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### ► To cite this version:

Jules Brochon, G. Coureaud, Cyril Hue, Bérénice Crochu, Isabelle Charrier. Odor discrimination in terrestrial and aquatic environments in California sea lions (*Zalophus californianus*) living in captivity. *Physiology & behavior*, 2021, 235, pp.113408. 10.1016/j.physbeh.2021.113408 . hal-03367320v2

**HAL Id: hal-03367320**

**<https://cnrs.hal.science/hal-03367320v2>**

Submitted on 8 Oct 2021

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1 Odor discrimination in terrestrial and aquatic environments in California sea  
2 lions (*Zalophus californianus*) living in captivity

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9 4 Jules Brochon<sup>1</sup>, Gérard Coureaud<sup>2</sup>, Cyril Hue<sup>3</sup>, Bérénice Crochu<sup>3</sup>, Isabelle Charrier<sup>1</sup>

10  
11  
12 5  
13  
14  
15 6 <sup>1</sup> Université Paris-Saclay, Université Paris-Sud, CNRS, UMR 9197, Institut des Neurosciences  
16  
17 Paris-Saclay, 91405 Orsay, France.

18  
19  
20  
21 8 <sup>2</sup> Centre de Recherche en Neurosciences de Lyon, Bron, France

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24 9 <sup>3</sup> Zoo de La Flèche, La Flèche, France

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33  
34 12 Corresponding Authors at: Institut des Neurosciences Paris Saclay (NeuroPSI), UMR 9197  
35  
36 13 CNRS, Université Paris Sud, 91405 Orsay, France (Isabelle Charrier) and at Centre de  
37  
38 14 Recherche en Neurosciences de Lyon (CRNL), INSERM U1028, CNRS UMR 5292, Université  
39  
40 15 Claude Bernard Lyon 1, Université Jean Monnet, CH Le Vinatier Bâtiment Neurocampus, 95  
41  
42 16 Boulevard Pinel, 69675 Bron cedex (Gérard Coureaud). E-mail addresses: isabelle.charrier@u-  
43  
44  
45  
46 17 psud.fr, gerard.coureaud@cnrs.fr

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19 **ABSTRACT**

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3 20 Pinnipeds, as any mammal species, use multimodal signals, including olfactory ones, to ensure  
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5 21 vital functions. Thus, some pinniped species seem able to use olfaction in both social and  
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7 22 foraging contexts and to discriminate between different odors in air including both natural and  
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9 23 artificial odors, but studies on that topic remain scarce. Here, we studied the olfactory  
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11 24 capabilities of California sea lions living in captivity at La Flèche Zoo (France) in both  
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13 25 terrestrial and aquatic environments. We used two categories of odors: social odors (from  
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15 26 familiar individuals of the same group, unfamiliar individuals from another Zoo, animal  
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17 27 zookeepers and a terrestrial carnivore) and non-social odors (food and odors identified as  
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19 28 repellents in certain vertebrates). Several behavioral parameters were measured and analyzed  
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21 29 as the number and duration of contact with the odor, mouth openings, vocalizations (air only)  
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23 30 and air bubble production (water only). Our results, although limited by the low number of  
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25 31 animals monitored (n=5), suggest that California sea lions are able to discriminate between  
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27 32 different odors both in the air and under water. In the aquatic environment, the process allowing  
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29 33 the perception of odors remains to be characterized. Applications to this work could be  
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31 34 considered in captive conditions as well as in the wild.

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33 35 **Keywords (6):** California sea lion, *Zalophus californianus*, olfaction, discrimination, aquatic  
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35 environment, social/food odors

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## 1. Introduction

In pinnipeds, the auditory system is considered as highly developed. Indeed, the majority of pinnipeds vocalize in a variety of social contexts, and the importance of acoustic signals in social recognition has been demonstrated [1,2]. For instance, vocalizations are involved in mother-pup recognition, territorial defense and rival assessment [1,2]. Regarding olfaction, pinnipeds, like all marine mammals, have long been considered ‘microsmatic’, i.e., having a poorly developed sense of smell [3]. However, some studies conducted in captivity and in the wild have pinpointed that olfaction plays a significant role in regulating the behavior of certain pinniped species, and that some of these species (at least) may perceive and discriminate olfactory stimuli at very low concentrations [4,5]. Regarding mother-young recognition, the mother accepts or rejects the young after intense sniffing in various pinnipeds species [1,6]. It has been demonstrated in Australian sea lion (*Neophoca cinerea*) that mothers are able to discriminate the odor of their pup from that of another one [7].

Olfactory signals are also important in social interactions occurring during the reproductive period. Male New Zealand fur seals (*Arctocephalus forsteri*), for example, sniff the facial and perineal regions of females, suggesting an olfactory examination of the female’s reproductive status [8]. Chemical analyses have shown that the odors of young Australian sea lions vary with age but not depending on the sex or body region. Body odors therefore appear to carry intraspecific information [9]. In addition, there is no similarity in chemical profiles of mothers and juveniles, thus ruling out the assumption of ‘phenotype matching’ in the process of olfactory recognition of pups by their mothers in this species [10]. However, a link between chemical profiles and genetic proximity has been found in Antarctic fur seal (*Arctocephalus gazella*) mother-pup pairs [11]. Moreover, it has been shown in Australian sea lions that the chemical profiles of individuals from two distinct colonies were different [10] and under the influence of the environment and/or genetic variability (even close colonies show high genetic variability

63 [12]). In addition to its involvement in social behavior, olfaction seems to be used by some  
64 pinnipeds in their search for food. Thus, harbor seals (*Phoca vitulina*) find areas of high forage  
65 value by using odor cues for spatial orientation and food detection [4,13].

66 Cape fur seals (*Arctocephalus pusillus pusillus*) discriminate between different  
67 monomolecular odors [14] and are able to memorize an odor stimulus that became significant  
68 by learning, even a few weeks after learning exposure. Another study highlighted that the sense  
69 of smell plays an underestimated role in regulating the behavior of these animals since it has  
70 been shown that these fur seals are able to discriminate between aliphatic odor [5]. A recent  
71 study also indicates that adults and sub-adults can discriminate between the odors of an adult  
72 male and a non-specific control odor, i.e., the odor of an alga present in the environment  
73 (Charrier et al., unpublished data).

74 While on land some pinnipeds appear to use olfaction to display a diversity of behaviors,  
75 the use of this sensory modality has never been demonstrated in the aquatic environment.

76 In this context of major gaps that still exist in the literature concerning olfactory capabilities  
77 of pinnipeds and their role both in the context of foraging and social interactions, the aim of our  
78 study was to test and compare, in terrestrial as in aquatic environments, the ability of captive  
79 California sea lions (1) to discriminate between food, social and repellent odors, and (2) to  
80 initiate the assessment of the use of olfaction under water. We carried out the experiments on  
81 captive animals, knowing the limits and advantages related to this context, in order to obtain  
82 results which could allow us in the future to continue this study in a natural environment and  
83 thus to have a comparative approach.

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## 85 **2. Materials and methods**

### 86 *2.1 Animals and housing conditions*

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87 Five captive-born California sea lion (*Zalophus californianus*) males (one intact and four  
88 castrated) living at La Flèche Zoo (La Flèche, France) were involved in our experiments. The  
89 sea lions had two separate enclosures at the zoo, one for the day and one for the night. They  
90 were locked into their indoor enclosure before the closure of the park (5:30 p.m. during the  
91 period of our study, conducted in February-March 2020). This building consists of a medical  
92 room where training and treatments were carried out as well as six individual pens. Animals  
93 went to their outdoor enclosure in the morning if the weather allowed it. Their outdoor facility  
94 comprised a concrete beach and a chlorinated pool.

95 In addition, the animals returned to their indoor enclosure daily in the afternoon to be taken  
96 out individually, or in pairs, to participate in training. During these daily trainings, which lasted  
97 about 20 minutes per sea lion, animals were rewarded with fish and received petting and  
98 praising from their zookeepers. During the day, animals were fed individually (in the indoor  
99 enclosure or during training) and collectively (several times a day). The food varied according  
100 to the season: fatty fish in winter (*Clupea harengus*) and lean fish in summer (*Merlangius*  
101 *merlangus*), but animals could also get sprat or roach in their rations. The amount of fish  
102 distributed per day varied from one individual to another (depending on their weight weekly  
103 checked).

104 This present study complies with the European Union Directive on the Protection of Animals  
105 Used for Scientific Purposes (EU Directive 2010/63/EU) and also with current French laws.  
106 Animal husbandry and care were under the management of the animal zookeepers of La Flèche  
107 Zoo, France.

108  
109 *2.2 Odor stimuli*

110 The tested odors were of animal, human or vegetal origin. All were collected and presented  
111 on sterile compresses (Mercurochrome, 20x20 cm, 100% cotton) by the experimenter or one  
112 zookeeper wearing nitrile gloves. The three types of odor used were:

113 - Animal odors collected a) from the California sea lions at La Flèche Zoo and from other  
114 California sea lions, castrated and intact males and females, at Beauval Zoo (France): the  
115 zookeepers rubbed the animal's head, neck and body with a sterile compress during 45s in  
116 the morning in the outdoor facility; b) from the male tiger (*Panthera tigris*) at La Flèche  
117 Zoo: the zookeepers rubbed during 30s with one hand the tiger's body through the enclosure  
118 fence as it approached; c) from herring (oily fish much appreciated by sea lions) and whiting  
119 (lean fish less appreciated): the experimenter rubbed the compress during 45s directly on  
120 thawed fish defrosted for 10 min intended for feeding the animals.

121 - Human odors collected from two of the four zookeepers dedicated to the sea lions at La  
122 Flèche Zoo. In our first experimental session, the zookeepers rubbed a sterile compress on  
123 their own face, neck and underarms during 30s. In our second session, two of the zookeepers  
124 wore a 100% cotton white t-shirt the night before the experiment. The t-shirts were collected  
125 in the morning and kept in an individual plastic bag until the experiment (3-4h later).

126 - Vegetal odors from organic essential oils of camphor (Herbes et Traditions, France) and  
127 black pepper (Pranarôm, France) known to trigger repulsion in terrestrial mammals  
128 [common vole (*Microtus arvalis*) and snowshoe hare (*Lepus americanus*)] [15,16] but also  
129 in a pinniped species, the harbor seal (Campagna S., personal observations): the  
130 experimenter poured 5 drops of essential oil on a sterile compress.

131 The collected odors were either used directly in the experiments or stored in the freezer in  
132 Ziploc bags for further presentations. Freezing was considered to allow a long-term odor  
133 retention with minimal degradation [17,18].

134 All these odors were separated into two categories: social odors (sea lion, tiger and zookeeper  
135 cues) and non-social odors (food/attractive and vegetal/repellent cues). Within the social odors,  
136 some were considered as familiar (California sea lion from La Flèche Zoo and their  
137 zookeepers), others as unfamiliar (California sea lion from Beauval Zoo, Saint Aignan, France,  
138 and the tiger from La Flèche Zoo). Among the familiar odors, those of the two zookeepers were  
139 sub-divided into "zookeeper 1", who was the first to be recruited in the aquatic team at La  
140 Flèche zoo (12 years of seniority) and "zookeeper 2", who was the last to be recruited in the  
141 team (3 years of seniority). Finally, the odors of the five sea lions were also divided into two  
142 categories as follows: "affinity -" vs. "affinity +" when the odor was from a group member with  
143 which the target animal displayed the least vs. the most affiliative interactions according to the  
144 zookeepers, respectively.

### 2.3 Experimental set-up

147 Animals were tested in two types of environment, terrestrial and aquatic. Two sessions (session  
148 1 and session 2) were carried out, 18 days apart, in order to limit the animals' habituation to the  
149 experimental devices and testing procedure.

150 In the aerial environment, 14 conditions were tested during session 1: 10 conditions with one  
151 target odor vs. water (herring, whiting, zookeeper 1, zookeeper 2, familiar conspecific,  
152 unfamiliar conspecific, pepper, camphor, affinity -, tiger vs. water) and 4 conditions with two  
153 target odors (herring vs. whiting, zookeeper 1 vs. zookeeper 2, familiar vs. unfamiliar, affinity  
154 - vs. affinity +). The "familiar vs. water" condition was identical to the "affinity + vs. water"  
155 condition.

156 During session 2, 6 conditions were tested: 1 condition with a single target odor (camphor vs.  
157 water) and 5 with two target odors (herring vs. whiting, zookeeper 1 vs. zookeeper 2, familiar



158 vs. unfamiliar, affinity - vs. affinity +, herring vs. herring + camphor). All experiments took  
1 place in the indoor enclosure, in each sea lion individual pens.

160 During session 1, the experimenter placed the compress impregnated with the target odor or  
161 control odor (pool water) at the end of a small metal rod (35 cm \* 5 cm) previously cleaned  
162 with alcohol. The compress was attached to the metal rod with a clamp, which was also cleaned  
163 with alcohol. The rod was then presented to the animal through the bars of its lodge for 30s  
164 after the animal's first contact with the compress. The animals had the opportunity of direct  
165 physical contact with the compress but they could not remove it from the rod. Each animal was  
166 tested with the two stimuli of a same condition sequentially. The order of odor presentation was  
167 random for each condition but remained the same for all animals in the session. The time  
168 interval between the two stimuli presentations was 30s. In session 2, the target and control odors  
169 were presented simultaneously to the animal at the end of two identical metal rods, each odor  
170 being separated by 40 cm. The position of the target and control odor, right or left, was  
171 randomly chosen but remained the same for all animals in the session.

172 In the aquatic environment, 2 conditions were tested during session 1 only, with one odor (water  
173 vs. herring, water vs. familiar). Conditions with food odors were carried out during session 2,  
174 but unfortunately without exploitable results. The experiments took place in the outdoor pool.  
175 The protocol was the same as in the terrestrial environment, except that the animal was tested  
176 in the presence of a zookeeper for safety reasons. The experimenter stood at the edge of the  
177 pool with the metal rod just below the water surface and the zookeeper joined him with the  
178 animal; the zookeeper remained close to the experimenter without giving any order to the  
179 animal. We expected that sea lions would approach the device by curiosity. Their behavior was  
180 then observed for 30s after the first contact with the compress. Within a test, the time interval  
181 between the two stimuli presentations was 30s. Each condition involved the five sea lions.  
182 Regardless of the environment, individuals were tested separately one after the other in a

183 random order, and they were tested twice a day with at least a 4-hour interval (morning and  
184 afternoon) for each session in a random environment (either in the air in the morning and in the  
185 water in the afternoon or conversely). The compresses were changed between each animal. The  
186 experimental device was cleaned with water between each animal and cleaned with alcohol  
187 between each testing condition. Animals were not rewarded following the experiment, but at  
188 the end of the session after all animals have been tested.

189

#### 190 *2.4 Behavioral responses*

191 The olfactory discrimination abilities of the sea lions in both terrestrial and aquatic  
192 environments were studied by quantifying several behavioral parameters recorded during the  
193 tests: the number and total duration a) of snout contacts with the compress, b) of vocalizations  
194 (terrestrial environment only), c) of bubble production (aquatic environment only), and d) of  
195 mouth openings. These variables were quantified *a posteriori*, during the analysis of video  
196 sequences recorded (GoPro Hero 3 camera) throughout the duration of the tests. Each 30-sec  
197 video was analyzed frame by frame using Avidemux software.

198 During session 1, the camera was attached to one end of the metal rod, with the compress  
199 attached at the other end, and thus the head of the animal was clearly visible on the video.  
200 During session 2, the camera was attached to the experimenter's chest so that the two  
201 compresses were in the camera field.

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#### 203 *2.5 Statistics*

204 The statistical analyses were performed using RStudio (R version 3.5.0). A PCA analysis was  
205 performed on our 6 behavioral parameters [number and duration of contacts, vocalizations (air

206 only), bubble production (aquatic only), mouth openings]. This allowed us to obtain a  
207 composite score of the behavioral response for each test performed on each individual. These  
208 composite scores were then used in mixed linear models as a "response" variable, allowing us  
209 to compare the responses obtained with the control odors to those obtained with the target odors,  
210 but also to compare the responses between two target odors. The odors, the odor categories  
211 (human, animal, vegetal) and categories of odor tests (social, non-social) were coded as "fixed  
212 factors". The order of presentation and individuals were coded as "random factors" to take into  
213 account repeated measures. Interactions between these different factors were implemented in  
214 the model or removed from the model if not significant (the model was then recalculated). When  
215 a significant effect was obtained, post-hoc tests were carried out by running the same models  
216 with data subsets allowing paired comparisons and sequential Bonferroni corrections were  
217 applied to account for multiple comparisons (Holm's procedure).

218

### 219 **3. Results**

220 All the behavioural responses obtained during our different tests can be found in Supplementary  
221 Table 1.

#### 222 *3.1 Tests in the terrestrial environment*

223 In the aerial environment, the PCA indicated that PC1 (first principal component) explained  
224 66.3% of the variability and had an eigenvalue > 1. The PC1 scores obtained for each test were  
225 therefore used for further analysis. Moreover, all behavioral variables were positively correlated  
226 to PC1 with the same magnitude (0.37 to 0.44). Strong reactions were therefore represented by  
227 positive and high PC1 scores.

228 Analysis of the composite scores showed that the factor interaction "odor x test type" was non-  
229 significant ( $\chi^2 = 2.75$ ,  $p = 0.6$ ), but odor ( $\chi^2 = 114.22$ ,  $p < 0.001$ ) and test type ( $\chi^2 = 90.58$ ,  $p <$

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2 230 0.001) showed a significant effect on the responses. Since the test type had a significant effect,  
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4 231 the data were analyzed separately for each of them.

5 232 *3.1.1 Session 1*

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8 233 Post-hoc analyses between the two odors of the same category revealed significant differences,  
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10 234 even after Bonferroni - Holm corrections (Figure 1A, B, C).

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14 235 The responses displayed by sea lions to food odors (fish) were significantly stronger than those  
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16 236 displayed to our control (water;  $\chi^2 > 35.38$ ,  $p < 0.001$ ) (Figure 1A). Responses to human odors  
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18 237 were also significantly stronger compared to water ( $\chi^2 > 9.24$ ,  $p < 0.01$ ). Concerning responses  
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20 238 to other animal odors, those displayed towards tiger odor did not differ significantly compared  
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22 239 to water ( $\chi^2 = 0.01$ ,  $p = 0.91$ ). For the tests involving odors from conspecifics, behavioral  
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24 240 responses to “affinity - “were weak and not significantly different from water ( $\chi^2 = 1.72$ ,  $p =$   
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26 241  $0.57$ ) but responses to familiar and unfamiliar odors were significantly higher or tended to be  
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28 242 higher than those to the control (familiar vs. water:  $\chi^2 = 6.26$ ,  $p = 0.06$ ; unfamiliar vs. water:  $\chi^2$   
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30 243  $= 15.90$ ,  $p < 0.001$ ) (Figure 1B, C). For plant odors, the results did not reveal any significant  
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32 244 differences in responsiveness with the control (camphor or pepper vs. water:  $\chi^2 < 3.26$ ,  $p$  values  
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34 245  $> 0.28$ ) (Figure 1D).

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51 249 Post-hoc analyses on PC1 scores for the two-odor tests did not reveal any significant differences  
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53 250 (affinity - vs. affinity +:  $\chi^2 = 2.21$ ,  $p = 0.28$ ; familiar vs. unfamiliar:  $\chi^2 = 0.49$ ,  $p = 0.49$ ;  
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55 251 zookeeper 1 vs. zookeeper 2:  $\chi^2 = 3.00$ ,  $p = 0.27$ ; herring vs. whiting:  $\chi^2 = 3.35$ ,  $p = 0.27$ ) (Figure  
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57 252 2). However, before applying the Bonferroni-Holm correction, PC1 scores tended to be higher  
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253 for the odor of herring compared to those of whiting ( $p = 0.07$ ) as well as for the odor of  
254 zookeeper 1 compared to those of zookeeper 2 ( $p = 0.08$ ).

Please, insert Figure 2 here

### 3.1.2 Session 2

259 Post-hoc analyses on PC1 scores (Figure 3A, B) showed that only the behavioral responses  
260 obtained with herring were significantly stronger than those obtained with herring + camphor  
261 ( $\chi^2 = 0.02$ ,  $p = 0.02$ ) (Figure 3A).

262 The responses obtained for all other tests (Figure 3A, B) were not found significantly different  
263 (herring vs. whiting:  $\chi^2 = 1.21$ ,  $p = 1.00$ ; water vs. camphor:  $\chi^2 = 0.02$ ,  $p = 1.00$ ; affinity - vs.  
264 affinity +:  $\chi^2 = 1.24$ ,  $p = 1.00$ ; familiar vs. unfamiliar:  $\chi^2 = 0.18$ ,  $p = 1.00$ ; zookeeper 1 vs.  
265 zookeeper 2:  $\chi^2 = 0.38$ ,  $p = 1.00$ ).

Please, insert Figure 3 here

### 3.2 Tests in the aquatic environment

270 In the aquatic environment, only 3 out of 5 sea lions approached our experimental device (metal  
271 rod) and were thus included in our analysis. Two conditions were tested: water vs. familiar and  
272 water vs. herring. During the odor investigations, the number and duration of contacts did not  
273 vary between the target odors (familiar or herring) and the water (Figure 4A). However, while

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2 274 the number of contacts did not vary significantly between the herring odor and water, the  
3 275 duration of contacts for herring was nearly three times longer than for water (Figure 4B).

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5 276 During the tests, we also observed some animals' production of bubbles and openings of the  
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7 277 mouth. The mouth opening occurred twice during the presentation of herring odor for one  
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9 278 individual, while the bubble production was observed for two sea lions with a total of 6  
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11 279 occurrences (3 in response to water, 2 to herring and 1 to the familiar odor).

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13 280 Due to the small number of animals approaching our device (n=3), no statistical tests could be  
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15 281 done on these data. However, according to our observations and the PC scores, the behavioral  
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17 282 responses to herring seemed to be stronger than to water (Figure 5A, B). In contrast, no clear  
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19 283 difference was observed between the responses displayed to the familiar odor and to water.

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#### 33 34 35 287 **4. Discussion**

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38 288 Our study aimed to determine whether captive California sea lions displayed spontaneous  
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40 289 behavioral responsiveness or preferences for certain odors depending on their nature/category  
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42 290 and the medium in which the odor stimuli were presented (air vs. water). The results showed  
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44 291 that California sea lions responded strongly to some odors, both in the air and under water,  
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46 292 demonstrating effective olfactory abilities for social and non-social odors.

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#### 50 51 52 294 *4.1 Odor perception in the air*

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295 In the aerial environment, when a fish odor - herring or whiting in our conditions - was  
296 presented sequentially to the individuals (session 1), one of the responses that we considered as  
297 behaviorally relevant, i.e., vocalizations, was significantly more often displayed by sea lions  
298 than during presentation of the control stimulus (water); this was not observed for any other  
299 odor stimulus compared to water (Figure 6).

Please, insert Figure 6 here

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Sea lions appear therefore able, as expected, to selectively respond to fish using olfaction. Interestingly, the behavioral variable contributing the most to the fish vs. water discrimination was their vocal production and not sniffing (i.e., olfactory investigation) as we should have expected. Moreover, vocalizations were only produced by the sea lions during the presentation of fish odors, and can be interpreted as a high-motivation trait. According to the zookeepers, the sea lions have a preference for herring, an oily fish, over whiting, a lean fish. Although this preference did not emerge significantly in our experiments, one may note that when the two with odors were presented sequentially, vocalizations were only observed for herring. Further trials including additional individuals would thus be necessary to corroborate this preference. Such food preference illustrated by stronger behavioral responsiveness to the preferred fish smell suggests that pinnipeds could use olfactory cues during foraging activities. Laska and colleagues (2008) demonstrated that captive Cape fur seals were able to discriminate the odors of two different fish mixtures, whatever these mixtures were highly different (i.e., from different species) or weakly different (i.e., one with, one without fish oil). These findings clearly illustrate their sharp sense of smell. Another study, on captive harbor seals, showed a high sensitivity for atmospheric DMS, a marker of high primary productivity [4]. The perception and discrimination among fish odors in air and/or under water would thus benefit pinnipeds to orient their foraging investigations and also to identify the preferred preys during their foraging trips at sea.

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320 Concerning the vegetal odors considered as "repellent" in other mammal species including a  
321 pinniped one, the harbor seal (Campagna S., personal observations), the group of sea lions  
322 involved in our study did not show distinct responsiveness to camphor or pepper vs. water.  
323 Camphor and pepper may not have a strong repellent value for California sea lions. Both these  
324 tested essential oils are known to have trigeminal properties in mammals. The trigeminal system  
325 is differently activated depending on the nature of the odorants: some are very active even at  
326 low concentration while others need very high concentration to activate this system [19]. When  
327 trigeminal activation occurs, odorants may generate different sensations such as "freshness"  
328 (peppermint, eucalyptus), "pain" (vinegar, acetone) or "warmth" (alcohol, cinnamon) [19,20].  
329 These sensations are linked to specific trigeminal receptors activated by specific odorants [21].  
330 In California sea lions, the lack of strong and clear repellent effects of camphor and pepper  
331 observed here suggests that the trigeminal system may not be activated by these odors, at least  
332 at the concentrations used in our conditions, or that the trigeminal system is not involved for  
333 olfactory assessment in this species. Further investigations using different concentrations of  
334 camphor and pepper, as additional olfactory-trigeminal odors, would be needed to conclude on  
335 the effective role of the trigeminal system on olfactory abilities in pinnipeds.

336 Another possible explanation of this absence of repellent effect is that the two stimuli were  
337 tested at the end of our experimental sessions. Therefore, the animals were putatively habituated  
338 to the procedure and this habituation effect may have impacted their responsiveness.

339 However, and interestingly, the results from the "fish vs. fish + camphor" condition used in  
340 session 2 highlighted that camphor may actually have a negative hedonic value in California  
341 sea lions since animals displayed a reduced response to the herring with camphor odor. Without  
342 having a powerful repellent value by itself in California sea lions, camphor essential oil could  
343 therefore have a negative effect when it is paired with an attractive food odor. This effect could  
344 be the result of interactions between molecules from the repellent and the food. Again, a more



345 in-depth study on that question would be useful to determine the putative repellent effect of  
1  
2 346 camphor in California sea lions and if this effect is effective over prolonged periods. Indeed, a  
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5 347 recent study has shown that the use of a chemical repellent, HaTe<sub>2</sub>, spread on plants is not  
6  
7 348 effective over time against a terrestrial mammal, the fallow deer (*Dama dama*) [22].  
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9  
10 349 The use of odors as pinniped repellents could have applications in the field, particularly to  
11  
12 350 prevent depredation caused by pinnipeds in aquaculture farms or in fishing traps [23], and thus  
13  
14 351 to limit their impact on fisheries – an impact experienced as very negative by fishermen.  
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17 352 The presentation of the odor of another carnivore, here a tiger (*Panthera tigris tigris*), did not  
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20 353 trigger particular responsiveness in sea lions. This clearly indicated that, in our conditions, sea  
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22 354 lions did not react to any odors presented in contrast to water. Here, this unfamiliar animal odor  
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25 355 did not appear to have any relevance to them. In the future, it will be interesting to test pinnipeds  
26  
27 356 for their responsiveness to odors from biologically relevant species such as competitor or  
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30 357 terrestrial predator. For instance, Cape fur seals could be tested with the odors of jackals or  
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32 358 hyenas, known to constitute some of their terrestrial predators [24].  
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35 359 Within the group of sea lions monitored at La Flèche Zoo, affinities between the five animals  
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38 360 were established and mostly based on their seniority at the zoo. While some individuals  
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40 361 displayed agonistic interactions between each other, in particular the animals called Tanguy  
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43 362 and Wally, this kind of interactions remained rare. This may thus explain the absence of  
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45 363 significance in their behavioral responses when they were tested with both odors "affinity +"  
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48 364 vs "affinity-". More data would be useful to further investigate the link that may exist between  
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50 365 odor-guided behavior and degree of affinity/dominance among conspecifics in these pinnipeds.  
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53 366 Similarly, when tested with familiar and unfamiliar conspecific odors, the sea lions reacted  
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55 367 significantly more often to both odors compared to water, but no significant difference was  
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58 368 observed when these odors were presented in the same session (in sequential or simultaneous  
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60 369 testing). This result was quite surprising as we expected that sea lions from La Flèche Zoo  
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370 would have shown a stronger reaction to the odor of unfamiliar individuals for instance, but this  
1  
2 371 was not the case. Social olfactory communication is used in pinnipeds in several interactions,  
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4 372 and it has been experimentally shown that Australian sea lion mothers discriminate between the  
5  
6 373 odor of their filial pup and those of non-filial pups [7]. Another study on Australian sea lions  
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8 374 had shown that animals from two different breeding colonies presented different chemical  
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10 375 profiles, which are related to both genetic and environmental differences [9]. Therefore, the  
11  
12 376 absence of such discrimination observed in our conditions could be explained by the fact that  
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14 377 the odors of familiar and unfamiliar individuals were considered as equally attractive to the  
15  
16 378 tested animals. It is also possible that our low sample size, a loss or change in odor quality  
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18 379 related to the freezing/thawing of our samples can have led to the lack of significant behavioral  
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20 380 responses. However, the freezing/thawing effect is unlikely since our samples triggered animal  
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22 381 responses when tested vs. water. Moreover, testing samples were frozen for 3-4 weeks only  
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24 382 while other studies conducted in Australian sea lions [9,10] and polar bears [18] showed a very  
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26 383 good conservation of odors during freezing and after thawing, even after several weeks or years.  
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29 384 Finally, considering the responsiveness of sea lions to human odors, our results pinpoint that  
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31 385 animals were able to discriminate between zookeepers' odors and water, regardless of how long  
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33 386 the zookeeper have been working at the zoo, with higher responsiveness to them. Since no  
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35 387 significant differences were displayed in the sequential or simultaneous presentation of the  
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37 388 odors of the two zookeepers, sea lions might not react to one zookeeper more than the other  
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39 389 based only on the sense of smell. Nevertheless, and interestingly, even if the result was not  
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41 390 statistically significant, animal responsiveness to zookeeper 1 (the one who has been working  
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43 391 at the zoo for the longest time) tended to be higher than to zookeeper 2 (recently recruited)  
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45 392 during the sequential presentation of these odors. Such responsiveness to human odors deserves  
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47 393 also to be further assessed, for instance by comparing the odors of sea lions' zookeepers vs.  
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49 394 zookeepers of other animals from the same zoo and/or vs. unfamiliar people (i.e., not working  
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395 at the zoo). If sea lions display a positive and preferred responsiveness to their own zookeepers'  
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2 396 odors, these stimuli could be used as positive cues to reduce the stress of the animals in certain  
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5 397 situations such as veterinary procedures or transport.  
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#### 11 399 *4.2 Odor perception under water*

14 400 In pinnipeds, the use of olfaction in the aquatic environment can not follow the same perceptual  
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16 401 processes as in the air since the animals cannot “sniff” under water, at risk of drowning. In some  
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19 402 other species such as the star-nosed mole (*Condylura cristata*) or the American water-shrew  
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21 403 (*Sorex palustris*), the use of olfaction under water is based on the production of air bubbles,  
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24 404 which are exhaled on objects of interest or on chemical tracks, and then inhaled by the animals  
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26 405 through the nose [25]. During our underwater experiment, we observed the production of air  
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29 406 bubbles via the nostrils during the test with herring, and also during the presentation of the  
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31 407 familiar odor and the water control. One may therefore assume that sea lions could detect and  
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33  
34 408 perceive odor stimuli under water by producing air bubbles towards an odor stimulus, which  
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36 409 would then be recaptured by the nostrils or the mouth. However, during our experiment, we  
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39 410 did not observe any case of re-inhalation of air bubbles via the mouth or the nostrils. Pinnipeds  
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41 411 do not breathe under water, but they might exhale or inhale the bubbles produced when in  
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43 412 contact with olfactory stimuli. Another possibility is that they might perceive the odor when the  
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45  
46 413 emitted bubbles pierce the surface of the water. Anyway, the interest displayed by sea lions for  
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48 414 the herring odor in our condition pinpoints their ability to perceive certain odor cues in the  
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51 415 aquatic environment. However, this interest might have been triggered by taste perception  
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53 416 rather than by odor. Further investigations are required to clearly determine whether bubble  
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56 417 sniffing could be used by some semi-aquatic mammals, such as pinnipeds.  
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419 *4.3 Issues with the method and animal welfare*

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3 420 In the wild, pinnipeds show high level of curiosity for novelty, approaching and sniffing any  
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5 421 new elements contained in the environment. This may have dramatic consequences when, for  
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8 422 instance, it led animals to become entangled in plastic debris (fishing lines and nets, plastics...)  
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10 423 [23]. When we started this study, we assumed that this natural curiosity of sea lions would  
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13 424 guarantee the interest in, and approach to, our experimental devices. Surprisingly, the animals  
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15 425 showed actually only a weak attention for our experimental devices, even though they were  
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18 426 introduced in their daily environment. This lack of interest in exploration of new elements  
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20 427 added in the environment may be a consequence of captivity or a consequence of a lack of  
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23 428 interest in enrichments. To stimulate their sea lions, zookeepers from La Flèche Zoo regularly  
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25 429 enrich the environment with ice cubes, balls, floating platform, food, but they have noticed that  
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27 430 the animals can get bored very quickly depending on the enrichment. In this context, the use of  
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30 431 odor enrichment may be relevant to improve attention of sea lions for novel objects, at least  
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32 432 during the periods of the day when they are not in contact with their zookeepers. To this end,  
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35 433 offering new, multi-sensory objects like floating platforms or submerged structures, on which  
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37 434 familiar sea lion sounds are broadcast and odors from familiar food or social sources, or from  
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40 435 the sea lions' natural environment are diffused could be developed. Moreover, it would be  
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42 436 interesting to test the response to novelty of captive sea lions from other zoos, which have less  
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45 437 training and/or contact with zookeepers than those from La Flèche Zoo, in order to determine  
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47 438 if the daily presence of the zookeepers reduces the attention of the animals to other stimuli than  
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50 439 those used in the training. Furthermore, familiar or unfamiliar odors could be directly used to  
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52 440 enrich the environment. Indeed, it was showed in California sea lions that the introduction of  
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54 441 different odors (i.e., familiar odors: soil, sand, kelp and sardine oil; unfamiliar odors: orange,  
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57 442 banana, vanilla extract and cinnamon) caused an increase in habitat utilization with less time  
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59 443 spent in the water [26] and, consequently, a reduction in the majority of stereotypical behaviors  
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2 445 [26]. A solution to enrich the environment and improve the attention of sea lions for novel  
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4 446 objects could then be to introduce odorized objects during training periods, and to encourage  
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7 447 zookeepers to promote interactions of sea lions with novel objects as targets to play with, in  
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9 both the indoor and the outdoor environments.

10 448 Finally, the lack of differential behavioral responses towards the majority of stimuli  
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12 449 combinations tested in this study might be the results of the experimental approach, based on  
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14 450 spontaneous preferences and aversions. Therefore, these results do not allow us to draw firm  
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17 451 conclusions as to the perceptual or discriminatory limits of their sensory system, but at least  
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19 452 they gave us some ideas for future directions. To deeply examine the olfactory abilities of  
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22 453 pinnipeds in-air and under water, we have for instance planned to run operant conditioning  
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24 454 procedures that have been successfully used in pinnipeds [4,5,14] and that could help us to  
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27 455 validate our hypotheses.

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### 31 32 33 457 **Acknowledgments**

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36 458 All animal zookeepers at La Flèche zoo involved in this study are gratefully acknowledged for  
37  
38 459 their help and support. We would also like to thank the animal zookeepers and Baptiste Mulot  
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41 460 at Beauval zoo for their contribution. This study was funded by CNRS (IC, GC, JB) and the  
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43 461 CNRS-IRP program SoCNetMM "Social Communication Network in Marine Mammals".  
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544 **Figures legends**

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3 545 Fig. 1: Boxplots of PC1 scores based on (A) food tests, (B) human tests, (C) animal test and  
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5 546 (D) repellent tests with a single experimental odor during the first session in the aerial  
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8 547 environment. The fat horizontal line indicated the median; the upper and lower limit of the box  
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10 548 itself represented the third and the first quartiles; and whiskers indicated the maximum and the  
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12 549 minimum value. Finally, the asterisk represented a significant difference in the behavioural  
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15 550 responses between two tested odors (significant level at  $p < 0.05$ ).

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21 552 Fig. 2: Boxplots of PC1 scores according to the tests carried out with 2 odors during the first  
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24 553 session in the aerial environment. The fat horizontal line indicated the median; the upper and  
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26 554 lower limit of the box itself represented the third and the first quartiles; and whiskers indicated  
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29 555 the maximum and the minimum value.

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35 557 Fig. 3: Boxplots of PC1 scores based on (A) food and repellent tests and (B) social tests during  
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37 558 the second session in the aerial environment. The fat horizontal line indicated the median; the  
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40 559 upper and lower limit of the box itself represented the third and the first quartiles; and whiskers  
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42 560 indicated the maximum and the minimum value. Finally, the asterisk represented a significant  
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45 561 difference in the behavioural responses between two tested odors (significant level at  $p < 0.05$ ).

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48 562  
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51 563 Fig. 4: Barplots of (A) the numbers of contacts and (B) duration of contacts according to the  
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54 564 tests carried out and the odors tested under water.

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566 Fig. 5: Boxplots of the (A) PC1 scores and (B) PC2 scores according to the tests carried out and  
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2 567 the odors tested under water. The fat horizontal line indicated the median; the upper and lower  
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4 568 limit of the box itself represented the third and the first quartiles; and whiskers indicated the  
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7 569 maximum and the minimum value.  
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10 570

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13 571 Fig. 6: Boxplots of the numbers of vocalizations based on (A) food tests, (B) human tests, (C)  
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16 572 animal test and (D) repellent tests with a single experimental odor during the first session in the  
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18 573 aerial environment. The fat horizontal line indicated the median; the upper and lower limit of  
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20  
21 574 the box itself represented the third and the first quartiles; and whiskers indicated the maximum  
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23 575 and the minimum value.  
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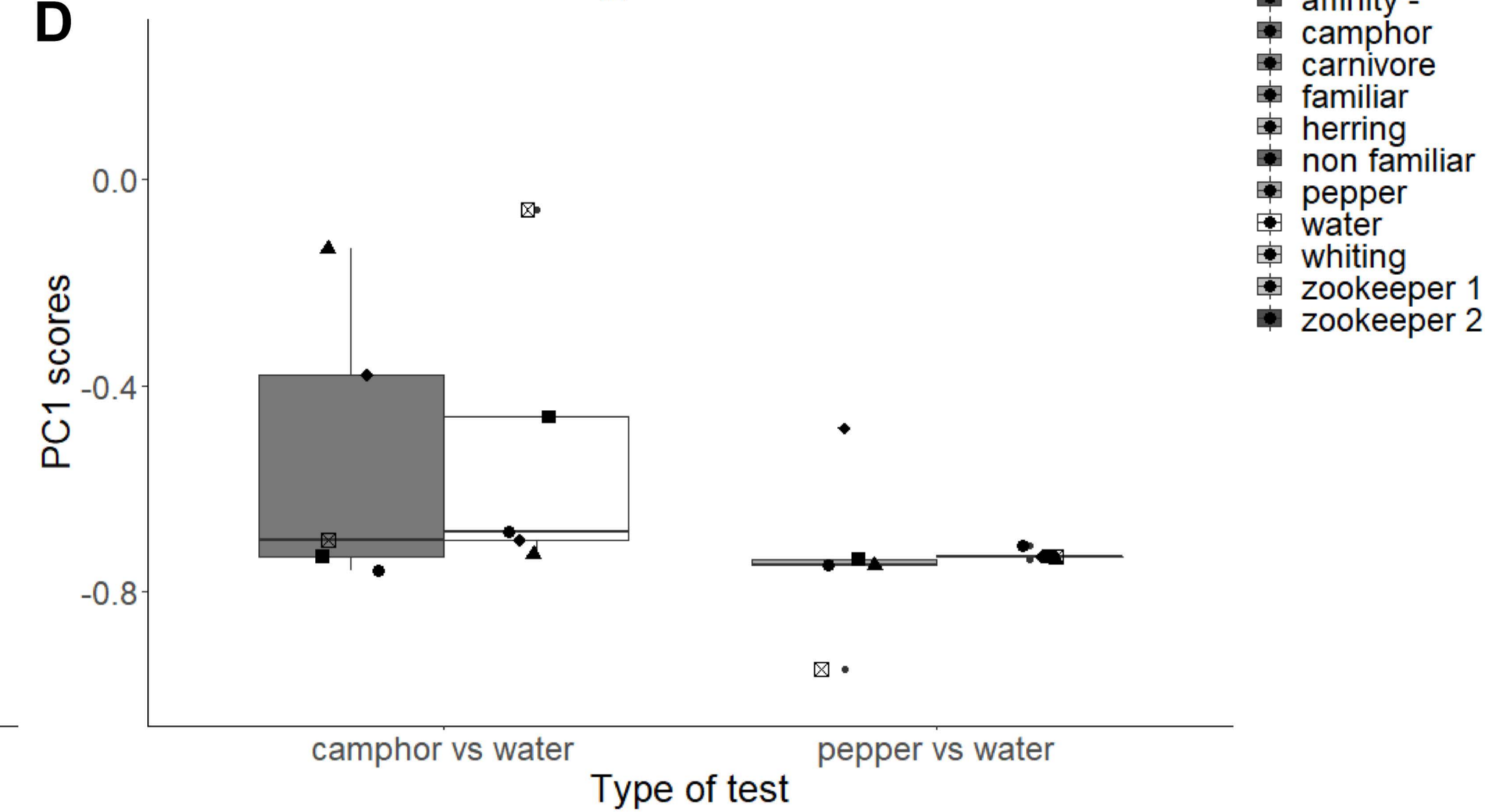
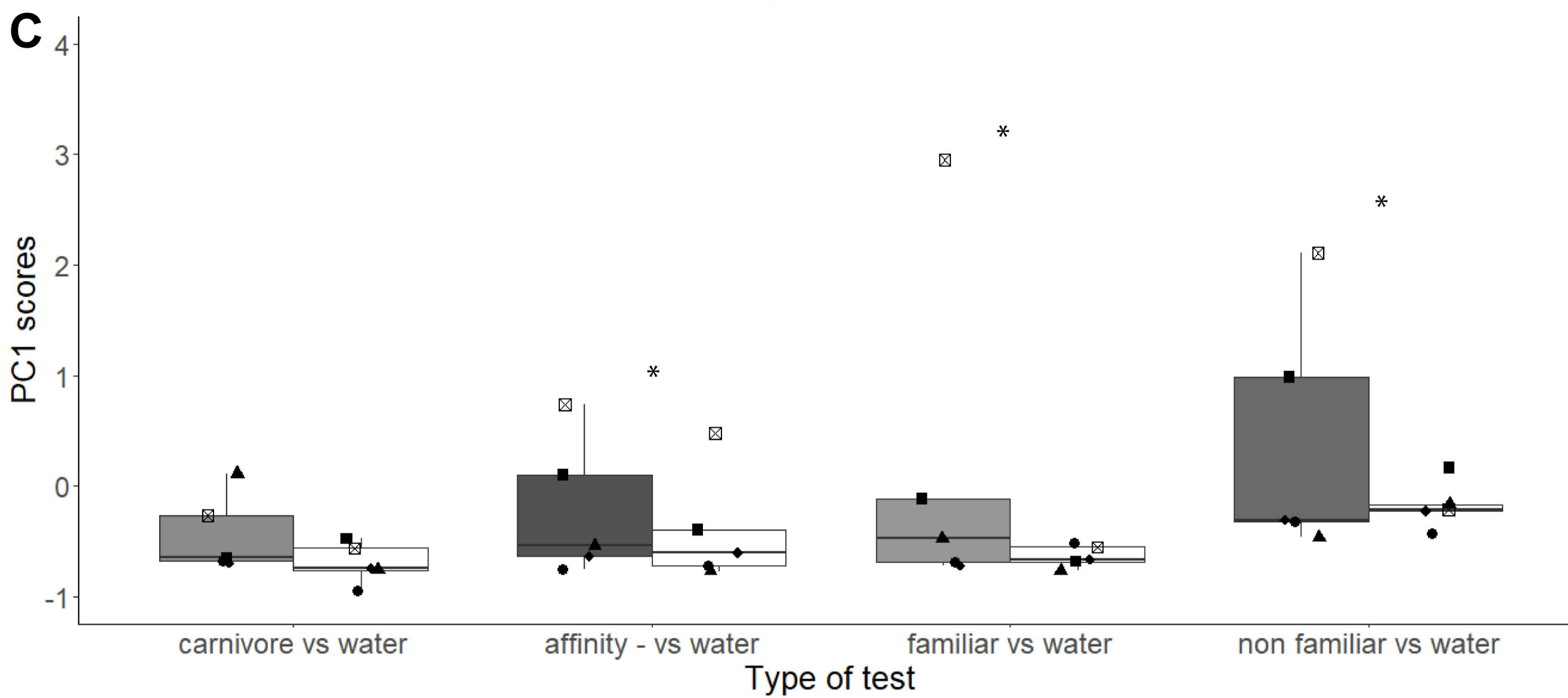
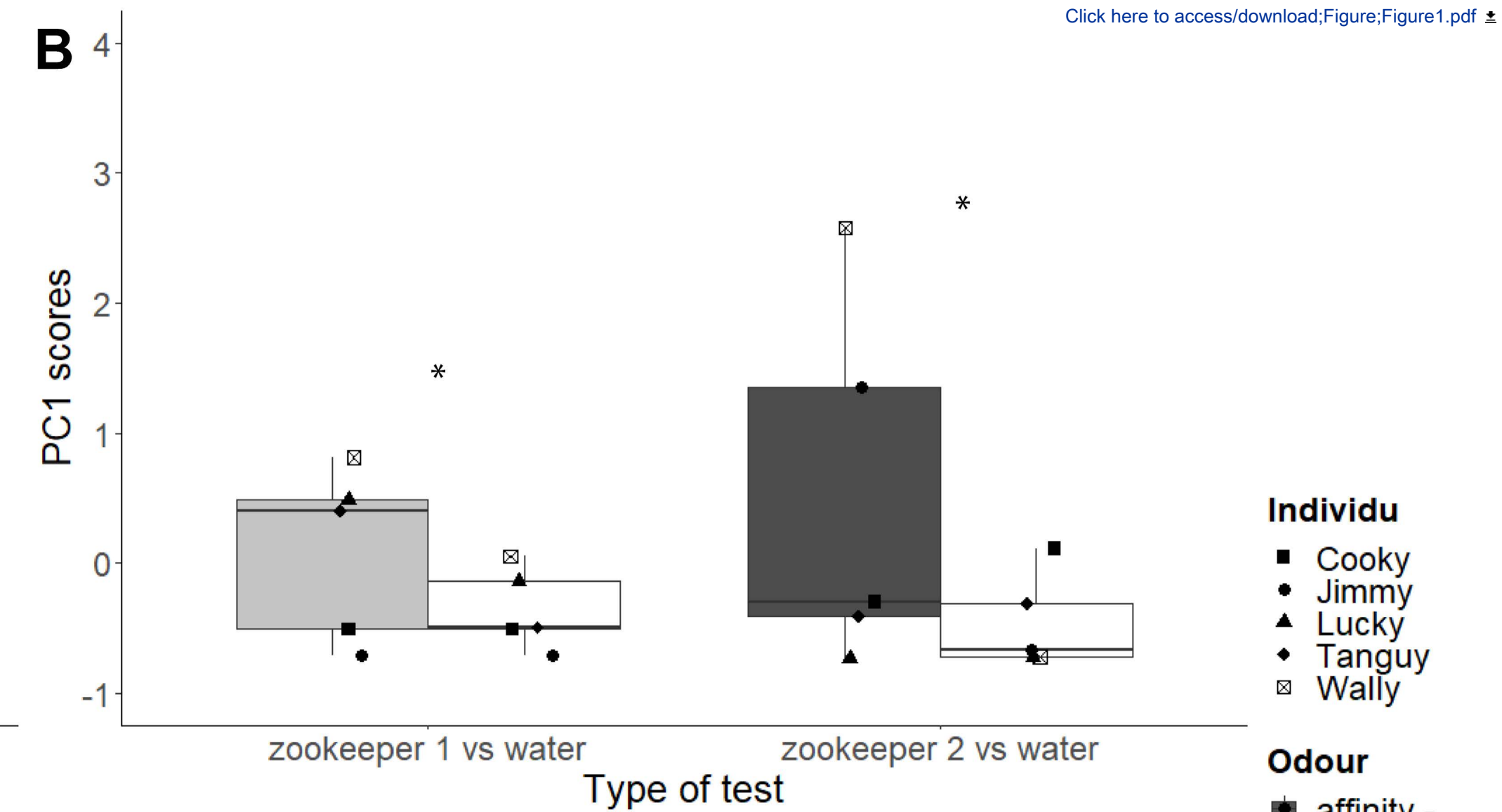
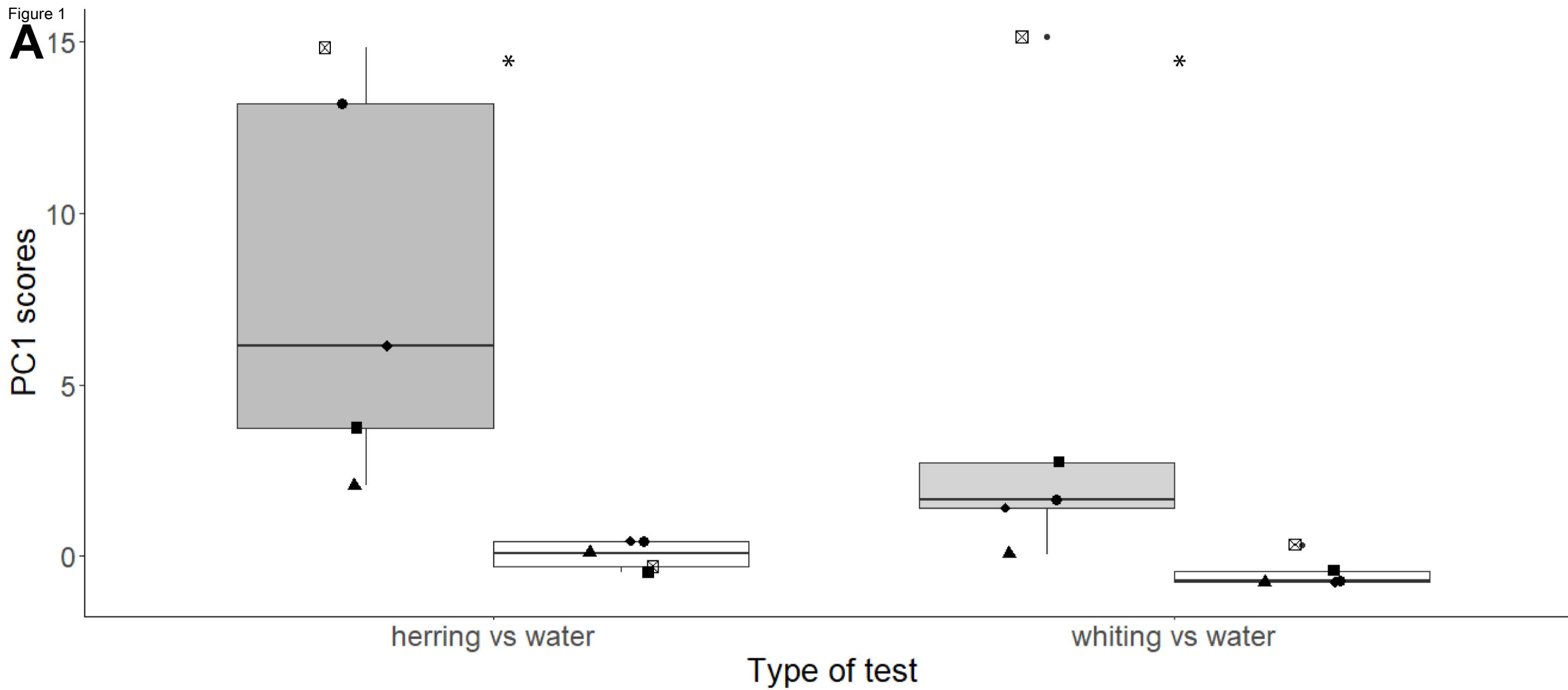
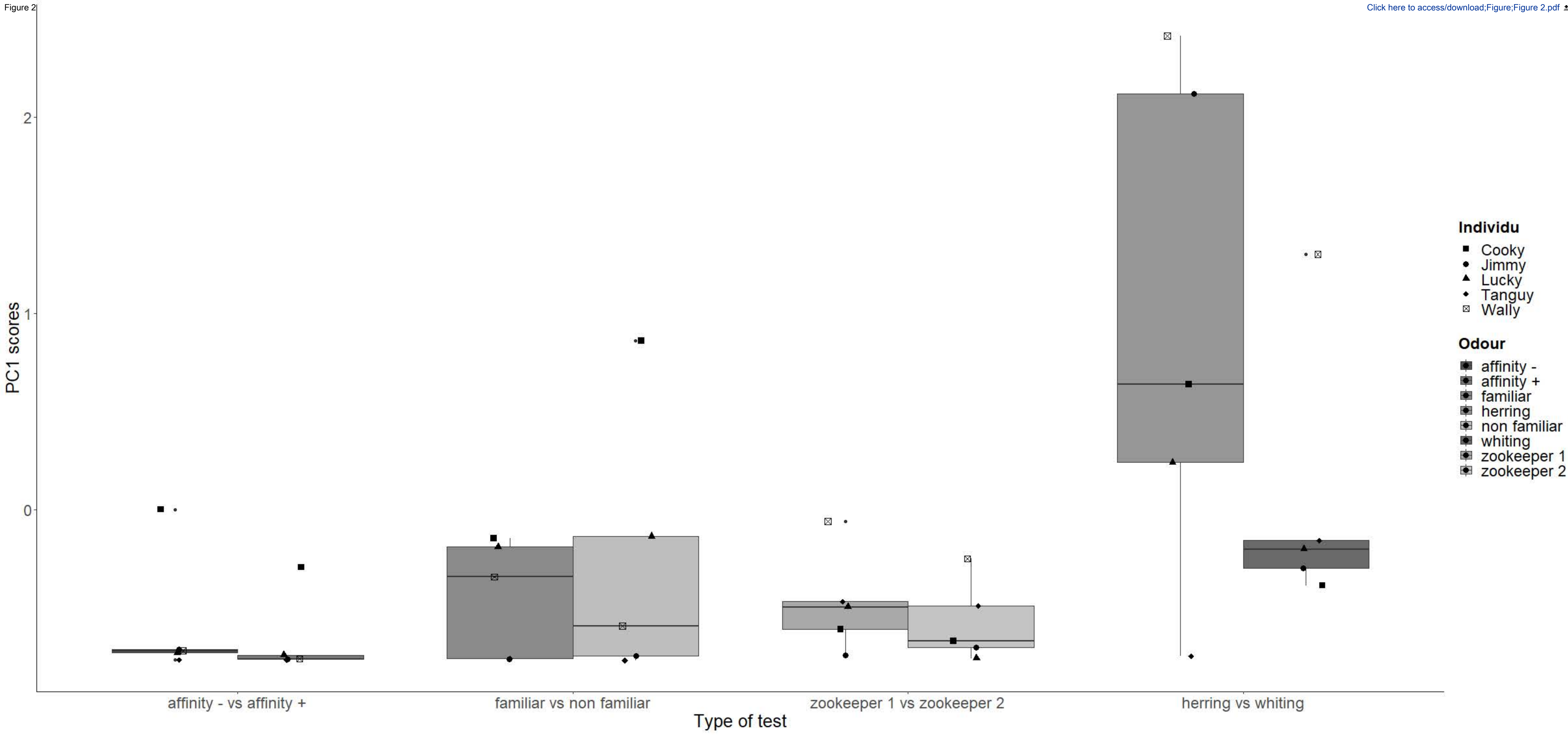
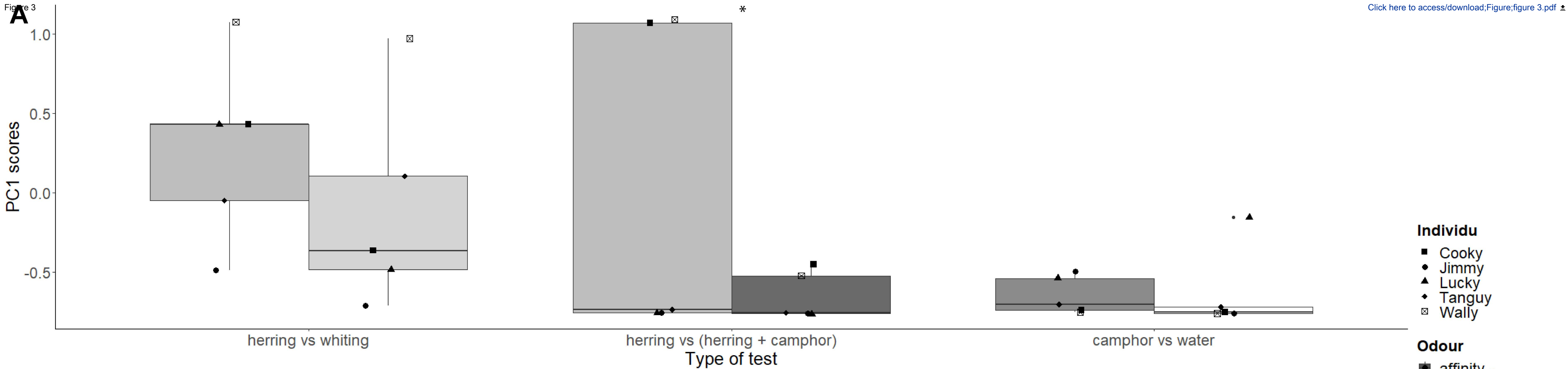


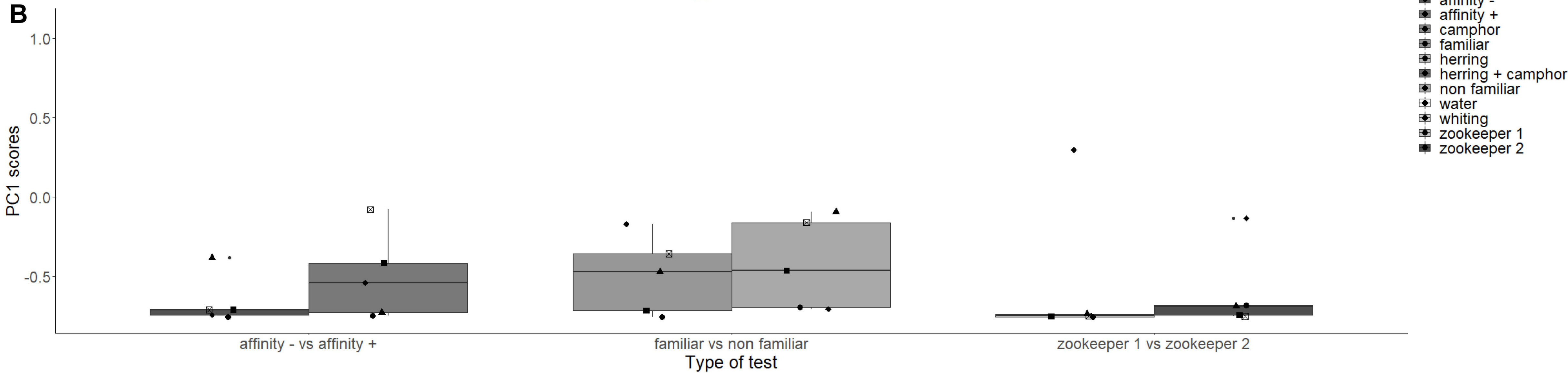
Figure 2

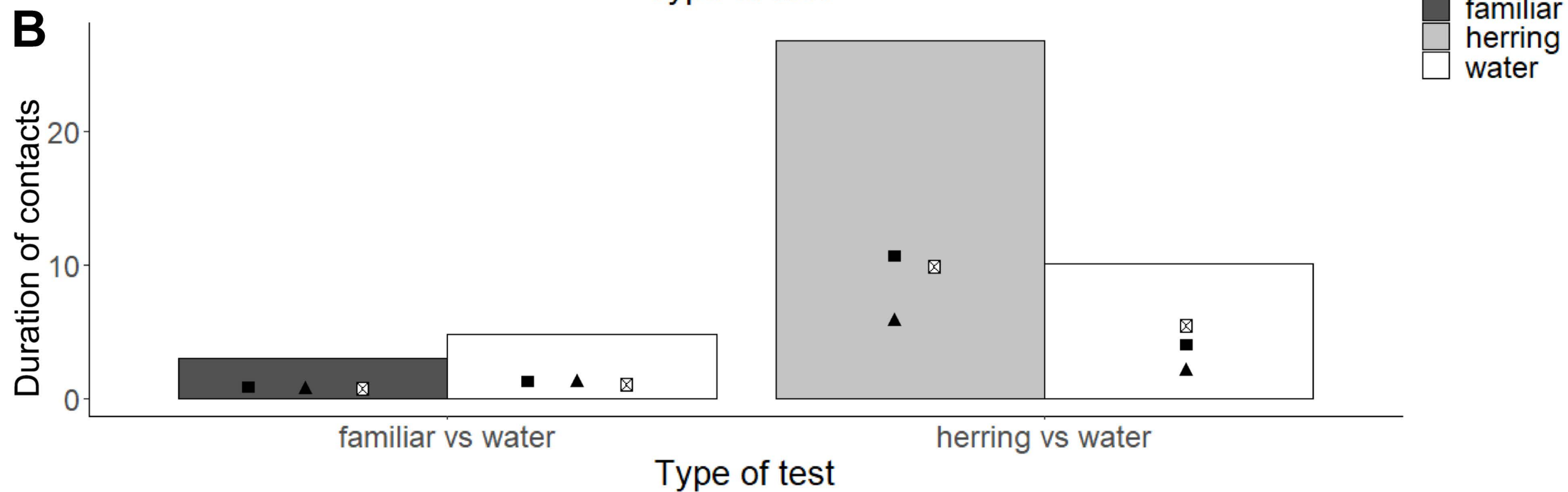
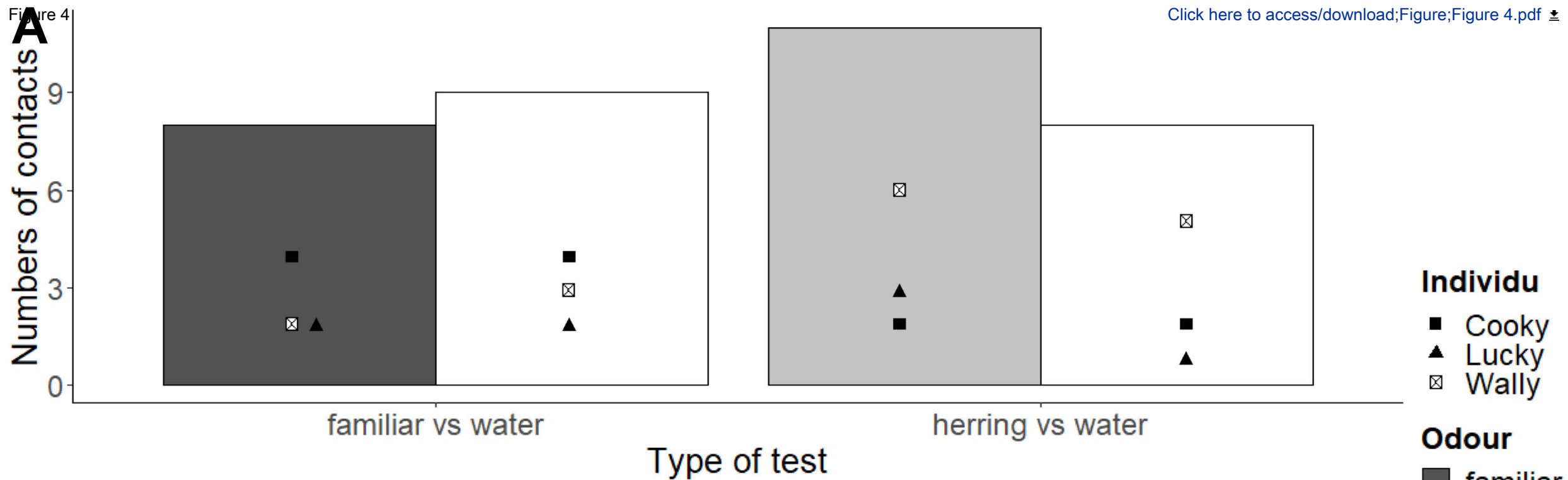


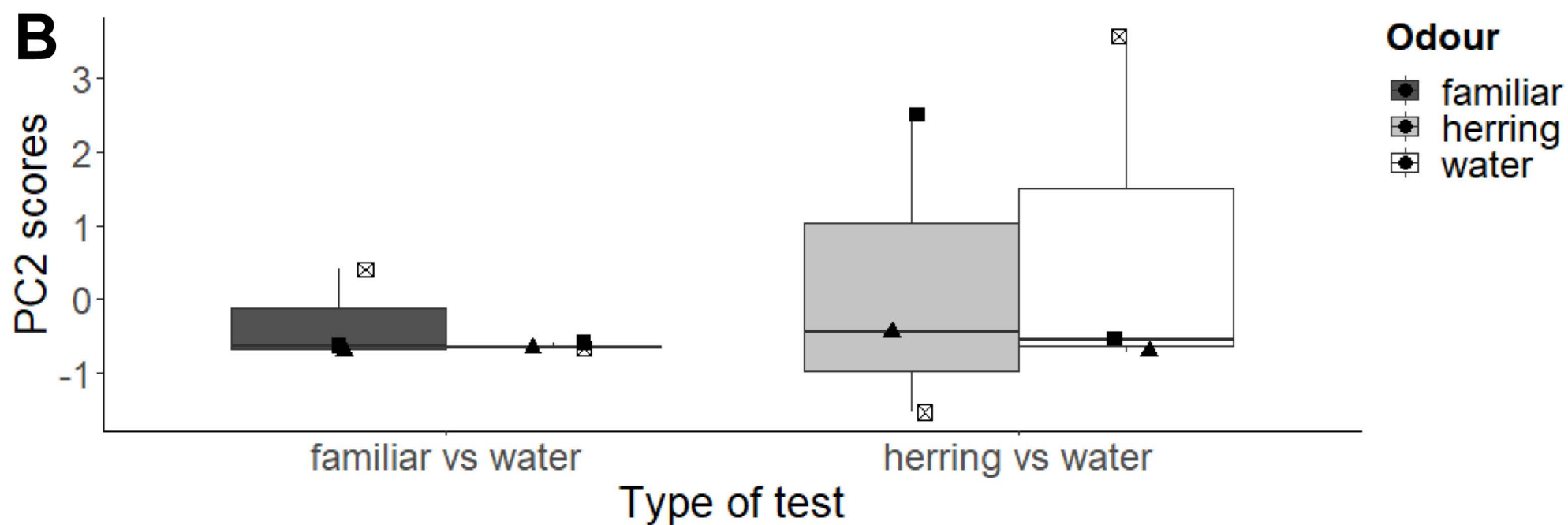
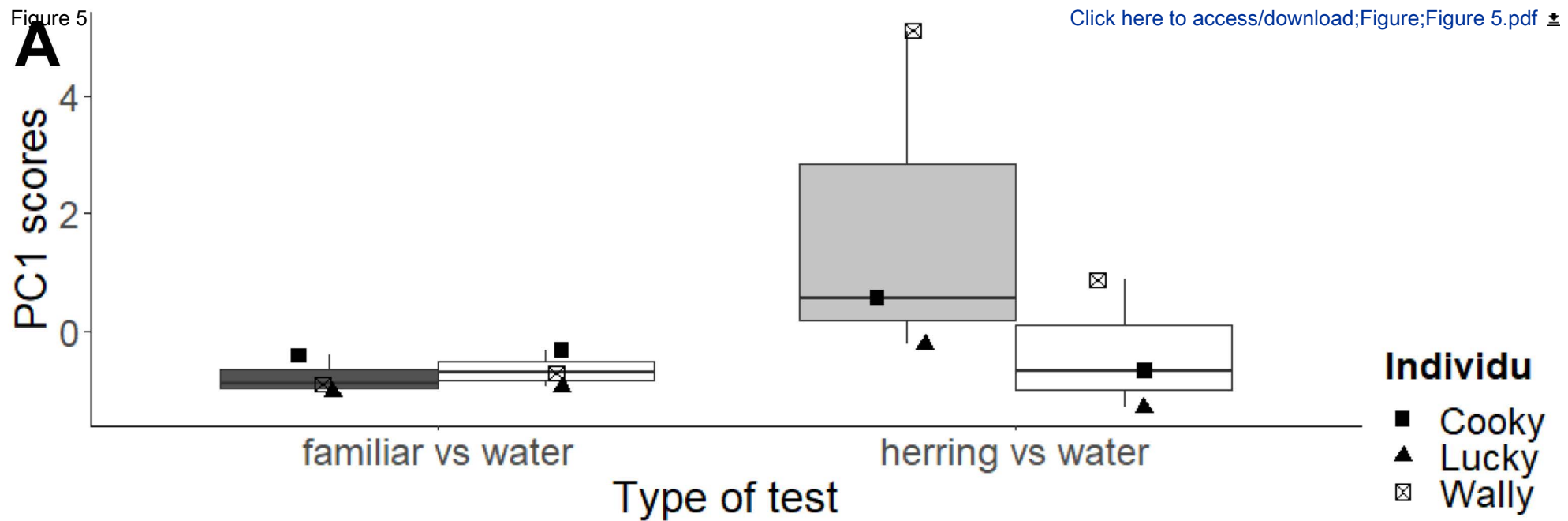
**A**



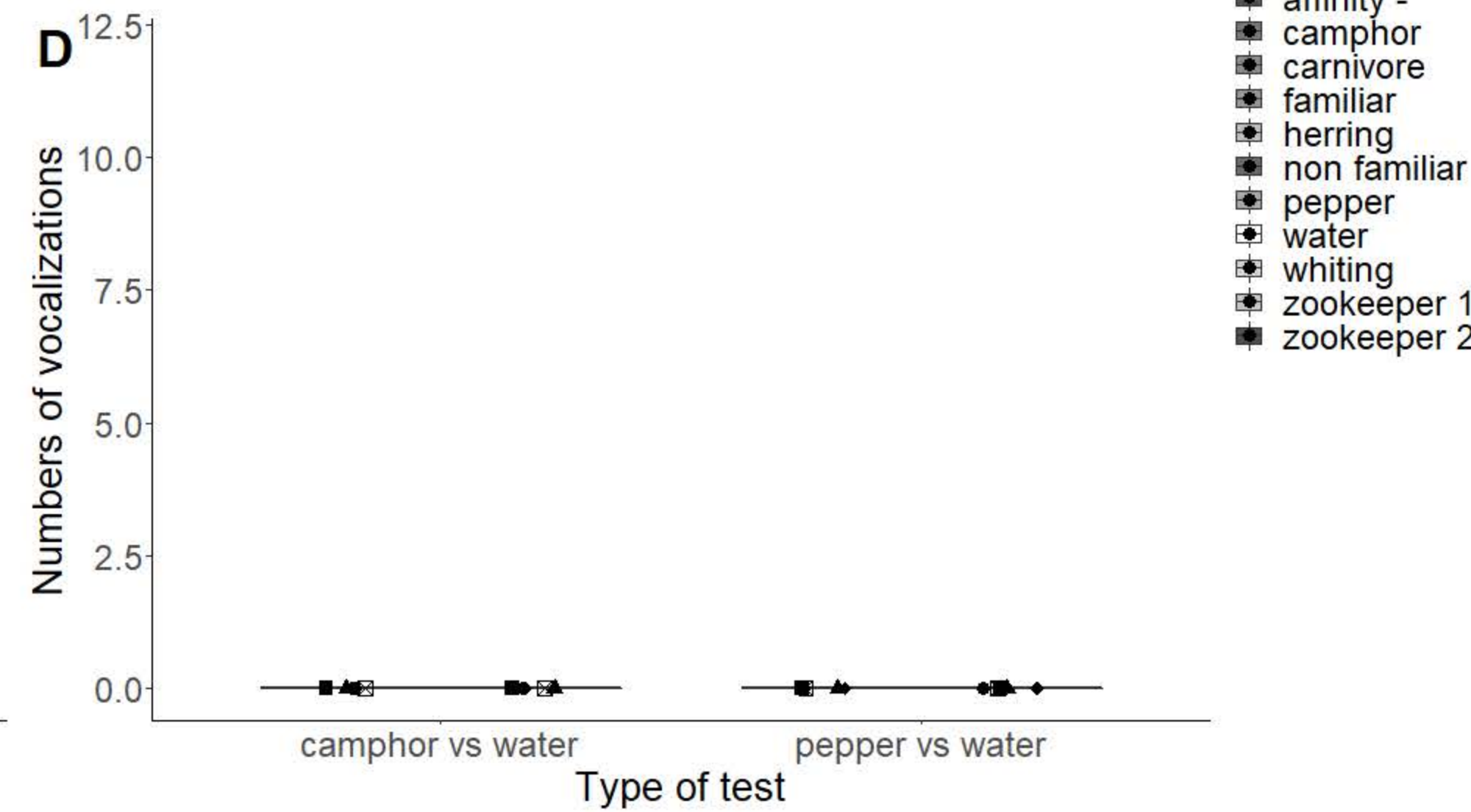
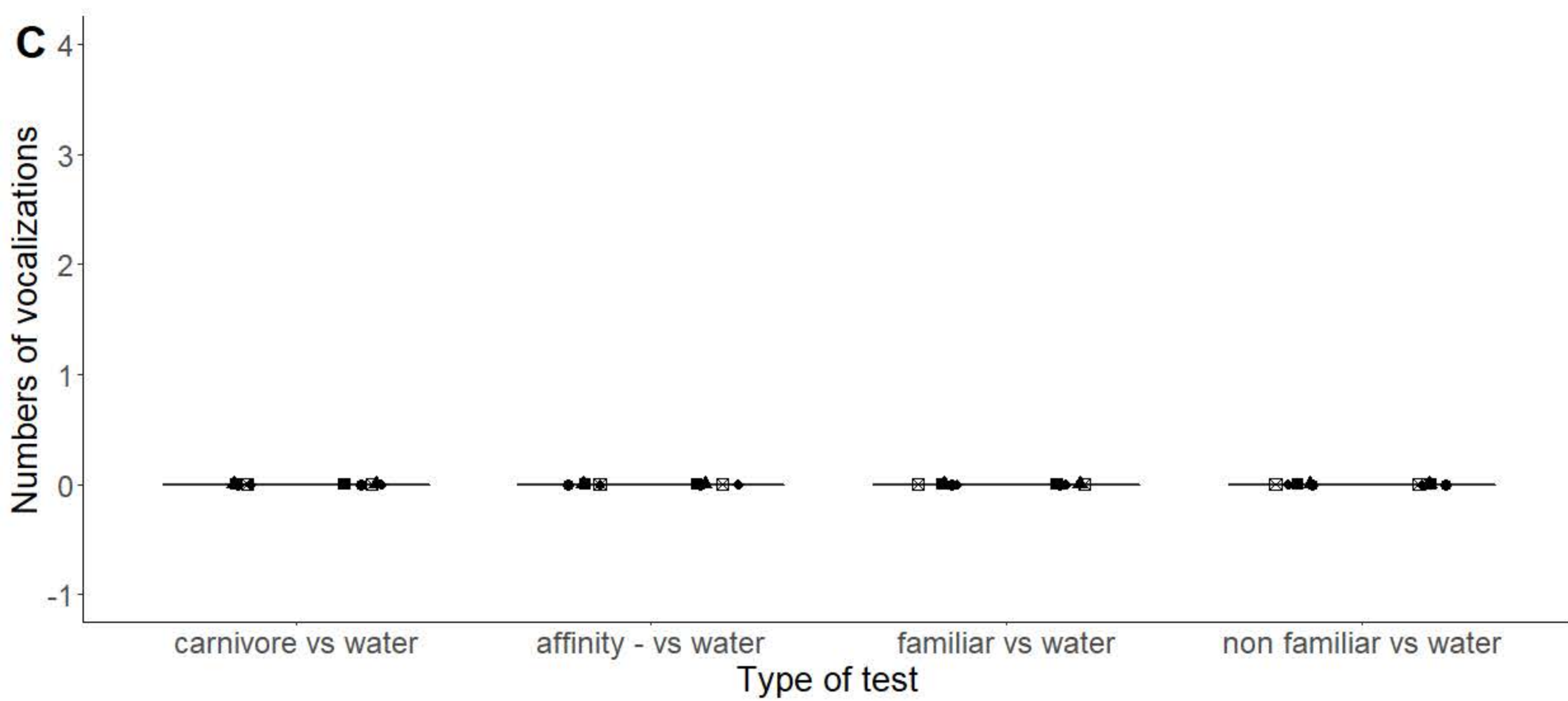
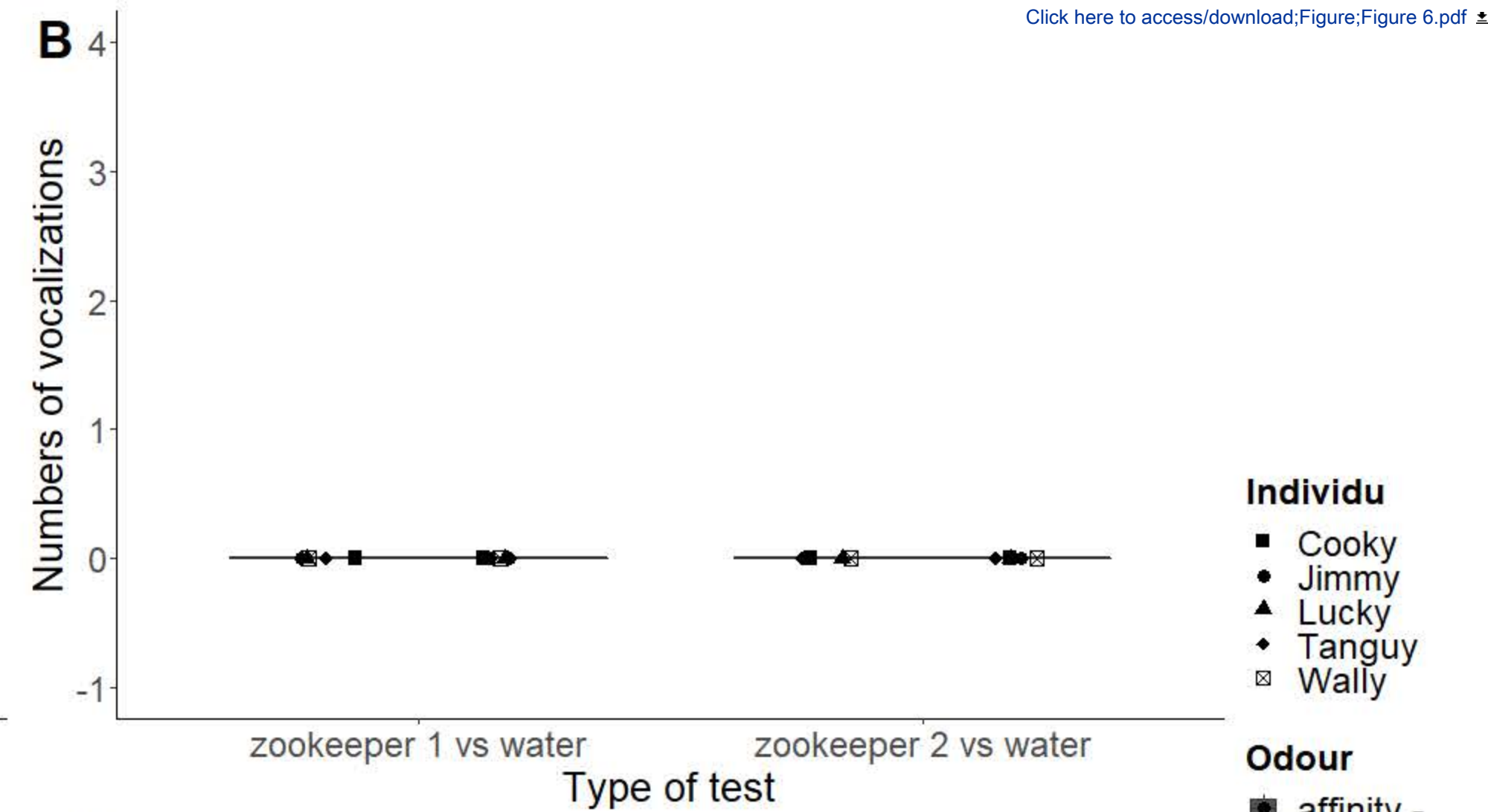
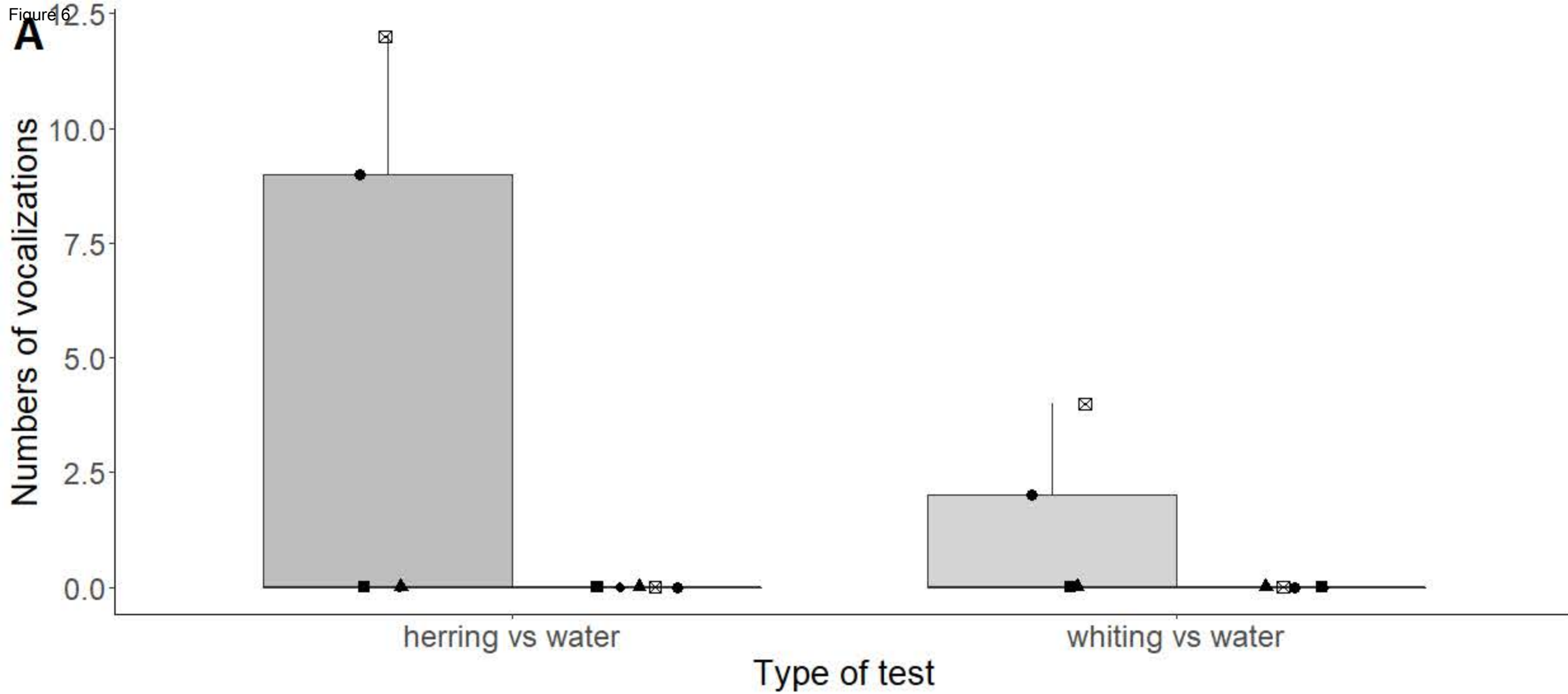
**B**











**Individu**

- Cookie
- Jimmy
- ▲ Lucky
- ◆ Tanguy
- ⊠ Wally

**Odour**

- affinity -
- camphor
- ▲ carnivore
- ◆ familiar
- ⊠ herring
- non familiar
- pepper
- ▲ water
- ◆ whiting
- ⊠ zookeeper 1
- zookeeper 2

Supplementary Table 1

[Click here to access/download;Table;Charrier\\_suppl\\_Table1.docx](#)

Individual	Session	Environment	Type of experience	Odour	Type of test	Type of odour	Numbers of contacts	Contact duration (s)	Percentage of contacts (%)	Vocalizations	duration of vocalizations (s)	Mouth opening	duration of mouth opening (s)	duration of bubble production (in s)	Nb of Bubble production events
Wally	1	aerial	1 odour	water	herring vs water	non-social	3	0,9796	3,27	0	0	0	0	NA	NA
Wally	1	aerial	1 odour	herring	herring vs water	non-social	10	12,51	41,71	12	7,677	6	1,084	NA	NA
Cooky	1	aerial	1 odour	water	herring vs water	non-social	1	2,294	7,65	0	0	0	0	NA	NA
Cooky	1	aerial	1 odour	herring	herring vs water	non-social	11	10,51	35,03	0	0	1	0,584	NA	NA
Jimmy	1	aerial	1 odour	water	herring vs water	non-social	5	3,922	13,07	0	0	0	0	NA	NA
Jimmy	1	aerial	1 odour	herring	herring vs water	non-social	12	14,89	49,64	9	10,468	2	0,983	NA	NA
Tanguy	1	aerial	1 odour	water	herring vs water	non-social	6	2,668	8,89	0	0	0	0	NA	NA
Tanguy	1	aerial	1 odour	herring	herring vs water	non-social	5	18,6	62	0	0	4	1,125	NA	NA
Lucky	1	aerial	1 odour	herring	herring vs water	non-social	3	18,98	63,25	0	0	0	0	NA	NA
Lucky	1	aerial	1 odour	water	herring vs water	non-social	4	2,628	8,76	0	0	0	0	NA	NA
Cooky	1	aquatic	1 odour	herring	herring vs water	non-social	2	10,97	36,56	NA	NA	0	0	1,085	2
Cooky	1	aquatic	1 odour	water	herring vs water	non-social	2	3,962	13,21	NA	NA	0	0	0	0
Jimmy	1	aquatic	1 odour	water	herring vs water	non-social	NA	NA	NA	NA	NA	NA	NA	NA	NA
Jimmy	1	aquatic	1 odour	herring	herring vs water	non-social	NA	NA	NA	NA	NA	NA	NA	NA	NA
Wally	1	aquatic	1 odour	herring	herring vs water	non-social	6	10,64	35,45	NA	NA	2	0,416	0	0
Wally	1	aquatic	1 odour	water	herring vs water	non-social	5	4,63	15,43	NA	NA	0	0	1,627	3
Lucky	1	aquatic	1 odour	water	herring vs water	non-social	1	1,501	5	NA	NA	0	0	0	0
Lucky	1	aquatic	1 odour	herring	herring vs water	non-social	3	5,172	17,24	NA	NA	0	0	0	0
Tanguy	1	aquatic	1 odour	herring	herring vs water	non-social	NA	NA	NA	NA	NA	NA	NA	NA	NA
Tanguy	1	aquatic	1 odour	water	herring vs water	non-social	NA	NA	NA	NA	NA	NA	NA	NA	NA
Cooky	1	aerial	1 odour	water	non familiar vs water	non-social	4	3,211	10,7	0	0	0	0	NA	NA
Tanguy	1	aerial	1 odour	water	non familiar vs water	non-social	3	1,543	5,14	0	0	0	0	NA	NA
Cooky	1	aerial	1 odour	non familiar	non familiar vs water	social	5	8,133	27,11	0	0	0	0	NA	NA
Tanguy	1	aerial	1 odour	non familiar	non familiar vs water	social	2	2,248	7,49	0	0	0	0	NA	NA

Jimmy	1	aerial	1 odour	water	non familiar vs water	non-social	2	1,292	4,31	0	0	0	0	NA	NA
Wally	1	aerial	1 odour	water	non familiar vs water	non-social	3	1,626	5,42	0	0	0	0	NA	NA
Lucky	1	aerial	1 odour	water	non familiar vs water	non-social	3	2,002	6,67	0	0	0	0	NA	NA
Jimmy	1	aerial	1 odour	non familiar	non familiar vs water	social	2	2,127	7,09	0	0	0	0	NA	NA
Wally	1	aerial	1 odour	non familiar	non familiar vs water	social	4	2,127	7,09	0	0	3	0,333	NA	NA
Lucky	1	aerial	1 odour	non familiar	non familiar vs water	social	2	1,043	3,48	0	0	0	0	NA	NA
Cooky	1	aquatic	1 odour	water	familiar vs water	non-social	4	1,834	6,11	NA	NA	0	0	0	0
Cooky	1	aquatic	1 odour	familiar	familiar vs water	social	4	1,084	3,61	NA	NA	0	0	0	0
Wally	1	aquatic	1 odour	water	familiar vs water	non-social	3	1,251	4,17	NA	NA	0	0	0	0
Wally	1	aquatic	1 odour	familiar	familiar vs water	social	2	0,918	3,06	NA	NA	0	0	0,375	1
Jimmy	1	aquatic	1 odour	water	familiar vs water	non-social	NA	NA	NA	NA	NA	NA	NA	NA	NA
Jimmy	1	aquatic	1 odour	familiar	familiar vs water	social	NA	NA	NA	NA	NA	NA	NA	NA	NA
Tanguy	1	aquatic	1 odour	water	familiar vs water	non-social	NA	NA	NA	NA	NA	NA	NA	NA	NA
Tanguy	1	aquatic	1 odour	familiar	familiar vs water	social	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lucky	1	aquatic	1 odour	water	familiar vs water	non-social	2	1,752	5,84	NA	NA	0	0	0	0
Lucky	1	aquatic	1 odour	familiar	familiar vs water	social	2	1	3,33	NA	NA	0	0	0	0
Lucky	1	aerial	1 odour	water	zookeeper 1 vs water	non-social	3	2,211	7,37	0	0	0	0	NA	NA
Lucky	1	aerial	1 odour	zookeeper 1	zookeeper 1 vs water	social	6	3,004	10,01	0	0	0	0	NA	NA
Jimmy	1	aerial	1 odour	water	zookeeper 1 vs water	non-social	1	0,5	1,67	0	0	0	0	NA	NA
Tanguy	1	aerial	1 odour	water	zookeeper 1 vs water	non-social	2	0,835	2,78	0	0	0	0	NA	NA
Cooky	1	aerial	1 odour	water	zookeeper 1 vs water	non-social	2	0,709	2,36	0	0	0	0	NA	NA
Wally	1	aerial	1 odour	water	zookeeper 1 vs water	non-social	4	2,337	7,79	0	0	0	0	NA	NA
Jimmy	1	aerial	1 odour	zookeeper 1	zookeeper 1 vs water	social	1	0,5	1,67	0	0	0	0	NA	NA
Wally	1	aerial	1 odour	zookeeper 1	zookeeper 1 vs water	social	6	5,492	18,31	0	0	0	0	NA	NA
Tanguy	1	aerial	1 odour	zookeeper 1	zookeeper 1 vs water	social	5	3,67	12,23	0	0	0	0	NA	NA

Cooky	1	aerial	1 odour	zookeeper 1	zookeeper 1 vs water	social	2	0,708	2,36	0	0	0	0	NA	NA
Cooky	1	aerial	1 odour	water	zookeeper 2 vs water	non-social	4	2,795	9,32	0	0	0	0	NA	NA
Jimmy	1	aerial	1 odour	water	zookeeper 2 vs water	non-social	1	0,835	2,78	0	0	0	0	NA	NA
Wally	1	aerial	1 odour	water	zookeeper 2 vs water	non-social	1	0,417	1,39	0	0	0	0	NA	NA
Tanguy	1	aerial	1 odour	water	zookeeper 2 vs water	non-social	2	2,211	7,37	0	0	0	0	NA	NA
Lucky	1	aerial	1 odour	water	zookeeper 2 vs water	non-social	1	0,417	1,39	0	0	0	0	NA	NA
Cooky	1	aerial	1 odour	zookeeper 2	zookeeper 2 vs water	social	2	2,294	7,65	0	0	0	0	NA	NA
Tanguy	1	aerial	1 odour	zookeeper 2	zookeeper 2 vs water	social	2	1,502	5,01	0	0	0	0	NA	NA
Jimmy	1	aerial	1 odour	zookeeper 2	zookeeper 2 vs water	social	3	2,99	9,97	0	0	1	0,584	NA	NA
Wally	1	aerial	1 odour	zookeeper 2	zookeeper 2 vs water	social	9	3,127	10,42	0	0	2	0,334	NA	NA
Lucky	1	aerial	1 odour	zookeeper 2	zookeeper 2 vs water	social	1	0,292	0,97	0	0	0	0	NA	NA
Cooky	1	aerial	1 odour	familiar	familiar vs water	social	3	2,376	7,92	0	0	0	0	NA	NA
Tanguy	1	aerial	1 odour	familiar	familiar vs water	social	1	0,459	1,53	0	0	0	0	NA	NA
Wally	1	aerial	1 odour	familiar	familiar vs water	social	7	5,337	17,79	0	0	2	0,626	NA	NA
Cooky	1	aerial	1 odour	water	familiar vs water	non-social	1	0,709	2,36	0	0	0	0	NA	NA
Tanguy	1	aerial	1 odour	water	familiar vs water	non-social	1	0,873	2,91	0	0	0	0	NA	NA
Wally	1	aerial	1 odour	water	familiar vs water	non-social	2	0,376	1,25	0	0	0	0	NA	NA
Jimmy	1	aerial	1 odour	familiar	familiar vs water	social	1	0,709	2,36	0	0	0	0	NA	NA
Jimmy	1	aerial	1 odour	water	familiar vs water	non-social	2	0,667	2,22	0	0	0	0	NA	NA
Lucky	1	aerial	1 odour	familiar	familiar vs water	social	2	0,96	3,2	0	0	0	0	NA	NA
Lucky	1	aerial	1 odour	water	familiar vs water	non-social	1	0,084	0,28	0	0	0	0	NA	NA
Lucky	1	aerial	1 odour	whiting	whiting vs water	non-social	3	3,712	12,37	0	0	0	0	NA	NA
Cooky	1	aerial	1 odour	whiting	whiting vs water	non-social	6	10,011	33,37	0	0	1	0,543	NA	NA
Jimmy	1	aerial	1 odour	whiting	whiting vs water	non-social	4	3,712	12,37	2	1,627	0	0	NA	NA
Tanguy	1	aerial	1 odour	whiting	whiting vs water	non-social	2	6,214	20,71	0	0	1	0,459	NA	NA
Wally	1	aerial	1 odour	whiting	whiting vs water	non-social	20	11,136	37,12	4	1	8	3,377	NA	NA
Cooky	1	aerial	1 odour	water	whiting vs water	non-social	2	1,334	4,45	0	0	0	0	NA	NA
Jimmy	1	aerial	1 odour	water	whiting vs water	non-social	1	0,459	1,53	0	0	0	0	NA	NA

Wally	1	aerial	1 odour	water	whiting vs water	non-social	5	3,171	10,57	0	0	0	0	NA	NA
Tanguy	1	aerial	1 odour	water	whiting vs water	non-social	1	0,157	0,56	0	0	0	0	NA	NA
Lucky	1	aerial	1 odour	water	whiting vs water	non-social	1	0,041	0,14	0	0	0	0	NA	NA
Wally	1	aerial	1 odour	water	affinity - vs water	non-social	5	4,253	14,18	0	0	0	0	NA	NA
Tanguy	1	aerial	1 odour	water	affinity - vs water	non-social	1	1,335	4,45	0	0	0	0	NA	NA
Cooky	1	aerial	1 odour	water	affinity - vs water	non-social	2	1,586	5,29	0	0	0	0	NA	NA
Jimmy	1	aerial	1 odour	water	affinity - vs water	non-social	1	0,417	1,39	0	0	0	0	NA	NA
Lucky	1	aerial	1 odour	water	affinity - vs water	non-social	1	0,042	0,14	0	0	0	0	NA	NA
Wally	1	aerial	1 odour	affinity -	affinity - vs water	social	6	4,921	16,4	0	0	0	0	NA	NA
Cooky	1	aerial	1 odour	affinity -	affinity - vs water	social	4	2,71	9,03	0	0	0	0	NA	NA
Jimmy	1	aerial	1 odour	affinity -	affinity - vs water	social	1	0,209	0,7	0	0	0	0	NA	NA
Lucky	1	aerial	1 odour	affinity -	affinity - vs water	social	2	0,5	1,67	0	0	0	0	NA	NA
Tanguy	1	aerial	1 odour	affinity -	affinity - vs water	social	1	1,084	3,61	0	0	0	0	NA	NA
Wally	1	aerial	2 odours	zookeeper 1	zookeeper 1 vs zookeeper 2	social	4	1,5	5	0	0	0	0	NA	NA
Tanguy	1	aerial	2 odours	zookeeper 1	zookeeper 1 vs zookeeper 2	social	2	1,042	3,47	0	0	0	0	NA	NA
Jimmy	1	aerial	2 odours	zookeeper 1	zookeeper 1 vs zookeeper 2	social	1	0,291	0,97	0	0	0	0	NA	NA
Cooky	1	aerial	2 odours	zookeeper 1	zookeeper 1 vs zookeeper 2	social	1	1,293	4,31	0	0	0	0	NA	NA
Lucky	1	aerial	2 odours	zookeeper 1	zookeeper 1 vs zookeeper 2	social	2	0,834	2,78	0	0	0	0	NA	NA
Tanguy	1	aerial	2 odours	zookeeper 2	zookeeper 1 vs zookeeper 2	social	2	0,871	2,9	0	0	0	0	NA	NA
Wally	1	aerial	2 odours	zookeeper 2	zookeeper 1 vs zookeeper 2	social	3	1,376	4,59	0	0	0	0	NA	NA
Jimmy	1	aerial	2 odours	zookeeper 2	zookeeper 1 vs	social	1	0,584	1,95	0	0	0	0	NA	NA

					zookeeper 2										
Cooky	1	aerial	2 odours	zookeeper 2	zookeeper 1 vs zookeeper 2	social	1	0,834	2,78	0	0	0	0	NA	NA
Lucky	1	aerial	2 odours	zookeeper 2	zookeeper 1 vs zookeeper 2	social	1	0,167	0,56	0	0	0	0	NA	NA
Lucky	1	aerial	1 odour	carnivore	carnivore vs water	social	3	4,129	13,76	0	0	0	0	NA	NA
Tanguy	1	aerial	1 odour	carnivore	carnivore vs water	social	1	0,626	2,09	0	0	0	0	NA	NA
Wally	1	aerial	1 odour	carnivore	carnivore vs water	social	2	2,545	8,48	0	0	0	0	NA	NA
Cooky	1	aerial	1 odour	carnivore	carnivore vs water	social	1	0,959	3,2	0	0	0	0	NA	NA
Jimmy	1	aerial	1 odour	carnivore	carnivore vs water	social	1	0,75	2,5	0	0	0	0	NA	NA
Tanguy	1	aerial	1 odour	water	carnivore vs water	non-social	1	0,25	0,83	0	0	0	0	NA	NA
Wally	1	aerial	1 odour	water	carnivore vs water	non-social	1	1,627	5,42	0	0	0	0	NA	NA
Cooky	1	aerial	1 odour	water	carnivore vs water	non-social	2	0,959	3,2	0	0	0	0	NA	NA
Jimmy	1	aerial	1 odour	water	carnivore vs water	non-social	0	0	0	0	0	0	0	NA	NA
Lucky	1	aerial	1 odour	water	carnivore vs water	non-social	1	0,125	0,42	0	0	0	0	NA	NA
Lucky	1	aerial	2 odours	non familiar	familiar vs non familiar	social	3	2,252	7,51	0	0	0	0	NA	NA
Cooky	1	aerial	2 odours	non familiar	familiar vs non familiar	social	2	1,001	3,34	0	0	1	0,542	NA	NA
Wally	1	aerial	2 odours	non familiar	familiar vs non familiar	social	1	1,419	4,73	0	0	0	0	NA	NA
Tanguy	1	aerial	2 odours	non familiar	familiar vs non familiar	social	1	0,083	0,28	0	0	0	0	NA	NA
Jimmy	1	aerial	2 odours	non familiar	familiar vs non familiar	social	1	0,25	0,83	0	0	0	0	NA	NA
Cooky	1	aerial	2 odours	familiar	familiar vs non familiar	social	4	0,834	2,78	0	0	0	0	NA	NA
Wally	1	aerial	2 odours	familiar	familiar vs non familiar	social	3	0,668	2,23	0	0	0	0	NA	NA
Tanguy	1	aerial	2 odours	familiar	familiar vs non familiar	social	1	0,167	0,56	0	0	0	0	NA	NA

Lucky	1	aerial	2 odours	familiar	familiar vs non familiar	social	4	0,5	1,67	0	0	0	0	NA	NA
Jimmy	1	aerial	2 odours	familiar	familiar vs non familiar	social	1	0,125	0,42	0	0	0	0	NA	NA
Lucky	1	aerial	2 odours	whiting	herring vs whiting	non-social	3	1,752	5,84	0	0	0	0	NA	NA
Tanguy	1	aerial	2 odours	whiting	herring vs whiting	non-social	3	2,083	6,94	0	0	0	0	NA	NA
Wally	1	aerial	2 odours	whiting	herring vs whiting	non-social	6	3,295	10,98	0	0	1	0,166	NA	NA
Cooky	1	aerial	2 odours	whiting	herring vs whiting	non-social	1	3,003	10,01	0	0	0	0	NA	NA
Jimmy	1	aerial	2 odours	whiting	herring vs whiting	non-social	3	1	3,33	0	0	0	0	NA	NA
Wally	1	aerial	2 odours	herring	herring vs whiting	non-social	9	8,927	29,76	1	0,626	0	0	NA	NA
Cooky	1	aerial	2 odours	herring	herring vs whiting	non-social	4	6,839	22,8	0	0	0	0	NA	NA
Tanguy	1	aerial	2 odours	herring	herring vs whiting	non-social	1	0,251	0,84	0	0	0	0	NA	NA
Jimmy	1	aerial	2 odours	herring	herring vs whiting	non-social	3	3,253	10,84	1	1,334	1	0,459	NA	NA
Lucky	1	aerial	2 odours	herring	herring vs whiting	non-social	5	2,461	8,2	0	0	0	0	NA	NA
Cooky	1	aerial	2 odours	affinity -	affinity - vs affinity +	social	4	1,959	6,53	0	0	0	0	NA	NA
Jimmy	1	aerial	2 odours	affinity -	affinity - vs affinity +	social	1	0,501	1,67	0	0	0	0	NA	NA
Wally	1	aerial	2 odours	affinity -	affinity - vs affinity +	social	1	0,459	1,53	0	0	0	0	NA	NA
Lucky	1	aerial	2 odours	affinity -	affinity - vs affinity +	social	1	0,376	1,25	0	0	0	0	NA	NA
Tanguy	1	aerial	2 odours	affinity -	affinity - vs affinity +	social	1	0,098	0,33	0	0	0	0	NA	NA
Cooky	1	aerial	2 odours	affinity +	affinity - vs affinity +	social	3	1,043	3,48	0	0	0	0	NA	NA
Tanguy	1	aerial	2 odours	affinity +	affinity - vs affinity +	social	1	0,108	0,36	0	0	0	0	NA	NA
Jimmy	1	aerial	2 odours	affinity +	affinity - vs affinity +	social	1	0,121	0,4	0	0	0	0	NA	NA
Wally	1	aerial	2 odours	affinity +	affinity - vs affinity +	social	1	0,142	0,47	0	0	0	0	NA	NA
Lucky	1	aerial	2 odours	affinity +	affinity - vs affinity +	social	1	0,292	0,97	0	0	0	0	NA	NA
Wally	1	aerial	1 odour	water	camphor vs water	non-social	3	2,838	9,46	0	0	0	0	NA	NA
Jimmy	1	aerial	1 odour	water	camphor vs water	non-social	1	0,709	2,36	0	0	0	0	NA	NA
Cooky	1	aerial	1 odour	water	camphor vs water	non-social	2	1,084	3,61	0	0	0	0	NA	NA
Tanguy	1	aerial	1 odour	water	camphor vs water	non-social	1	0,584	1,95	0	0	0	0	NA	NA
Wally	1	aerial	1 odour	camphor	camphor vs water	non-social	1	0,584	1,95	0	0	0	0	NA	NA

Jimmy	1	aerial	1 odour	camphor	camphor vs water	non-social	1	0,125	0,42	0	0	0	0	NA	NA
Cooky	1	aerial	1 odour	camphor	camphor vs water	non-social	1	0,334	1,11	0	0	0	0	NA	NA
Tanguy	1	aerial	1 odour	camphor	camphor vs water	non-social	2	1,711	5,7	0	0	0	0	NA	NA
Lucky	1	aerial	1 odour	water	camphor vs water	non-social	1	0,376	1,25	0	0	0	0	NA	NA
Lucky	1	aerial	1 odour	camphor	camphor vs water	non-social	3	2,252	7,51	0	0	0	0	NA	NA
Lucky	1	aerial	1 odour	water	pepper vs water	non-social	1	0,291	0,97	0	0	0	0	NA	NA
Tanguy	1	aerial	1 odour	water	pepper vs water	non-social	1	0,333	1,11	0	0	0	0	NA	NA
Jimmy	1	aerial	1 odour	water	pepper vs water	non-social	1	0,501	1,67	0	0	0	0	NA	NA
Wally	1	aerial	1 odour	water	pepper vs water	non-social	1	0,334	1,11	0	0	0	0	NA	NA
Cooky	1	aerial	1 odour	water	pepper vs water	non-social	1	0,334	1,11	0	0	0	0	NA	NA
Wally	1	aerial	1 odour	pepper	pepper vs water	non-social	0	0	0	0	0	0	0	NA	NA
Jimmy	1	aerial	1 odour	pepper	pepper vs water	non-social	1	0,208	0,69	0	0	0	0	NA	NA
Cooky	1	aerial	1 odour	pepper	pepper vs water	non-social	1	0,292	0,97	0	0	0	0	NA	NA
Tanguy	1	aerial	1 odour	pepper	pepper vs water	non-social	2	0,917	3,06	0	0	0	0	NA	NA
Lucky	1	aerial	1 odour	pepper	pepper vs water	non-social	1	0,209	0,7	0	0	0	0	NA	NA
Cooky	2	aerial	2 odours	whiting	herring vs whiting	non-social	2	1,835	6,12	0	0	0	0	NA	NA
Cooky	2	aerial	2 odours	herring	herring vs whiting	non-social	4	5,255	17,52	0	0	0	0	NA	NA
Wally	2	aerial	2 odours	whiting	herring vs whiting	non-social	8	4,046	13,49	0	0	0	0	NA	NA
Wally	2	aerial	2 odours	herring	herring vs whiting	non-social	7	6,173	20,58	0	0	0	0	NA	NA
Tanguy	2	aerial	2 odours	whiting	herring vs whiting	non-social	3	4,087	13,62	0	0	0	0	NA	NA
Tanguy	2	aerial	2 odours	herring	herring vs whiting	non-social	3	2,919	9,73	0	0	0	0	NA	NA
Jimmy	2	aerial	2 odours	whiting	herring vs whiting	non-social	1	0,5	1,67	0	0	0	0	NA	NA
Jimmy	2	aerial	2 odours	herring	herring vs whiting	non-social	2	0,876	2,92	0	0	0	0	NA	NA
Lucky	2	aerial	2 odours	whiting	herring vs whiting	non-social	2	0,917	3,06	0	0	0	0	NA	NA
Lucky	2	aerial	2 odours	herring	herring vs whiting	non-social	5	3,921	13,07	0	0	0	0	NA	NA
Wally	2	aerial	2 odours	familiar	familiar vs non familiar	social	2	1,876	6,25	0	0	0	0	NA	NA
Wally	2	aerial	2 odours	non familiar	familiar vs non familiar	social	3	2,044	6,81	0	0	0	0	NA	NA



Cooky	2	aerial	2 odours	familiar	familiar vs non familiar	social	1	0,458	1,53	0	0	0	0	NA	NA
Cooky	2	aerial	2 odours	non familiar	familiar vs non familiar	social	2	1,052	3,51	0	0	0	0	NA	NA
Tanguy	2	aerial	2 odours	familiar	familiar vs non familiar	social	2	3,295	10,98	0	0	0	0	NA	NA
Tanguy	2	aerial	2 odours	non familiar	familiar vs non familiar	social	1	0,542	1,81	0	0	0	0	NA	NA
Lucky	2	aerial	2 odours	familiar	familiar vs non familiar	social	2	0,986	3,29	0	0	0	0	NA	NA
Lucky	2	aerial	2 odours	non familiar	familiar vs non familiar	social	2	3,88	12,93	0	0	0	0	NA	NA
Jimmy	2	aerial	2 odours	familiar	familiar vs non familiar	social	1	0,167	0,56	0	0	0	0	NA	NA
Jimmy	2	aerial	2 odours	non familiar	familiar vs non familiar	social	1	0,626	2,09	0	0	0	0	NA	NA
Tanguy	2	aerial	2 odours	zookeeper 1	zookeeper 1 vs zookeeper 2	social	3	5,547	18,49	0	0	0	0	NA	NA
Tanguy	2	aerial	2 odours	zookeeper 2	zookeeper 1 vs zookeeper 2	social	2	3,587	11,96	0	0	0	0	NA	NA
Cooky	2	aerial	2 odours	zookeeper 1	zookeeper 1 vs zookeeper 2	social	1	0,169	0,56	0	0	0	0	NA	NA
Cooky	2	aerial	2 odours	zookeeper 2	zookeeper 1 vs zookeeper 2	social	1	0,241	0,8	0	0	0	0	NA	NA
Wally	2	aerial	2 odours	zookeeper 1	zookeeper 1 vs zookeeper 2	social	1	0,209	0,7	0	0	0	0	NA	NA
Wally	2	aerial	2 odours	zookeeper 2	zookeeper 1 vs zookeeper 2	social	1	0,186	0,62	0	0	0	0	NA	NA
Jimmy	2	aerial	2 odours	zookeeper 1	zookeeper 1 vs zookeeper 2	social	1	0,148	1,39	0	0	0	0	NA	NA
Jimmy	2	aerial	2 odours	zookeeper 2	zookeeper 1 vs zookeeper 2	social	1	0,709	2,36	0	0	0	0	NA	NA

Lucky	2	aerial	2 odours	zookeeper 1	zookeeper 1 vs zookeeper 2	social	1	0,292	0,97	0	0	0	0	NA	NA
Lucky	2	aerial	2 odours	zookeeper 2	zookeeper 1 vs zookeeper 2	social	1	0,667	2,22	0	0	0	0	NA	NA
Cooky	2	aerial	2 odours	affinity -	affinity - vs affinity +	social	1	0,501	1,67	0	0	0	0	NA	NA
Cooky	2	aerial	2 odours	affinity +	affinity - vs affinity +	social	2	1,419	4,73	0	0	0	0	NA	NA
Wally	2	aerial	2 odours	affinity -	affinity - vs affinity +	social	1	0,501	1,67	0	0	0	0	NA	NA
Wally	2	aerial	2 odours	affinity +	affinity - vs affinity +	social	3	2,67	8,9	0	0	0	0	NA	NA
Tanguy	2	aerial	2 odours	affinity -	affinity - vs affinity +	social	1	0,24	0,8	0	0	0	0	NA	NA
Tanguy	2	aerial	2 odours	affinity +	affinity - vs affinity +	social	2	0,471	1,57	0	0	0	0	NA	NA
Jimmy	2	aerial	2 odours	affinity -	affinity - vs affinity +	social	1	0,148	1,39	0	0	0	0	NA	NA
Jimmy	2	aerial	2 odours	affinity +	affinity - vs affinity +	social	1	0,231	0,77	0	0	0	0	NA	NA
Lucky	2	aerial	2 odours	affinity -	affinity - vs affinity +	social	2	1,669	5,56	0	0	0	0	NA	NA
Lucky	2	aerial	2 odours	affinity +	affinity - vs affinity +	social	1	0,375	1,25	0	0	0	0	NA	NA
Tanguy	2	aerial	1 odour	water	camphor vs water	non-social	1	0,459	1,53	0	0	0	0	NA	NA
Tanguy	2	aerial	1 odour	camphor	camphor vs water	non-social	1	0,584	1,95	0	0	0	0	NA	NA
Cooky	2	aerial	1 odour	water	camphor vs water	non-social	1	0,208	0,69	0	0	0	0	NA	NA
Cooky	2	aerial	1 odour	camphor	camphor vs water	non-social	1	0,292	0,97	0	0	0	0	NA	NA
Jimmy	2	aerial	1 odour	water	camphor vs water	non-social	1	0,143	0,48	0	0	0	0	NA	NA
Jimmy	2	aerial	1 odour	camphor	camphor vs water	non-social	2	0,833	2,78	0	0	0	0	NA	NA
Lucky	2	aerial	1 odour	water	camphor vs water	non-social	3	2,092	6,97	0	0	0	0	NA	NA
Lucky	2	aerial	1 odour	camphor	camphor vs water	non-social	2	0,5	1,67	0	0	0	0	NA	NA
Wally	2	aerial	1 odour	water	camphor vs water	non-social	1	0,143	0,48	0	0	0	0	NA	NA
Wally	2	aerial	1 odour	camphor	camphor vs water	non-social	1	0,201	0,67	0	0	0	0	NA	NA
Tanguy	2	aerial	2 odours	herring + camphor	herring vs (herring + camphor)	non-social	1	0,167	0,56	0	0	0	0	NA	NA
Tanguy	2	aerial	2 odours	herring	herring vs (herring + camphor)	non-social	1	0,333	1,11	0	0	0	0	NA	NA

Cooky	2	aerial	2 odours	herring + camphor	herring vs (herring + camphor)	non-social	2	1,168	3,89	0	0	0	0	NA	NA
Cooky	2	aerial	2 odours	herring	herring vs (herring + camphor)	non-social	6	7,466	24,89	0	0	0	0	NA	NA
Wally	2	aerial	2 odours	herring + camphor	herring vs (herring + camphor)	non-social	2	0,625	2,08	0	0	0	0	NA	NA
Wally	2	aerial	2 odours	herring	herring vs (herring + camphor)	non-social	7	6,298	20,99	0	0	0	0	NA	NA
Jimmy	2	aerial	2 odours	herring + camphor	herring vs (herring + camphor)	non-social	1	0,146	0,49	0	0	0	0	NA	NA
Jimmy	2	aerial	2 odours	herring	herring vs (herring + camphor)	non-social	1	0,179	0,6	0	0	0	0	NA	NA
Lucky	2	aerial	2 odours	herring + camphor	herring vs (herring + camphor)	non-social	1	0,096	0,32	0	0	0	0	NA	NA
Lucky	2	aerial	2 odours	herring	herring vs (herring + camphor)	non-social	1	0,153	0,51	0	0	0	0	NA	NA