



HAL
open science

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

Samara Danel, Jules Chiffard-Carricaburu, Francesco Bonadonna, Anna P Nesterova

► **To cite this version:**

Samara Danel, Jules Chiffard-Carricaburu, Francesco Bonadonna, Anna P Nesterova. Exclusion in the field: wild brown skuas find hidden food in the absence of visual information. *Animal Cognition*, 2021, 24 (4), pp.867-876. 10.1007/s10071-021-01486-4 . hal-03324991

HAL Id: hal-03324991

<https://hal.science/hal-03324991>

Submitted on 24 Aug 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

[Click here to view linked References](#)

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

3 Samara Danel^{1,2*}, Jules Chiffard-Carricaburu^{3*}, Francesco Bonadonna³⁺, & Anna P.
4 Nesterova^{3,4+}

5 ¹Laboratory for the Study of Cognitive Mechanisms, University of Lyon, Bron Rhône-Alpes
6 69500, France.

7 ²Max-Planck-Institute for Ornithology, 82319 Seewiesen, Germany.

8 ³CEFE UMR 5175, CNRS, University of Montpellier, Paul- Valéry Montpellier University -
9 EPHE, Montpellier, Cedex 5, France.

10 ⁴PRC, CNRS, INRAE, Université de Tours, UMR 7247, 37380 Nouzilly, France.

11 *These two authors contributed equally to this work and share the first-authorship

12 +These two authors contributed equally to this work and share the last-authorship

13 **Corresponding authors:** correspondence concerning this article should be addressed to

14 Samara Danel: samara.danel@gmail.com

15

16 16-digit ORCID identifier:

17 Francesco Bonadonna - 0000-0002-2702-5801

18 Jules Chiffard-Carricaburu - 0000-0002-7767-8106

19 Samara Danel - 0000-0003-0233-2343

20 Anna P. Nesterova - 0000-0003-3225-901X

21

22 **Acknowledgments of support**

23 This work was financed by the French Polar Institute (IPEV): project ETHOTAAF 354 to

24 FB. We are very grateful to Yoanna Marescot for helping with the experiments on the field.

25 **Abstract**

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

43

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

46

47

48

49

50 **Introduction**

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

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

70 The ability to choose by exclusion has been found in various animals such as elephants
71 (Plotnick et al. 2014), dogs (Aust et al. 2008; Erdőhegyi et al. 2007), goats (Nawroth et al.
72 2014), or non-human primates (Hill et al. 2011; Sabbatini et al. 2008; Schmitt et al. 2009). In
73 birds, mainly in Corvids and Parrots, some species pass the cups task (e.g. carrion crows
74 *Corvus corone*, Mikolasch et al. 2012; Clark’s nutcracker, *Nucifraga Columbiana*, Tornick

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

79 Whilst some researchers have supported hypotheses about ecological factors promoting
80 the emergence of exclusion in specific animal orders (e.g., ‘the adapted intelligence
81 hypothesis’ in food-caching corvids e.g. Mikolasch et al. 2012; Schloegl et al. 2009; Schloegl
82 2011, but see Shaw et al. 2013; ‘social complexity’ in primates e.g. Petit et al. 2015), others
83 have proposed this ability to be a fundamental cognitive capacity (‘general intelligence’;
84 Pepperberg et al. 2013), or, lately, to be of higher importance in flexible foraging species
85 (Nawroth et al. 2014).

86 A good way to further understand the possible drivers favouring the emergence and
87 evolution of exclusion is to expand the spectrum of species studied with this paradigm in
88 species possessing traits associated with this ability (Marsh et al. 2015; Mikolasch et al.
89 2011; Schloegl et al. 2009). Moreover, experiments with free-living animal populations are
90 crucial to understand how exclusion performance – and cognitive processes more generally –
91 operates under natural conditions (Byrne and Bates 2011; Cauchoix et al. 2017; Völter and
92 Call 2017).

93 However, as testing individuals in the wild is often prohibitively challenging (Shaw et al.
94 2015), we still lack studies about the use of exclusion in wild individuals. For instance,
95 species can show high neophobia (preventing their willingness to participate in the task), be
96 non-territorial (struggling with locating individuals when several trials need to be
97 administrated), or live in groups (making difficult their isolation from conspecifics; Shaw et
98 al. 2015). To our knowledge, only two captive exclusion experiments have been conducted

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

101 This study aims to assess exclusion performance in a new avian model: the wild brown
102 skua (*Catharacta antarctica* ssp *lonnbergi*). This large gull-like seabird frequents Antarctic
103 Peninsula and Subantarctic islands of Atlantic, Indian and Pacific Oceans (Carneiro et al.
104 2014, 2015; Furness et al. 2018). Skuas are top marine predators that display a wide range of
105 feeding techniques i.e. aerial and terrestrial hunting, cannibalism, fishing, kleptoparasitism,
106 and scavenging (Moncorps et al. 1998; Mougeot et al. 1998; Schreiber and Burger 2002).
107 When spatial or seasonal fluctuations in prey availability occur, these birds exhibit high
108 degree of flexibility by adjusting their movements and switching to different resources
109 (Burton 1968; Carneiro et al. 2015). Moreover, skuas can be locally highly selective in their
110 prey intakes and show preferences for hunting specific seabird species (e.g. blue petrel,
111 *Halobaena caerulea*), while others seem to be avoided (e.g. diving petrels, *Pelecanoides*
112 *urinatrix*; Mougeot et al. 1998). Both previous characteristics, behavioural flexibility and
113 selectivity, have been suggested as explanatory factors for exclusion skills in animals
114 (Nawroth et al. 2014). Indeed, some highly flexible species may show higher aversion to
115 losses through the avoidance of the empty container (Nawroth et al. 2014).

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

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

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

135 **Methods**

136 Study population

137 Between Feb 2010 – and Mar 2012, 26 wild brown skuas were tested at Cape Ratmanoff,
138 Courbet Peninsula, Kerguelen Island (48°25'-50°00'S; 68°27'-70°35'E). All birds had a
139 minimum age of 1 year (i.e. colour pattern, uniformity, distinct wing flashes of the body
140 plumage, Furness et al. 2018). Eighteen subjects were individually identified based on leg
141 bands coloured by Darvik©, 2 based on temporary coloured dye sprays (Porcimark©,
142 Langeskov, Denmark, 22 Feb 2010 – 3 Mar 2010), and 6 based on specific aspects of their
143 appearance (i.e. body plumage, presence/absence of scars on the feet' webbing, 2 Mar 2012 –
144 10 Mar 2012). In both field seasons, trials were performed between 7 a.m. and 5 p.m. and
145 each subject was tested separately (a second experimenter prevented conspecifics from
146 entering the test area, by approaching and making the intruders leave within approximately 5
147 meters radius of the setup). Prior to the current study, no skua had ever been tested in any
148 exclusion task.

149 Experimental setup and Materials

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

159 < Fig. 1 about here >

160 Procedure

161 ***Familiarization phase.***

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

167 ***Test phase.***

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

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

178 *Full information condition.* In this condition, we wanted the birds to learn that they would
179 have to make a choice. For that purpose, one reward was hidden under one cup by the
180 experimenter behind the blind. Then, the experimenter removed the blind and both cups were
181 simultaneously lifted so the subject could locate visually which cup contained the food. After
182 3 sec, both containers were put down in same places and the skua could choose between one
183 of them (see S1 in supplementary material). If the subject lifted the rewarded cup, it was
184 allowed to consume the food. Conversely, if the subject chose the unrewarded cup, the
185 experimenter stopped the trial to prevent the bird from obtaining the food. Each subject
186 received 10 trials in total (60 sec each, max. 10 per day, between 10 sec-1 min apart).

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

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

198 Analysis

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

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

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

225 **Results**

226 Model tree I: test conditions and food position

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

230 < Fig. 2 about here >

231 There was a difference in performance between the control condition and the exclusion/full
232 information condition ($p < 0.001$; Node 1). Food position had an effect on success probability
233 but only within the control condition ($p = 0.023$; Node 2): birds' success probability was $P_s =$
234 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
235 $- 0.75$] when the reward was located on the right (Node 4). Thus, there was a mean side bias
236 towards the right container during this condition. At the individual scale, we could detect
237 birds 100% lateralized (Left side: $N = 1$, right side: $N = 3$). Skuas were on average more
238 successful in the full information condition ($P_s = 0.74$ [95% IC: $0.63 - 0.83$]) than in the
239 exclusion condition ($P_s = 0.64$ [95% IC: $0.53 - 0.74$]) ($p = 0.024$; Node 5).

240 Model tree II: test conditions and learning

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

244 < Fig. 3 about here >

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

248 a difference between the exclusion and full information condition ($p = 0.021$; Node 3).
249 During the exclusion condition, there was a difference between the first 12 trials and the last
250 8 trials ($p = 0.021$; Node 4), with an average success probability $P_s = 0.58$ [95% IC: 0.49 –
251 0.67] during the first 12 trials (Node 5), and an average success probability $P_s = 0.71$ [95%
252 IC: 0.62 – 0.79] during the last 8 trials (Node 6). Thus, there was a learning effect emerging
253 over the course of the exclusion condition. During the full information condition (Node 7),
254 mean success probability was $P_s = 0.72$ [95% IC: 0.64 – 0.80].

255 **Discussion**

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

261 When no information was available (control condition), most birds failed in locating the
262 baited cup above chance. This result is not surprising when we refer to the species' biological
263 and behavioural features. Skuas possess small olfactory bulbs and display no reaction when
264 faced to striking odour changes of a same food item (Furness et al. 2018). Noteworthy, a
265 mean side bias emerged over trials in the control condition with a mean preference to select
266 the right cup in tested individuals. At the individual level, four subjects chose constantly the
267 same side (three skuas selected the right one, one the left one). This behaviour is not
268 uncommon when subjects are confronted with two-way object-choice tasks (e.g. Danel et al.
269 2018; Gagne et al. 2012; Ketchaisri et al. 2019), and represents a useful strategy when
270 environmental stimuli are unpredictable, such as in our control condition (Jacobs and Osvath
271 2015; Ketchaisri et al. 2019; Plotnik et al. 2013; Tebbich et al. 2007). In contrast, skuas were
272 able to derive relevant information from the full information and exclusion conditions

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

274 Similarly to other avian species (e.g., African grey parrots, Mikolasch et al. 2011,
275 Pepperberg et al. 2013, Schloegl et al. 2012; carrion crows, Mikolasch et al. 2012; Clark's
276 nutcrackers, Tornick and Gibson 2013; Eurasian jays, Shaw et al. 2013; jackdaws, Schloegl
277 et al. 2011; keas, Schloegl et al. 2009; ravens, Schloegl et al. 2009; red-tailed black
278 cockatoos, Subias et al. 2019), skuas chose significantly more the rewarded cup over the
279 unrewarded one in the full information condition (success probability $P_s = 0.72$ [95% IC:
280 $0.64 - 0.80$]). Our results indicate that this species was able to rely on direct visual
281 information for solving the task. We also suggest that skuas showed spontaneous object
282 permanence (Piaget 1954), i.e. the understanding that hidden objects do not cease to exist
283 (Pepperberg et al. 2013), as they successfully selected the opaque container covering the food
284 reward.

285 Crucially, this species was also able to use indirect information (i.e. the view of the empty
286 cup) to choose substantially more the baited cup over the unbaited one in the critical
287 exclusion condition (success probability $P_s = 0.64$ [95% IC: $0.53 - 0.74$]). Unlike other
288 captive avian species (e.g., Schloegl et al. 2009), skuas in this experiment did not require
289 extensive training and all birds were naive to experimental testing. In this case, the subjects
290 may not have had the time to learn the causal cues (low-level explanation i.e. avoidance of
291 the empty cup) required to solve the task (Nawroth et al. 2014; Shaw et al. 2013; Schloegl
292 2011; Schloegl et al. 2009). Moreover, exclusion performance might not normally require
293 elementary associative learning when a limited number of tests is proposed (Darmaillacq et
294 al. 2018; Shaw et al. 2013). However, we found a progressive amelioration in subjects'
295 performance over trials within the exclusion condition. We therefore cannot rule out the
296 possibility that subjects have used a non-costly cognitive strategy through the avoidance of
297 the empty cup in the following trials (Call 2006; Paukner et al. 2009; Mikolasch et al. 2012;

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

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

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

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

336 **References**

- 337 Allaire J, Xie Y, McPherson J, Luraschi J, Ushey K, Atkins A, Wickham H, Cheng J, Chang
338 W, Iannone R (2020). *rmarkdown: Dynamic Documents for R*. R package version
339 2.3, <https://github.com/rstudio/rmarkdown>.
- 340 Aust U, Range F, Steurer M, Huber L (2008) Inferential reasoning by exclusion in pigeons,
341 dogs, and humans. *Anim cogn* 11:587-597.
- 342 Burton RW (1968) Breeding biology of the brown skua, *Catharacta skua lonnbergi*
343 (Mathews), at Signy Island, South Orkney Islands. *Brit Antarct Surv B* 15:9-28.
- 344 Byrne RW and Bates LA (2011) Cognition in the wild: exploring animal minds with
345 observational evidence. *Biol Lett* 7:619-622.
- 346 Call J (2004) Inferences about the location of food in the great apes (*Pan paniscus*, *Pan*
347 *troglodytes*, *Gorilla gorilla*, and *Pongo pygmaeus*). *J Comp Psychol* 118:232-241.

348 Call J (2006) Inferences by exclusion in the great apes: the effect of age and species. Anim
349 Cogn 9:393-403.

350 Carneiro APB, Manica A, Phillips RA (2014) Foraging behaviour and habitat use by brown
351 skuas *Stercorarius lonnbergi* breeding at South Georgia. Mar Biol 161:1755-1764.

352 Carneiro AP, Manica A, Trivelpiece WZ, Phillips RA (2015) Flexibility in foraging strategies
353 of Brown Skuas in response to local and seasonal dietary constraints. J
354 Ornithol 156:625-633.

355 Cauchoix, M., Hermer, E., Chaine, A. S., & Morand-Ferron, J. (2017). Cognition in the field:
356 comparison of reversal learning performance in captive and wild passerines. Sci
357 Rep 7:1-10.

358 Chester SR (1993) Antarctic birds and seals. Wandering Albatross, San Mateo.

359 Danel S, von Bayern AM, Osiurak F (2019) Ground-hornbills (*Bucorvus*) show means-end
360 understanding in a horizontal two-string discrimination task. J Ethol 37:117-122.

361 Darmaillacq AS, Dickel L, Avargues-Weber A, Duboscq J, Dufour V, Jozet-Alves C
362 2018 Cognition animale: perception, raisonnement et représentations. Dunod.

363 De Kort SR and Clayton NS (2006) An evolutionary perspective on caching by corvids. Proc
364 R Soc B 273:417-423.

365 Erdőhegyi Á, Topál J, Virányi Z, Miklósi Á (2007) Dog-logic: inferential reasoning in a two-
366 way choice task and its restricted use. Anim Behav 74:725-737.

367 Fokkema M, Smits N, Zeileis A, Hothorn T, Kelderman H (2018) Detecting Treatment-
368 Subgroup Interactions in clustered Data With Generalized Linear Mixed-Effects Model
369 Tree Behav Res Methods 50:2016-2034.

370 Furness RW (1987) The Skuas. Carlton, Pyser Press.

371 Furness RW, Boesman P, Garcia EFJ (2018) The Brown Skua (*Catharacta antarctica*). In:
372 del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E (eds) Handbook of the Birds
373 of the World Alive. Lynx Edicions, Barcelona.

374 Gagne M, Levesque K, Nutile L, Locurto C (2012) Performance on patterned string problems
375 by common marmosets (*Callithrix jacchus*). Anim Cogn 15:1021-1030.

376 Gajdon GK, Fijn N, Huber L (2004) Testing social learning in a wild mountain parrot, the
377 kea (*Nestor notabilis*). Anim Learn Behav 32:62-71.

378 Garland A, Low J, Armstrong N, Burns KC (2014) Wild robins (*Petroica longipes*) respond
379 to human gaze. Anim Cogn 17:1149-1156.

380 Grant PB and Samways MJ (2015) Acoustic prey and a listening predator: interaction
381 between calling katydids and the bat-eared fox. Bioacoustics 24:49-61.

382 Grether WF and Maslow AH (1937) An experimental study of insight in monkeys. J Comp
383 Psychol 24:127-134.

384 Hahn S, Peter, HU (2003) Feeding territoriality and the reproductive consequences in brown
385 skuas *Catharacta antarctica lonnbergi*. Polar Biol 26:552-559.

386 Hill A, Collier-Baker E, Suddendorf T (2011). Inferential reasoning by exclusion in great
387 apes, lesser apes, and spider monkeys. J Comp Psychol 125:91-103.

388 Jelbert SA, Taylor AH, Gray RD (2015) Reasoning by exclusion in New Caledonian crows
389 (*Corvus moneduloides*) cannot be explained by avoidance of empty containers. J Comp
390 Psychol 129:283-290.

391 Ketchaisri O, Siripunkaw C, Plotnik JM (2019) The use of a human's location and social cues
392 by Asian elephants in an object-choice task. Anim Cogn 22:907-915.

393 Lee WY, Han YD, Jablonski PG, Jung JW, Kim JH (2016) Antarctic skuas recognize
394 individual humans. Anim Cogn 19:861-865.

- 395 Marsh HL, Vining AQ, Levendoski EK, Judge PG (2015) Inference by Exclusion in Lion-
396 Tailed Macaques (*Macaca silenus*), a Hamadryas Baboon (*Papio hamadryas*),
397 Capuchins (*Sapajus apella*), and Squirrel Monkeys (*Saimiri sciureus*). J Comp Psychol,
398 3:256-267.
- 399 Mikolasch S, Kotrschal K, Schloegl C (2011) African grey parrots (*Psittacus erithacus*) use
400 inference by exclusion to find hidden food. Biol Lett 7:875-877.
- 401 Mikolasch S, Kotrschal K, Schloegl C (2012) Is caching the key to exclusion in corvids? The
402 case of carrion crows (*Corvus corone corone*). Anim Cogn 15:73-82.
- 403 Moncorps S, Chapuis J, Haubrex D, Bretagnolle V (1998) Diet of the Brown Skua
404 *Catharacta skua lonnbergi* on the Kerguelen archipelago: comparisons between
405 techniques and between islands. Polar Biol 19:9-16.
- 406 Morand-Ferron J, Sol D, Lefebvre L (2007) Food stealing in birds: brain or brawn? Anim
407 Behav 74:1725-1734.
- 408 Mougeot F, Bretagnolle V (2000) Predation as a cost of sexual communication in nocturnal
409 seabirds: an experimental approach using acoustic signals. Anim Behav 60: 647-656.
- 410 Mougeot F, Genevois F, Bretagnolle V (1998) Predation on burrowing petrels by the brown
411 skua (*Catharacta skua lonnbergi*) at Mayes Island, Kerguelen. J Zool 244:429-438.
- 412 Nawroth C, von Borell E, Langbein J (2014) Exclusion performance in dwarf goats (*Capra*
413 *aegagrus hircus*) and sheep (*Ovis orientalis aries*). PLoS One 9:e93534.
- 414 O'Hara M, Auersperg AM, Bugnyar T, Huber L (2015) Inference by exclusion in Goffin
415 cockatoos (*Cacatua goffini*). PLoS One 10:e0134894.
- 416 O'Hara M, Schwing R, Federspiel I, Gajdon GK, Huber L (2016) Reasoning by exclusion in
417 the kea (*Nestor notabilis*). Anim Cogn 19, 965-975.

418 Paukner A, Huntsberry ME, Suomi SJ (2009) Tufted capuchin monkeys (*Cebus apella*)
419 spontaneously use visual but not acoustic information to find hidden food items. J
420 Comp Psychol 123:26-33.

421 Paxton Gazes R, Chee NW, Hampton, RR (2018) Monkeys choose, but do not learn, through
422 exclusion. Anim Behav Cogn 5:1-25.

423 Penn DC, Povinelli, DJ (2007) Causal cognition in human and nonhuman animals: a
424 comparative, critical review. Annu Rev Psychol 58:97-118.

425 Pepperberg IM, Koepke A, Livingston P, Girard M, Hartsfield LA (2013) Reasoning by
426 inference: Further studies on exclusion in grey parrots (*Psittacus erithacus*). J Comp
427 Psychol 127:272-281.

428 Petit O, Dufour V, Herrenschildt M, De Marco A, Sterck EH, Call J (2015). Inferences
429 about food location in three cercopithecine species: an insight into the socioecological
430 cognition of primates. Anim Cogn 4:821-830.

431 Piaget J (1954) *The construction of reality in the child*. New York, NY: Basic Books.

432 Plotnik JM, Pokorny JJ, Keratimanochaya T, Webb C et al (2013) Visual cues given by
433 humans are not sufficient for Asian elephants (*Elephas maximus*) to find hidden food.
434 PLoS One 8:e61174.

435 Plotnik JM, Shaw RC, Brubaker DL, Tiller LN, Clayton, SC (2014) Thinking with their
436 trunks: elephants use smell but not sound to locate food and exclude nonrewarding
437 alternatives. Anim Behav 88:91-98.

438 Premack D, Premack AJ (1994) Levels of causal understanding in chimpanzees and children.
439 Cognition 50:347-362.

440 R Core Team (2019) R: A language and environment for statistical computing. R Foundation
441 for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

442 Rice WR (1982) Acoustic location of prey by the marsh hawk: adaptation to concealed prey.
443 The Auk 19:403-413.

444 Ricklefs RE (2004) The cognitive face of avian life histories: the 2003 Margaret Morse Nice
445 lecture. *Wilson J Ornithol* 116:119-133.

446 Sabbatini G and Visalberghi E (2008) Inferences about the location of food in capuchin
447 monkeys (*Cebus apella*) in two sensory modalities. *J Comp Psychol* 122:156-166.

448 Schloegl C (2011) What you see is what you get-reloaded: can jackdaws (*Corvus monedula*)
449 find hidden food through exclusion? *J Comp Psychol* 125:162-174.

450 Schloegl C, Dierks A, Gajdon GK, Huber L, Kotrschal K, Bugnyar T (2009) What you see is
451 what you get? Exclusion performances in ravens and keas. *PloS One* 4:e6368.

452 Schloegl C, Schmidt J, Boeckle M, Weiß BM, Kotrschal, K (2012) Grey parrots use
453 inferential reasoning based on acoustic cues alone. *Proc R Soc B* 279:4135-4142.

454 Schmitt V and Fischer J (2009) Inferential reasoning and modality dependent discrimination
455 learning in olive baboons (*Papio hamadryas anubis*). *J Comp Psychol* 123:316-325.

456 Schreiber EA, Burger J 2002 *Biology of marine birds*. CRC Press, Boca Raton, FL.

457 Shaw RC, Boogert NJ, Clayton NS, Burns KC (2015) Wild psychometrics: evidence for
458 ‘general’ cognitive performance in wild New Zealand robins, *Petroica longipes*. *Anim*
459 *Behav* 109:101-111.

460 Shaw RC, Plotnik JM, Clayton NS (2013) Exclusion in corvids: The performance of food-
461 caching Eurasian jays (*Garrulus glandarius*). *J Comp Psychol* 127:428-435.

462 Sittler B, Aebischer A, Gilg O (2011) Post-breeding migration of four Long-tailed Skuas
463 (*Stercorarius longicaudus*) from North and East Greenland to West Africa. *J Ornithol*
464 152: 375-381.

465 Spear LB, Howell SNG, Oedekoven CS, Legay D, Bried J (1999) Kleptoparasitism by brown
466 skuas on albatrosses and giant-petrels in the Indian ocean. *Auk* 116:545-548.

467 Subias L, Griffin AS, Guez, D (2019) Inference by exclusion in the Red-tailed Black
468 Cockatoo (*Calyptorhynchus banksii*). *Integr Zool* 14:193-203.

- 469 Tebbich S, Seed AM, Emery NJ, Clayton NS (2007) Non-tool-using rooks, *Corvus*
470 *frugilegus*, solve the trap-tube problem. *Anim Cogn* 10:225-231.
- 471 Tornick JK and Gibson BM (2013) Tests of inferential reasoning by exclusion in Clark's
472 nutcrackers (*Nucifraga columbiana*). *Anim Cogn* 16:583-597.
- 473 Trivelpiece W, Butler RG, Volkman NJ (1980) Feeding territories of Brown Skuas
474 (*Catharacta lonnbergi*). *Auk* 97:669-676.
- 475 Völter CJ and Call J (2017) *Causal and inferential reasoning in animals*. In J Call, GM
476 Burghardt, IM Pepperberg, CT Snowdon, & T Zentall (Eds.), *APA handbooks in*
477 *psychology*®. *APA handbook of comparative psychology: Perception, learning, and*
478 *cognition* (p. 643–671). American Psychological Association.
- 479 Watanabe S and Huber L (2006) Animal logics: decisions in the absence of human
480 language. *Anim Cogn* 9:235-245.

481 **Figure captions**

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

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

496 **Fig. 3** Model tree II: test conditions and learning. The Tree shows skuas’ estimated mean
497 success probabilities in each of the terminal nodes during the different test conditions,
498 including the potential effect of learning through trial number (ID_trial) during the exclusion
499 condition. The black bars show the 95% confidence intervals associated with estimated
500 means. Dots show the observed performance of each individual during the different tests
501 between 0 and 1 (0 to 100% success), dots’ colour include transparency so that darker dots
502 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.





