

Wild skuas can follow human-given behavioural cues when objects resemble natural food

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Running head: HUMAN BEHAVIOURAL CUES IN SKUAS

- 1 Wild skuas can follow human-given behavioural cues when objects resemble
- 2 natural food
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Abstract

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The capacity to follow human cues provides animals with information about the environment and can hence offer obvious adaptive benefits. Most studies carried out so far, however, have been on captive animals with previous experience with humans. Further comparative investigation is needed in order to properly assess the factors driving the emergence of this capacity under natural conditions, especially in species that do not have longstanding interactions with humans. Wild brown skuas (Catharacta antarctica ssp. lonnbergi) are nonneophobic seabirds that live in human-free habitats. In test 1, we assessed this species' capacity to use human behavioural cues (i.e., pecking at the same object previously picked up and lifted by a human experimenter) when the items presented were food objects: anthropogenic objects (wrapped muffins) and natural-food-resembling objects (plaster eggs). In test 2, we examined the response of another skua population towards non-food objects (sponges). Although all skuas in test 1 pecked at the object, they pecked significantly more at the same previously handled items when they resembled natural food (plaster eggs). Most skuas in test 2, however, did not approach or peck the non-food objects presented. Our results lead us to suggest that the use of human-behavioural cues may be influenced by skuas' foraging ecology, which paves the way to further field studies assessing whether this capacity is directed specifically towards food objects and/or develops after previous interaction with humans.

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Keywords: choice task · human-animal communication · neophobia · skua · social cue · social learning

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Introduction

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The capacity to use human behavioural cues has been demonstrated in numerous non-human species and has remained the focus of extensive research over the last decade (e.g., gulls, Larus argentatus: Goumas et al. 2020; dogs, Canis lupus familiaris: Bhattacharjee et al. 2020; elephants, *Elephas maximus*: Ketchaisri et al. 2019; goats, *Capra hircus*: Nawroth et al. 2020; horses, Equus caballus: Lovrovich et al. 2015; kangaroos, Macropus fuliginosus fuliginosus, Macropus giganteus, Macropus rufus: McElligott et al. 2020; monkeys, Cebus [Sapajus] apella: Essler et al. 2017; pigs, Sus scrofa domestica: Nawroth et al. 2016; sealions, Zalophus californianus: Malassis and Delfour 2015). A widely-used method for investigating this capacity is the two-way object-choice paradigm, where subjects are presented with a choice between two containers, only one hiding a food reward, and the identity of the correct container is indicated through experimenter-given cues (such as gazing and pointing e.g., Clark et al. 2019; Danel et al. 2022). However, interpreting subjects' success on the task (i.e., through the selection of the correct container) can be difficult when the human experimenter makes contact directly with (e.g., provides the cue by touching) - or is in close proximity to - the rewarded container (Kaminski et al. 2005). The reason for the ambiguity is that cues given in proximity to a target can trigger responses through local enhancement: a form of social information use relying on attraction to a specific location merely due to the presence of other conspecifics there (Thorpe 1963). As such, responses may reflect an attraction to the location where the object is manipulated rather than an understanding of the cues presented. So far, most studies have been restricted to captive populations, where rigorous controls can easily be administered. Field experiments, however, are crucial to elucidating whether and how human-given cue use operates under natural conditions. Moreover, recently, it has been suggested that the capacity to use human behavioural cues, including through local

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enhancement, may be facilitated in wild animals that often interact with humans and show low levels of neophobia ('fear of novelty'; Goumas et al. 2020). For instance, when two anthropogenic objects are directly visible (as opposed to hidden under containers), urban herring gulls (Larus argentatus) peck at the object previously handled by the human experimenter only when it is food-related (wrapped blueberry flapjack: Goumas et al. 2020). Here, we assessed whether a population (île Verte site) of wild brown skuas (Catharacta antarctica ssp. lonnbergi) follows human cues in two-way object-choice tasks involving the use of familiar and unfamiliar food objects ('Test 1: food objects' i.e., anthropogenic: wrapped muffins and natural-food-resembling objects: plaster eggs). To evaluate whether skuas are attracted towards non-food objects and to prevent familiarity with the experimental set-up from influencing results (Goumas et al. 2020), we tested a second skua population (Ratmanoff site) with non-food objects only ('Test 2: non-food objects' i.e., anthropogenic non-food objects: sponges). Skuas are closely related to gulls (Furness et al. 2018) and share behavioural traits believed to facilitate adaptation to changing environments (Wong et al. 2015) and exploitation of anthropogenic resources, such as boldness, behavioural flexibility, fast learning, generalism, and opportunism (Carneiro et al. 2014, Carneiro et al. 2015). However, skuas inhabit human-free habitats, do not have longstanding interactions with humans, and are not familiar with anthropogenic resources. Investigation in closely related species that differ in terms of their previous exposure to humans is crucial to determine the predictors of the capacity to follow human cues, and understand its evolution. Moreover, skuas are non-neophobic and highly territorial (Furness et al. 2018; see also Danel et al. 2021; Danel et al. 2022), which facilitates greatly the study of their cognition in the wild. Based on this species' almost complete absence of neophobia and lack of longstanding interactions with humans, we first expected skuas from the first population (île Verte site) to approach all food objects ('test 1: food-objects' i.e., wrapped muffins, plaster eggs), but to peck

significantly more at salient, experience-based food objects (i.e., plaster eggs), without following human behavioural cues. For comparative purposes (Goumas et al. 2020), we also administered a test with non-food objects to skuas from the second population (Ratmanoff site). We predicted subjects to approach (without pecking at) non-food objects ('test 2: non-food objects' i.e., sponges).

Methods

Study population

Two populations of adult wild brown skuas participated in this study, each located at a different geographical site within the Kerguelen archipelago, in the Southern Indian Ocean: 18 birds at île Verte, Morbihan gulf (test 1: food objects) and 18 individuals at Cape Ratmanoff, Courbet peninsula (test 2: non-food objects). These sites are located approximately 67 km from each other, and thus represent independent populations. Experiments were conducted between November 2020 and February 2021. Tests were administered between 7 a.m. and 6 p.m. Only the subjects of test 1: food objects had previously interacted with humans: this consisted of cognitive experiments conducted over a very short period (i.e., 2.5 weeks) between December 2019 and January 2020.

Experimental setup and Materials

In test 1: food objects, we used two food objects: (i) 'Cookie Creations' chocolate muffins in green liners wrapped in transparent packaging (8 cm in length x 7 cm in width; 40 g) as anthropogenic food objects, and (ii) two plaster blue petrel (*Halobaena caerulea*) eggs (6.5 cm in length x 4 cm in width; 90 g) inserted into plastic zip lock bags as natural-food-resembling objects, given that eggs are part of skuas' diet (Furness et al. 2018) (Figure 1). Given the extent of resemblance, the insertion of the eggs into transparent bags was necessary in order to prevent skuas' swallowing attempts (SD, personal observation). In test 2: non-food objects, we used green sponges (10 g) of the same size and shape as the previous

anthropogenic food objects (wrapped muffins). Although skuas are familiar with blue petrel eggs, our subjects had never encountered wrapped muffins and green sponges previously.

Procedure

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Our general procedure was similar to the one used with gulls (Goumas et al. 2020). When a target individual was in view on the ground, the experimenter approached the skua holding in each hand a platform covered by a white plastic container. When the bird was approximately 8 m from the human experimenter, she crouched down on the ground, spaced the two platforms at a distance of 70 cm using a marked stick, and removed simultaneously both containers to reveal the objects. Then, the experimenter picked up one of the two objects, stood up straight and moved the object towards her face while mentally counting up to 20 s (continuously reorienting her body to keep facing the skua in case it did not stand still). The experimenter then put the object down in same place, stood up, took the white containers, and walked backwards up to a distance of about 6 m. Subjects received two trials (test 1: food objects: two types of objects, île Verte site) or one trial (test 2: non-food objects: one type of object, Ratmanoff site) in total (each trial lasting 120 s maximum, 2 trials per day maximum, minimum 1 h apart). Objects were always presented using the same side and orientation. The experimenter alternated the manipulation of the right and left object between trials (test 1: food objects). In test 1: food objects, the order of presentation of the objects was counterbalanced across subjects (bird 1 was first presented with wrapped muffins, then plaster eggs, bird 2 was first presented with plaster eggs, then wrapped muffins, etc.).

Data analysis

We used a Generalized Linear Mixed Model (GLMM) following a binomial distribution to test whether skuas' choice was influenced by the type of object manipulated by the human experimenter (matching/non-matching the experimenter's choice, measured by *pecking*, i.e.

behaviour that consists of touching with the beak the same (matching) or different (non-
matching) object previously handled by the human experimenter) in test 1: food objects (i.e.,
anthropogenic: wrapped muffins or natural-food-resembling objects: plaster eggs). Subjects'
identity was included as a random variable, and the following fixed variables were
considered as additional predictors: latency of contact and distance between the skua and the
objects.
At the individual level, we also used two binomial tests (α set at 0.05; α at 0.025 with
Bonferroni correction) to assess whether skuas pecked at previously handled food objects
(i.e., plaster eggs or wrapped muffins) more than would be expected by chance.
Finally, we ran two Fisher's exact tests (two-tailed, α set at 0.05; α at 0.025 with
Bonferroni correction) to evaluate whether the proportion of skuas that pecked at or
approached the objects differed significantly between the two populations (île Verte site and
Ratmanoff site). GLMM analysis, binomial tests, and Fisher's exact test focusing on pecking
behaviours were conducted on 17 individuals at île Verte site, since one skua approached but
did not peck at any object. All the analyses were conducted with R version 3.6, and the
package lme4 (Bates et al. 2015) was used to perform the GLMM analysis.
Results
The variable type of object (wrapped muffins vs plaster eggs) had a significant effect on
birds' choices. More precisely, skuas matched significantly more (pecked at the same object
previously manipulated by the experimenter) when the objects were plaster eggs rather than
wrapped muffins (binomial GLMM, $Z = -3.36$, $p \le 0.001$; Table 1). Latency of contact and
distance between the skua and the objects had no significant effect on skuas' choices.
At the individual level, skuas pecked at the same previously handled item more than
would be expected by chance when the food objects presented were plaster eggs (14 out of 17
subjects; binomial test: $p = 0.01$, adjusted p with Bonferroni correction = .02), but not when

they were wrapped muffins (7 out of 17 subjects; binomial test: p = .48, adjusted p with Bonferroni correction = .96). We could not test whether skuas from the Ratmanoff site pecked indiscriminately at non-food objects as too few subjects pecked at non-food objects.

All skuas at île Verte (test 1: food objects: n = 18) approached the food objects (wrapped muffins and plaster eggs), while at the Ratmanoff site (test 2: non-food objects: n = 18), only 5 individuals did so when exposed to non-food objects (sponges). This difference was

significant (Fisher's exact test: $p \le 0.001$). Seventeen out of 18 skuas at île Verte and 4 out of

18 skuas at Ratmanoff pecked at the objects presented. This difference was also significant

(Fisher's exact test: $p \le 0.001$).

< Figure 2 and Table 1 about here >

Discussion

Although most free-ranging skuas pecked at both food objects (wrapped muffins and plaster eggs: île Verte site), they used human behavioural cues only when the objects resembled natural food (plaster eggs). Furthermore, few skuas approached and pecked at objects in test 2: non-food objects (Ratmanoff site).

Thus, at the île Verte site (test 1: food objects), handled food seemed more attractive when objects resembled natural (plaster eggs) rather than unfamiliar, anthropogenic food (wrapped muffins). This suggests that local enhancement (attraction to the handled object; Thorpe 1963) is driven by ecologically relevant, context-specific stimuli in wild skuas. Due to their identification as familiar food items, plaster eggs may have represented highly salient stimuli when manipulated by the human experimenter (Furness et al. 2018). This behaviour may originate from skuas' tendency for piracy (Kanaujia et al. 2014), also known as kleptoparasitism, which consists of stealing food already procured by others (Morand-Ferron et al. 2007). Skuas seem particularly attracted by food held by conspecifics and other species

- and they may have been able to generalize this behaviour towards humans, as is the case for some other kleptoparasites (e.g., gulls: Rock 2005).

At the Ratmanoff site (test 2: non-food objects), few skuas approached and/or pecked at anthropogenic non-food objects. Despite an almost total lack of neophobia, this result shows that skuas from this population do not necessarily approach - or are attracted towards - novel objects. In this context, one can relate exploration and the salience of - or attraction towards - ecologically-relevant stimuli (plaster eggs) discussed above to the results obtained with free-ranging herring gulls (Goumas et al. 2020). More specifically, when skuas and urban gulls are confronted with *repeated* food-human learning associations in their environment (i.e., skuas at île Verte and urban gulls), they may be more inclined to peck at all objects presented by humans, but also to follow their cues particularly when food objects are ecologically relevant (i.e., skuas: plaster eggs, gulls: wrapped blueberry flapjacks). The rapidity with which skuas may have acquired this food-human association is intriguing and may relate to this species' ecology (e.g., the necessity to form quickly new associations regarding prey availability and foraging behaviour in fluctuating environments: Carneiro et al. 2015).

However, at this stage, further studies are necessary to control for and draw firm conclusions about whether the types of objects presented (food vs. non-food objects) affected subjects' interest, for example by eliciting more peck and approach behaviours when they resembled food items, or whether short food-mediated contact with humans played a significant role in the development of interspecific local enhancement (i.e., by testing the same individuals at the Ratmanoff site with food objects, and those at the île Verte site with non-food objects).

Beyond showing that the use of human handling as a cue is food-specific (Goumas et al. 2020), our findings suggest that this capacity is influenced by a species' foraging ecology. This experiment contributes to to-date small number of cognitive studies investigating the use

of human behavioural cues in the wild, especially in populations that live in human-free
habitats. By testing animals that vary in their fear of novelty, history of past interactions with
humans, and ecology (e.g., urban vs. non-urban vs. outside of anthropogenic habitats), we
will be able to obtain a fuller picture of the selective forces acting on the development of this
skill in the wild.

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228	Conflicts of interest/Competing interests
229	The authors declare that they have no conflict of interest.
230	Ethics approval
231	This article does not contain any studies with human participants performed by any of the
232	authors. The protocols were carried out in accordance with published guidelines of the
233	Association for the Study of Animal Behaviour (ASAB) and the Animal Behavior Society
234	(ABS). The experiment was approved by the French Ethical Committee (n°
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290 **Tables**

Table 1 – Results of the GLMM analysis for test 1: food objects.

	Estimate	SE	Z	p
Test 1: food objects				
Intercept	10.56	3.82	2.76	\leq 0.001
Type of object (wrapped muffins and plaster eggs)	-20.01	5.94	-3.36	≤ 0.001

Figure legends

Figure 1 Objects and experimental set-up presented to wild brown skuas. (a) Test 1: food objects i.e., wrapped muffins and plaster eggs. (b) Test 2: non-food objects i.e., sponges. (c) An example of the experimental set-up with sponges (test 2: non-food objects).

a. Test 1: food objects - île Verte

