies also demonstrate the ability of many captive or wild-caught species with considerable human exposure to use human-given cues to locate food, regardless of their domestication level or their social organization (e.g. Clark's nutcrackers: Tornick et al., 2010; cotton-top tamarins, *Saguinus oedipus*, rhesus monkeys, *Macaca mulatta*, and chimpanzees: Wood et al., 2007; dogs and some wolves: Hare & Tomasello, 1999; Virányi et al., 2008; goats: Kaminski et al., 2005; gorillas, *Gorilla gorilla*: Peignot & Anderson, 1999). For instance, in a comparative study with chimpanzees and orangutans (*Pongo abelii*), the only subject that successfully selected hidden food from one of three containers was an enculturated orangutan (Tomasello et al., 1997). Therefore, it is possible that a lack of exposure to humans may prevent individuals from learn specific aspects of human-given cues.

Future research in the cooperative social context may assess whether skuas are able to learn to follow heterospecific cues after extended interaction with humans. For instance, tests may involve (i) more test trials in total, as other species show this capacity after 16 trials (e.g. Giret et al., 2009; Tornick et al., 2010), (ii) the presentation of only a single cue at a time (e.g. Kano et al., 2018; Tornick et al., 2010), (iii) longer duration of the cues (e.g. in a dynamic-sustained manner: e.g. Maros et al., 2008; Nawroth et al., 2014), or (iv) intensive training (e.g. Neiworth et al., 2002; Shapiro et al., 2003). Finally, future work may assess whether individuals that failed the task can learn to use cues in the presence of an informed conspecific (e.g. Schloegl et al., 2008), and if learned social cues can be transferred within and across species (e.g. Essler et al., 2017).

To conclude, our study illustrates the need to assess past and present human-animal interactions when investigating responses to human cues and, more generally, in cognitive studies

requiring the exchange of information between a human experimenter and an animal subject (Cibulski et al., 2014). What and how wild animals, and birds more particularly, understand about human cues remains understudied. Probably due to their evolutionary isolation and lack of experience with humans, wild skuas do not seem to be sensitive to human cues, either in a cooperative or a competitive social context. Increasing work on the ability to use human-given cues is fundamental to map the distribution of this capacity throughout the animal kingdom (Miklósi & Soproni, 2006; Proops et al., 2010). Once more experiments assess whether wild animals, that vary widely in their socio-ecology and prior interactions with humans, use and respond to human cues, we will be able to better pinpoint the evolutionary and developmental drivers of this ability.

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Tables**Table 1***Results of the GLMM and GLM Analysis in the Cooperative and Competitive Contexts, Respectively*

Fixed effects	Estimate	SE	z	p
GLMM the cooperative context				
Experimental condition	0.256	0.129	1.983	0.047
Side choice	-0.778	0.187	-4.148	< .001
GLM in the competitive context				
Body away/toward	-2.592	1.073	-2.417	0.015
Side away/toward	2.484	0.978	2.738	0.011
Head away/toward	1.874	1.176	1.594	0.110
Eyes away/toward	1.911	1.177	1.624	0.104
Face occluded/chest occluded	2.009	1.192	1.685	0.091
Mouth occluded/eyes occluded	2.009	1.192	1.685	0.091

Table 2

Number of Correct Choices Out of the Total Number of Trials and Side Bias (Right Choices/Choices in

Total)

Subjects	Touch	Head	Point	Point + Head	Control	Right
Cooperative context						
01A	7/16	9/16	7/16	4/16	8/16	
03A	8/16	9/16	7/16	7/16	9/16	
11A	7/15	7/14	7/15	5/15	7/14	5
12A	7/12	6/12	4/12	6/12	5/12	3
13A	0/1	0/1	1/1	-	1/1	
21A	6/16	7/16	9/16	9/16	8/16	
Sourcil blanche	9/14	5/14	5/14	8/15	8/15	6
Blond	3/5	2/5	2/6	1/5	3/5	
Subjects	Body away/toward	Side away/toward	Head away/toward	Eyes away/toward	Face occluded/chest occluded	M occlu oc
Competitive context						
01A	0/1	1/1	0/1	0/1	0/1	
02A	0/1	1/1	1/1	1/1	1/1	
03A	0/1	0/1	0/1	0/1	0/1	
05A	0/1	0/1	-	1/1	-	
06A	0/1	-	0/1	-	0/1	
11A	0/1	1/1	0/1	1/1	1/1	
18A	1/1	1/1	0/1	0/1	1/1	
12A	0/1	1/1	1/1	0/1	1/1	
13A	0/1	0/1	0/1	0/1	0/1	
21A	1/1	1/1	1/1	1/1	1/1	
22A	0/1	1/1	0/1	0/1	0/1	
32A	0/1	-	0/1	-	-	
Boiteuse	0/1	0/1	1/1	0/1	0/1	
Sourcil b.	0/1	1/1	1/1	1/1	0/1	

Note. A correct choice in the cooperative context consists of choosing the container indicated by a human cue, while a correct choice within the competitive context consists of selecting the platform that is not within the view of the human experimenter).

* $p < .05$.

Figures

Figure 1

Schematic Representation of the Experimental Conditions Used in the (A) Cooperative and (B) Competitive Contexts of the Object-Choice Paradigm

Experiment 1 - cooperation context



Experiment 2 - competition context

