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1 Remote islands as natural laboratories: human-food association increases
2 attraction to humans and novelty exploration in a seabird

3

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19 **Abstract**

20

21 Increased attraction to humans and their objects often arises after repeated and
22 positive human-wildlife encounters (e.g., food provided in tourist settings). Causes of
23 this ‘over-attraction’, which may result from a learned association between humans
24 and food, are still poorly studied in wild animals. Understanding the influence of
25 humans on animals’ responses is yet crucial to prevent negative effects (e.g.,
26 aggression). We presented three novel objects to two groups of free-ranging brown
27 skuas (*Catharacta antarctica* ssp. *lonnbergi*) in the remote sub-Antarctic, where their
28 habitats show no or minimal human disturbance. Skuas in one group (Verte) had
29 previously participated in repeated food-rewarded behavioural and cognitive tasks
30 with a human experimenter; skuas in the other group (Ratmanoff) had never done so.
31 Objects consisted of (i) one natural-food-resembling object (plastic fish), (ii) one
32 anthropogenic food object (real cake slice), and (iii) one anthropogenic non-food
33 object (yellow glove). Verte group skuas approached the human experimenter and
34 pecked significantly more and sooner at novel objects. Human-food association may
35 have thus resulted in increased attraction to humans and novelty exploration in
36 previously naive brown skuas, making this species a useful model for investigating
37 the consequences of experience with humans on wildlife behaviour.

38

39 **Keywords:** exploration, field experiment, human-food association, human-animal
40 interaction, insular bird, skua

41 1. Introduction

42

43 Due to humans' ongoing population growth, human-wildlife conflict has been rising
44 at alarming rates over the last decades [1], and now represents one of the most
45 significant threats facing wildlife. To develop relevant conservation practices,
46 experiments assessing whether wild animals are sensitive to – and can interpret –
47 human behavioural cues (e.g. [2, 3]) have become a burgeoning focus for research [4].
48 A related, poorly-tested question, concerns whether and how extrinsic factors, such as
49 association between humans and food (“rewarding humans”: [4]), influence animal
50 behaviour in the wild. For instance, in free-ranging capuchins (*Cebus libidinosus*),
51 interest in visitors is associated with food-mediated interactions with humans [5].
52 Similarly, at Uluwatu Temple, Indonesia, long-tailed macaques (*Macaca fascicularis*)
53 have learnt to rob human visitors and barter their objects for food with the temple
54 staff [6]. Attraction to human settlements and artifacts can sometimes give rise to
55 serious human-wildlife conflicts, threatening wildlife species of conservation interest.
56 This suggests that human-food association is a key factor affecting attraction to
57 humans and their objects [4, 7-10]. However, research on the extent to which this
58 factor affects wild populations that frequent habitats with no or minimal human
59 disturbance is scant [4]. Using distinct past histories of association between humans
60 and food may help reveal whether and how this factor influences variation in
61 attraction to humans and novelty exploration in the wild [4, 11].

62 Here, we assessed exploration tendencies (measured as the first pecking event) in
63 two populations of wild brown skuas (*Catharacta antarctica* ssp. *lonnbergi*) that
64 inhabit the remote Kerguelen archipelago during the breeding season. Much of these
65 protected islands is devoid of anthropogenic disturbance and temporary activities (e.g.,
66 governmental research) are subject to legal controls and rigorous biosecurity
67 measures. The Kerguelen archipelago thus represents a relevant ‘natural laboratory’
68 for conducting comparative behavioural studies. Due to their low predation pressure
69 and isolation, wild skuas at this location share similar characteristics with captive
70 animals, which usually live in risk-free environments, such as low neophobia [12] and
71 naivety [13]. This species also possesses specific traits associated with exploration
72 propensity [14], such as foraging flexibility, generalism, high opportunism,
73 innovation, and kleptoparasitism [12, 15-16]. Therefore, Kerguelen’s skuas represent
74 an ideal species to examine how wild animals are influenced by humans in their

75 natural environment.

76 In this study, we tested skuas from two populations: skuas from the Verte group
77 had previously interacted with humans and their objects during food-rewarded
78 behavioural and cognitive experiments, whereas skuas from the Ratmanoff group had
79 had no such experience and bred at sites free from human disturbance. Due to this
80 species' naivety, and considering reduced predation pressure associated with most
81 island environments (resulting in low costs associated with novel situations, [17-19]),
82 we expected skuas from both groups to show low levels of fear of humans (prediction
83 1). However, based on previously formed associations between humans and food,
84 skuas in the Verte group should be motivated to approach the human experimenter
85 (prediction 2). We also predicted birds from the Verte group to peck more (prediction
86 3) and sooner (i.e., with a shorter latency; prediction 4) at the novel objects, compared
87 to those from the Ratmanoff group. Finally, if exploration is driven by context-
88 specific stimuli [11], skuas should preferentially peck at ecologically-relevant,
89 natural-food-resembling objects (i.e., plastic fish), compared to other food and non-
90 food novel objects (prediction 5).

91

92 **2. Material and methods**

93

94 2.1. Study populations

95 During January 2023, we tested 22 breeding wild brown skuas (*Catharacta antarctica*
96 *ssp. lonnbergi*) within the Kerguelen archipelago (68–70 °E, 48–50 °S). At the end of
97 the chick-rearing period, data were collected at two geographical sites: 11 skuas (6
98 females, 5 males) were tested at île Verte, Morbihan gulf (Verte group) and 11 skuas
99 (7 females, 4 males) at Cape Ratmanoff, Courbet peninsula (Ratmanoff group). The
100 two locations were approx. 48 km apart. Over four consecutive austral summers
101 (2019-2020 to 2022-2023 breeding seasons), skuas at île Verte had participated in
102 food-rewarded behavioural and cognitive tests mediated mostly by the same
103 experimenter ([e.g., 11, 20, 21]; see supplementary material).

104

105 2.2. Experimental set-up

106 The three objects (**Fig. 1**) consisted of a plastic fish (natural-food-resembling item:
107 [22]; 22 cm in length x 9 cm in width), a real cake slice (anthropogenic food item; 9
108 cm in length x 7 cm in width), and a Simond® yellow glove (anthropogenic non-food

109 item; 17 cm in length x 10 cm in width). To safeguard subjects (habituated skuas can
110 try to steal and ingest novel items, SD pers. obs.), each novel object needed to be
111 presented in a transparent zip lock bag attached with a sisal cord to a square wooden
112 platform (30 cm in length x 22 cm in width x 0.5 cm in height). Before each trial, the
113 platform and the objects were covered by an opaque white piece of fabric (25 cm in
114 length x 25 cm in width).

115

116 < Insert Figure 1 about here >

117

118 2.3. Procedure

119 When the focal skua was present in the absence of its breeding partner, the
120 experimenter (i.e., unfamiliar to the skuas) approached the bird slowly with a platform
121 supporting one of the novel objects covered by fabric. At a distance of approx. 8
122 meters from the skua, she then kneeled, placed the platform on the ground, and
123 removed the fabric to reveal the object. The experimenter then immediately took the
124 object, stood up straight, and moved the object towards her face for a duration of 20 s.
125 She then replaced the object in its previous location and orientation on the platform,
126 put a stone on the platform covering a small part of the zip lock bag (to prevent it
127 from being blown away by the often-strong winds at the study locations [23]), turned
128 on a stopwatch, and walked backwards up to a distance of about 8 m. For each subject,
129 3 trials in total were administered (1 trial per day for each object, based on previous
130 two-object choice tasks e.g., [2, 11]: trials lasted 120 s maximum). The same
131 procedure was repeated the next day and the day after with the two remaining objects
132 in an order randomised across subjects. On each test day, from 10 a.m. to 4 p.m., the
133 experimenter visited skuas' nesting territories in a consistent order. Trials started
134 when the experimenter stood up to manipulate the novel object, and ended either (i)
135 when the skua pecked at the novel object with its beak or (ii) after the maximum trial
136 length had elapsed.

137

138 2.4. Data collection and analysis

139 Tests were coded live and subsequently from video recordings. We recorded skuas'
140 avoidance (moving at least two steps *away* from the experimenter when she stood up
141 to manipulate the object), approach (moving at least two steps *towards* the
142 experimenter; defined as in [24]), exploration (whether skuas *pecking at* objects), and

143 exploration latency (the time elapsed from when the experimenter stepped away from
144 the platform to when the bird pecked at the object). Each trial required birds to remain
145 within a distance of maximum 10 meters from the platform supporting the novel
146 object. Videos were coded by (SB), and subsequently checked by (SD). Both
147 observers were not blind to the experiment. Inter-rater reliability (calculated on a
148 random 20% of 14 out of 69 videos) was high ($p < .001$; $0.545 < ICC < 0.939$).

149 We used Generalized Linear Mixed Models (GLMMs) following a binomial
150 distribution (Models 1, 2, & 3) and one Cox proportional hazards model with mixed
151 effects (Model 4) [25] in R version 3.6 [26]. This latter survival analysis technique is
152 useful for handling censored data (no approach within the 120-second trial duration).
153 First, we checked the absence of collinearity among predictors (function *vif*, package:
154 *car* [27]; GLMM models). Second, we modelled how our response variables varied
155 with fixed effects (packages: *lme4* [28], *coxme* [29]; GLMM and Cox models). Third,
156 we conducted an exhaustive model selection procedure using Akaike Information
157 Criterion corrected for small sample sizes (AICc, package: *MuMIn* [30]; GLMM and
158 Cox models). As any model within two AICc units of the lowest value is, by
159 convention, considered to fit the data just as well [31], we retained the best model
160 within this interval with the largest number of fixed effects. In case of equality
161 regarding the maximum number of variables, both models were implemented.

162 After fitting the selected best-fitting models, deviance tables were extracted
163 (function *Anova*, package: *car* [27]) to assess the significance of the fixed effects in
164 both GLMM and Cox models. For qualitative variables with two modalities, Wald
165 tests from the models were used to assess the significance of the difference between
166 the two modalities. For variables with more than two modalities, post-hoc tests were
167 conducted to assess the significance of contrast differences (package: *emmeans* [32]).

168 Additionally, odds ratios (ORs, [33]) were calculated by exponentiating the
169 coefficients (log-odds) extracted from the models. Effects were categorized as follows:
170 small (OR close to 1.68), moderate (OR close to 3.47), and large (OR close to 6.71).
171 Finally, both marginal and conditional R^2 (as described in [34], package: *MuMIn* [30])
172 were calculated (see supplementary material). For all three GLMM models, *Subjects'*
173 *identity* was included as a random variable, and fixed effects were *group* (Verte group
174 vs. Kerguelen group), *sex* (male vs. female), *object presentation order* (1st trial vs. 2nd
175 trial vs. 3rd trial), and *object type* (yellow glove vs. cake slice vs. plastic fish). The
176 response variable was *avoidance* (coded as: 1 = moving away, or 0 = not moving

177 away) for *Prediction 1: skuas from neither group avoid humans* (Model 1); *approach*
178 (coded as: 1 = approach, or 0 = no approach) for *Prediction 2: skuas from the Verte*
179 *group are more likely to approach humans than skuas from the Ratmanoff group*
180 (Model 2); and *exploration* (i.e., coded as: 1 = pecking, or 0 = no pecking) for
181 *Prediction 3: skuas from the Verte group are more exploratory towards novel objects*
182 *than skuas from the Ratmanoff group* (Model 3). To assess *Prediction 5: skuas peck*
183 *more at the plastic fish than at the other novel objects*, we evaluated the effect of
184 *object type* (yellow glove vs. cake slice vs. plastic fish) in Model 3. As a final step, we
185 present the results of the best model.

186 For the Cox proportional hazards model with mixed effects (i.e., non-independence
187 of observations), we followed the same model selection process and included
188 identical fixed factors (i.e. *group*, *sex*, *object presentation order*, and *object type*). The
189 response variable was *pecking latency* for *Prediction 4: skuas from the Verte group*
190 *peck sooner at the novel objects than skuas from the Ratmanoff group* (Model 4). The
191 models contained data on 22 subjects ($n = 11$ skuas in each test group), each
192 presented with three objects (i.e., $22 \times 3 = 66$).

193

194 **3. Results**

195

196 3.1. Prediction 1: skuas from neither group avoid humans

197 Four skuas in the Verte group moved away from the human experimenter compared
198 to 3 skuas in the Ratmanoff group (**Fig. 2**). The best-fitting Model 1a included *object*
199 *presentation order* ($\chi^2 = 2.55$, $p = 0.280$) and *sex* ($\chi^2 = 2.58$, $p = 0.107$). The best-
200 fitting Model 1b included *object type* ($\chi^2 = 2.55$, $p = 0.280$) and *sex* ($\chi^2 = 2.58$, $p =$
201 0.107 : see [25] and supplementary material). Fixed factors did not lead to significant
202 results for both models (see [25]).

203

204 < Insert Figure 2 about here >

205

206 3.2. Prediction 2: skuas from the Verte group approach humans more than skuas from 207 the Ratmanoff group

208 Eight skuas in the Verte group approached the human experimenter compared to 3
209 skuas in the Ratmanoff group (**Fig. 2**). The best-fitting Model 2 included *group* and
210 *object presentation order* (*object presentation order*: $\chi^2 = 2.37$, $p = 0.305$, *group*: χ^2

211 = 6.06, $p = 0.013$: see [25] and supplementary material). Wald tests from the GLMM
212 showed that skuas in the Verte group were more likely to approach humans than those
213 in the Ratmanoff group (binomial GLMM, 2.07 ± 0.842 , $z = 2.46$, $p = 0.013$; ORs of
214 *group* was 7.95, indicating a large effect: see [25]).

215

216 3.3. Prediction 3: skuas in the Verte group peck more at the novel objects than skuas
217 in the Ratmanoff group

218 All 11 skuas in the Verte group pecked at least at one novel object compared to 6
219 skuas in the Ratmanoff group (Prediction 3; **Fig. 2**). The best-fitting Model 3 included
220 *group*, along with *object type*, since our last aim (see 3.5. below) was to investigate a
221 preference towards the ecologically-relevant object (plastic fish; *group*: $\chi^2 = 13.15$, p
222 ≤ 0.001 , *object type*: $\chi^2 = 0.21$, $p = 0.896$: see [25] and supplementary material).

223 Wald tests showed that skuas in the Verte group pecked significantly more at novel
224 objects than skuas in the Ratmanoff group (binomial GLMM, 3.36 ± 9.26 , $z = 3.62$, p
225 ≤ 0.001 ; ORs of *group* was 28.68, indicating a large effect: see [25]).

226

227 3.4. Predictions 4: skuas in the Verte group peck at the novel objects sooner than
228 skuas in the Ratmanoff group

229 The best-fitting Model 4 included *group*, *object presentation order*, and *sex* (Model 4:
230 *group*: $\chi^2 = 18.95$, $p < 0.001$, *object presentation order*: $\chi^2 = 7.19$, $p = 0.027$, *sex*: χ^2
231 $= 0.027$, $p = 0.884$: see [25] and supplementary material). Wald tests showed that
232 skuas in the Verte group pecked significantly sooner at novel objects than skuas in the
233 Ratmanoff group (cox model, 3.04 ± 0.700 , $z = 4.35$, $p \leq 0.001$; ORs of *group* was
234 21.1, indicating a large effect. Post-hoc tests showed that skuas took longer to peck at
235 the objects after their second trial (ORs of *object presentation order* was 3.23,
236 indicating a moderate effect: see **Table 1** and [25]).

237

238 3.5. Prediction 5: skuas in both groups are more exploratory towards the ecologically-
239 relevant object (plastic fish) than the other novel objects

240 Post-hoc tests of the variable *object type* (yellow glove vs. cake slice vs. plastic
241 fish; Model 3) did not reveal a significant effect on birds' exploration: skuas did not
242 peck significantly more at the plastic fish (see **Table 1** and [25]).

243

< Insert Table 1 about here >

244

245

246 **4. Discussion**

247

248 The hypothesis that attraction to humans and novelty exploration are influenced by
249 previous food-mediated interaction with humans has rarely been tested in wild insular
250 species. Yet, this question is crucial to understanding whether and how these species,
251 and generalist species more particularly [24], adapt to environmental changes. Groups
252 (Verte vs. Ratmanoff) did not seem to differ in their levels of avoidance towards the
253 human experimenter. However, only a few free-ranging skuas in the Ratmanoff group
254 (i.e., those with no participation in previous food-rewarded experiments) pecked at
255 food and non-food anthropogenic objects (cake slice, yellow glove) and natural-food-
256 resembling objects (plastic fish), while all individuals that had previously interacted
257 with humans (Verte group) pecked more and sooner at all the objects. Moreover, the
258 suggested ecological salience of stimuli features did not seem to influence the
259 likelihood of exploration – birds pecked at the novel objects irrespective of whether
260 they resembled a natural food item or not.

261 In skuas that frequent Kerguelen islands, different groups or populations may
262 differ in their degree of fear of humans (e.g., due to habitat variability or competition),
263 which may impact skuas' behaviours. This latter aspect, and not human-food
264 association *per se*, may explain the difference found between our two field sites (i.e.,
265 more pecking behaviours at the objects with shorter latencies in the Verte group). We
266 did not find a difference in avoidance behaviour between test groups. Based on our
267 limited sample size, however, this result still needs to be interpreted cautiously.

268 Together, our results rather suggest that human-food association, formed during
269 previous positive interactions between skuas and human experimenters, strongly
270 influences attraction to humans and novelty exploration. From an ecological
271 perspective, unhabituated skuas (Ratmanoff group) may not 'need' to approach
272 humans and explore novelty since, at least at this location, the likelihood of
273 encountering man-made objects of high nutritional value is very low. Furthermore,
274 since Ratmanoff group skuas did not seem more wary than Verte group skuas in the
275 presence of the experimenter, and had not had the opportunity to form an association
276 between food and humans, we suggest that at present they lack interest in humans and
277 their objects [11].

278 The ecological relevance of the object itself (where this was judged to be the
279 highest for the plastic fish, a natural-prey-resembling stimulus) did not seem to
280 influence the decision to explore in skuas. In the Verte group, all novel objects
281 elicited pecking behaviours, a form of exploration. This finding supports previous
282 observations made on wild brown skuas, where all individuals tested at île Verte
283 pecked at both artificial and ecologically-relevant food objects [11]. Exploration of
284 novelty may result from inadvertent experimenter's cues during trials, inciting skuas
285 to peck at novel objects. However, skuas do not respond to experimenters' cues (e.g.,
286 gaze, head direction) during food-rewarded tasks [2], which makes this explanation
287 unlikely. By showing that novelty exploration is still maintained when Verte group
288 skuas are presented with novel *non-food* objects, we argue that food-mediated contact
289 with humans plays a significant role in this species' behaviour. Nevertheless, we
290 found a moderate effect of the order of objects presented. After repeated presentations,
291 longer latencies in pecking at novelty may be explained by the absence of
292 reinforcement (i.e., food). To draw firm conclusions about exploration behaviour in
293 skuas, however, further studies are required with larger sample sizes.

294 Although, at first glance, skuas' behavioural flexibility may provide them with
295 advantageous foraging opportunities, we suggest that attraction to humans and
296 novelty exploration may become detrimental for this species' survival (i) when certain
297 human interventions are administered for conservation purposes (e.g., the spreading
298 of brightly coloured poisoned pellets to eradicate introduced invasive species), or (ii)
299 in an anthropized world (due to skuas' insular-related naivety [2, 10]). Intriguingly,
300 the île Verte skuas' learning and flexibility was evident after very short fieldwork
301 durations already. Although the impact of food-human associations is still poorly
302 studied [4], skuas' learned attraction to humans and their objects is in line with
303 previous literature in various species such as bottlenose dolphins (*Tursiops* sp.) [8],
304 capuchins [5], or least chipmunks (*Tamias minimus*) [35] (see also [36]). Overall, our
305 results support the idea that rewarding humans can deeply *act* on developing
306 organisms, by affecting their attraction towards humans and responses to novelty [4].
307 More research on the effect of animal-human 'positive' interactions will provide
308 indispensable insights towards the development of conservation strategies that
309 minimise the negative consequences of wild animals' learned attraction to humans
310 and their artifacts [4, 37].

311

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316

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319

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439 **Figures and tables.**

440 **Figure legends.**

441 **Figure 1.** Novel objects and experimental set-up presented to wild brown skuas at the
442 two field sites (île Verte and Cape Ratmanoff).

443 **Figure 2.** Total number of avoidance, approach, and pecking behaviours reported for
444 both groups (Verte vs. Ratmanoff). Images at the top show the location of the two
445 field sites within the Kerguelen archipelago. Details about pecking behaviours (i.e.,
446 top: total number, down: mean latency) are also provided on the right.

447 **Tables.**

448 **Table 1.** Post-hoc tests for the fixed effects *object* (Model 3) and *object presentation*
449 *order* (Model 4).

Contrasts	Estimate \pm SE	ORs	<i>z</i>	<i>p</i>
<i>Model 3</i>				
Yellow glove – cake slice	0.331 \pm 0.817	1.39	0.405	0.913
Cake slice – plastic fish	> 0.001 \pm 0.814	1.00	0.000	1.000
Yellow glove – plastic fish	0.331 \pm 0.817	1.39	0.405	0.913
<i>Model 4</i>				
Object order 2 – object order 1	0.190 \pm 0.420	1.21	0.452	0.893
Object order 1 – object order 3	0.983 \pm 0.466	2.67	2.11	0.088
Object order 2 – object order 3	1.17 \pm 0.455	3.23	2.58	0.027

450

anthropogenic food

resembling-natural food



Cake slice



Plastic fish

anthropogenic non-food



Yellow glove



8 meters





Île Verte
n = 11



Cape Ratmanoff
n = 11

Legend



= avoid humans



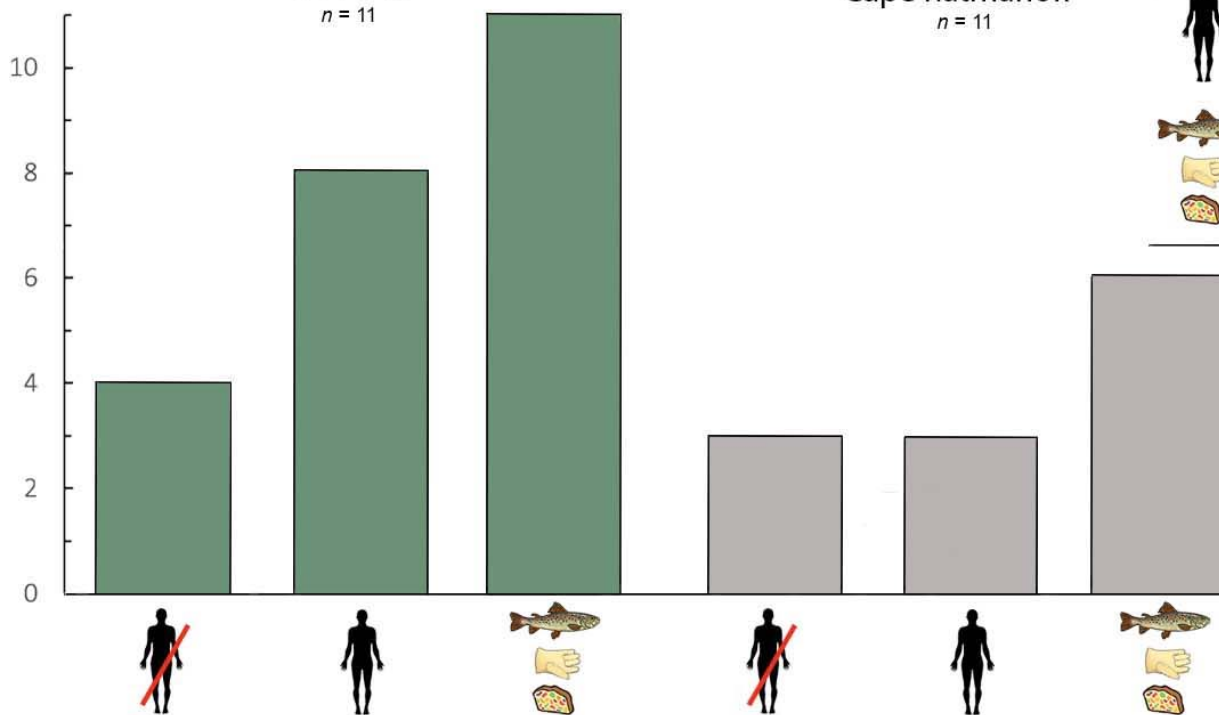
= approach humans



= explore objects



Total number of skuas



Pecking numbers

Verte	Ratmanoff
29	8

Pecking latencies

Verte	Ratmanoff
26 s	97 s