



21 **Abstract**

22 Self-recognition is the ability to recognise stimuli originating from oneself. Humans and most  
23 great apes show evidence of true self-recognition in the mirror test. They use their reflection  
24 to remove a mark that is only visible in the mirror. Not all animals, however, rely primarily on  
25 vision. In lizards, chemical cues are important in social interactions. A number of lizard species  
26 show chemical self-recognition but it has never been investigated in a gecko species. Here,  
27 we test the tokay gecko (*Gekko gecko*) a territorial species with parental care on their ability  
28 to discriminate their own skin and faecal chemicals from those of same-sex, unfamiliar  
29 conspecifics. Geckos show a higher response rate towards chemicals from unfamiliar  
30 individuals compared to self-produced chemicals and a water control. Lizards showed self-  
31 directed behaviour, responded stronger to skin chemicals and females responded more than  
32 males. Our study provides first evidence towards self-recognition and for a social function of  
33 chemical present on faeces in tokay geckos but further tests are needed to confirm true self-  
34 recognition. Tokay geckos are an excellent model species to investigate individual recognition  
35 to demonstrate more sophisticated social cognitive abilities than have previously been  
36 attributed to reptiles.

37

38 *Keywords:* chemical discrimination, cognition, communication, *Gekko gecko*, reptile,

39

40

## 41 **Introduction**

42 Self-recognition is the ability to recognise cues that represent/ originate from oneself (visual  
43 images, olfactory cues, acoustic stimuli) (Gallup, 1970; Gallup et al., 2011; Platek et al., 2004).  
44 Research into self-recognition aims to uncover self-awareness (the ability to become the  
45 object of one's own attention) and its' emergence across humans and non-human animals  
46 (Gallup, 1970; Gallup et al., 2011). The method of choice is the mirror self-recognition (MSR)  
47 test. In this test, a subject is confronted with a mirror and provided with a mark that can only  
48 be seen using the reflection in the mirror. Confirmation of MSR occurs when the subject  
49 inspects the mark and attempts to remove it using their reflection (Gallup, 1970). Two  
50 important control conditions need to be implemented. First, an invisible mark has to be used  
51 to exclude that physical irritation caused by the mark itself or the process of marking is  
52 triggering the behaviour (Gallup, 1970). Second, a mark has to be applied in a spot that can  
53 be seen without the use of the mirror to confirm the subjects' motivation to remove marks in  
54 general (Gallup and Anderson, 2018). Humans and most great apes show MSR (Gallup, 1970;  
55 Gallup et al., 2011) while evidence in other species has led to controversial discussion (Gallup  
56 and Anderson, 2018; 2020).

57 Not all species primarily depend on their visual sense. This has led to the development  
58 of the sniff-test for self-recognition used in dogs whose primary sense is smell (Cazzolla Gatti,  
59 2016). These studies have demonstrated that dogs discriminate between their own odour and  
60 that of conspecifics. They sniff the urine of unfamiliar dogs for longer than their own urine  
61 (Cazzolla Gatti, 2016; Horowitz, 2017). Furthermore, they sniff their own odour longer when it  
62 is modified than the modifier by itself (Horowitz, 2017). Nonetheless, some researchers have  
63 criticised these studies as not being a true equivalent to the MSR test because dogs do not  
64 show self-directed behaviour in the sniff-test which is an important criterion in the MSR test  
65 (Gallup and Anderson, 2018). Interestingly, chemical self-recognition tests are a fairly  
66 common test in lizards (Aguilar et al., 2009; Alberts, 1992; Aragón et al., 2001; Bull et al.,  
67 2000; Cooper, 1999; Graves and Halpern, 1991; López et al., 1997). Particularly one study in  
68 male desert iguanas (*Dipsosaurus dorsalis*) showed that these animals perform self-directed

69 behaviour after detection of their own femoral gland sections but did not show this behaviour  
70 towards the secretions of unfamiliar males (Alberts, 1992). Following the critique voiced  
71 regarding the results in dogs, this study demonstrates more conclusive evidence for self-  
72 recognition using chemicals in lizards.

73         Generally, reptiles rely strongly on chemicals (i.e. pheromones) when it comes to  
74 individual recognition, territoriality, social interactions and mate choice (Norris and Lopez,  
75 2001). In lizards, pheromones might originate from the skin or specialised glands such as  
76 femoral glands which are most pronounced in males (Norris and Lopez, 2001). Many species  
77 also possess cloacal glands that deposit pheromones onto the faeces (Norris and Lopez,  
78 2001). This is especially important in scat piling lizards which defecate repeatedly in the same  
79 location (Bull et al., 1999a). Similar to latrines in mammals (e.g. Green et al., 2015; King et  
80 al., 2017), these scat piles can have a social function by communicating, for example, territory  
81 ownership (Bull et al., 1999a; 1999b) and group identity (Bull et al., 2000; but see Shah et al.,  
82 2006). Lizards detect pheromones using tongue-flicks (TF), protrusions of the tongue forward  
83 towards a stimulus (e.g. on the ground or on a swab) to collect chemicals (Cooper, 1994), and  
84 generally show increased TF rates towards stimuli from unfamiliar conspecifics (e.g. Alberts,  
85 1992; Aragón et al., 2001; Cooper et al., 1999; Graves and Halpern, 1991).

86         Discrimination of self-produced chemicals and chemicals produced by unfamiliar,  
87 same-sex conspecifics has never been shown in a gecko species although leopard geckos  
88 (*Eublepharis macularius*) discriminate sex based on pheromones (Cooper and Steele, 1997;  
89 Mason and Gutzke, 1990) and thick-tailed geckos (*Nephurus milii*) recognise their own scats  
90 to add additional faecal matter (Carpenter and Duvall, 1995). Many gecko species scat pile  
91 which suggests either a communicative function aimed at conspecifics, an anti-predatory  
92 function to avoid detection of refuges or both (Bull et al., 1999a; Carpenter and Duvall, 1995).  
93 Here, we test the tokay gecko (*Gekko gecko*), a large (up to 185 mm Snout Vent Length),  
94 nocturnal, insectivorous, scat piling gecko species from tropical South-East Asia (Grossmann,  
95 2006). The aims of this study were to

96 (1) investigate if tokay geckos can discriminate between self-produced chemicals and  
97 chemicals produced by unfamiliar, same-sex conspecifics on cotton swabs  
98 (Cooper, 1998).

99 (2) We were also interested in finding out if chemicals originating from scats were as  
100 effective as chemicals originating from the skin as stimuli.

101 We predicted, that if geckos are able to recognize their own odour they would show  
102 lower responses towards their own odour than the conspecific odour (e.g. Alberts, 1992;  
103 Cooper et al., 1999; Graves and Halpern, 1991). If geckos are capable of self-recognition, we  
104 expected to find both stimulus directed and ground directed TFs as a sign of comparison  
105 between the two stimuli when confronted with their own and unfamiliar conspecific odour. We  
106 predicted, however, less ground directed responses when confronted with their own odour as  
107 it is familiar and can be recognised easier. We also predicted that faecal chemicals were as  
108 effective as skin chemicals in eliciting a response if scats had a communicative function.

109

## 110 **Methods**

111 Study animals, housing and husbandry

112 We tested 22 captive bred, adult tokay geckos, 10 males (SVL range = 11.35-15.02 cm) and  
113 12 females (SVL range = 11.29-13.72 cm). Animals were acquired from different breeders  
114 across Europe and approximately 2-6 years old at the time of the study. Animals were naïve  
115 to the experimental procedure used in this study.

116 At our facility, geckos are kept singly in plastic terraria (females – 45 L x 45 B x 70 H  
117 cm; males – 90 L x 45 B x 100 H cm). Enclosures are equipped with a drainage layer of clay  
118 pebbles and a layer of organic rainforest soil (Dragon BIO-Ground) on top separated by a  
119 mosquito mesh to prevent mixing of the layers. On the soil surface we spread autoclaved red  
120 oak leaves. Collembola, isopods and earth worms in the soil break down the faecal matter  
121 produced by the geckos. Each enclosure also includes a compressed cork back wall, cork

122 branches, refuges made out of cork branches cut in half and hung on the back wall as well as  
123 plants.

124 Enclosures are located in a fully controlled environment with a reversed photo period.  
125 Because tokay geckos are nocturnal, the dark cycle (when geckos are active) lasts from 6am  
126 to 6pm while the light period (when geckos are asleep) lasts from 6pm to 6am. Each enclosure  
127 is equipped with an additional light to provide lizards with UVB (Exo Terra Reptile UVB 100,  
128 25 W) during the light cycle. The system automatically simulates a sunrise and sunset.  
129 Temperature is automatically control and reaches approximately 25 °C during the night cycle  
130 and 31 °C during the day cycle. To allow animals to thermoregulate, a heat mat (TropicShop)  
131 is fixed to the outside of each enclosure increasing the temperature by ~5 °C. To simulate the  
132 tropical condition this species experiences in the wild, the room humidity is kept at 50% and  
133 daily rainfall (osmotic water, 30s every 12h at 5pm and 4am) increases the humidity within  
134 enclosures to 100%. Humidity decreases with time until the next rainfall event. All enclosures  
135 are set up on shelves with small enclosures on the top and large enclosures on the bottom.  
136 Animals are spread evenly across two rooms.

137 Lizards are fed three times per week on Monday, Wednesday and Friday with adult  
138 crickets (*Acheta domesticus*). Before feeding, crickets are gut loaded using cricket mix (reptile  
139 planet LDT), Purina Beyond Nature's Protein™ Adult dry cat food and fresh carrots to ensure  
140 that they provided optimal nutrition (Vitamin D and calcium). Each individual lizard receives 3-  
141 5 crickets each feeding with tweezers to be able to monitor the food intake. A water bowl  
142 provides water *ad libitum*. Once a month geckos are captured and weighed to ensure healthy  
143 weight.

144

145 Experimental setup and stimuli

146 Lizards were tested in their home enclosures to reduce stress of handling (Langkilde and  
147 Shine, 2006) between 10<sup>th</sup> of August to 30<sup>th</sup> September 2021. Testing was conducted under  
148 red light (PHILIPS TL-D 36W/15 RED). The light we use has a red component at 718 nm

149 which is not detectable by the tokay geckos' photoreceptors (Loew 1994). Furthermore, a blue  
150 UV-C component at 282 nm is also produced which is visible to the geckos (Loew 1994) and  
151 promotes gecko activity (personal observation).

152         Because animals were spread across two rooms, each room was tested on a different,  
153 non-feeding day (either Tuesday or Thursday) once a week. Each individual was tested in a  
154 random order each day and the stimuli (control, own, same sex unfamiliar) and treatment  
155 (skin, faeces – i.e. scat) were also randomised across trials. As a positive control we used the  
156 odour of tap water on a paper towel. To create the control stimulus, one side of a cotton swab  
157 was taped 10 times on a moistened paper towel. As the familiar odour we used the individuals  
158 own odour either from their skin collected by gently rubbing one side of a cotton swab over its'  
159 back and/or sides 10 times or from a fresh (no older than 2 days) scat. The cotton swab was  
160 rubbed on the scat until a stain was visible. To create the same-sex unfamiliar stimulus we  
161 took chemicals from the skin or scats of a same sex individual from the second room. Although  
162 animals never had direct contact with each other within a room we were unsure if the smell of  
163 individuals could spread within a room. To ensure true unfamiliarity, we used the individuals  
164 from the second room located across a small hallway. The same methods as for collecting  
165 individuals own odour was used. Each individual was tested on their reaction towards the  
166 odour of three different same-sex conspecifics. From each conspecific both chemicals from  
167 skin and faeces were used to be able to compare the reaction across treatments while  
168 controlling for identity. All cotton swabs were marked at the back to indicate on which side the  
169 stimulus was applied. This was done so the experimenter could present each cotton swab  
170 with the stimulus facing downwards to exclude the use of visual information originating from  
171 faeces or UV-reflecting chemicals (Mason 1992).

172



**Figure 1.** Setup of cotton swabs in clay bowls. For each focal subject swabs were placed in a separate clay bowl. Swabs were placed in the testing order. The experimenter made sure that swab tips covered in chemical stimuli never touched each other. To prevent excessive degradation of stimuli, individuals within a room were divided into two groups and the second group set up after the first group finished testing.

182

### 183 Experimental procedure

184 At the start of a test day stimuli were set up as follows: First, all swabs for the control were  
185 prepared. Next, all swabs with lizards own odour were prepared and lastly, all swabs with the  
186 unfamiliar odour were prepared. This was done to leave enough time (20-30 minutes) between  
187 stimulus collection and test of focal individuals to recover from stimulus collection (skin  
188 treatment). All swabs were placed in clay bowls in the order of presentation (Figure 1). We  
189 first set up half of the individuals, tested their reaction and then set up and tested the second  
190 half. This was done to prevent excessive degradation of chemical stimuli. After all individuals  
191 finished testing, cotton swabs were discarded and clay bowls thoroughly cleaned with hot  
192 water and a sponge. Then they were dried upside down until the next test day. The  
193 experimenter ensured that the inside of the bowls was never touched. Furthermore, they  
194 ensured that the cotton swabs within a bowl never touched.

195 After set up, we first tested all individuals with the first cotton swab, then all with the  
196 second and finally with the third. This was done to leave about 10-15 minutes between  
197 stimulus presentations and reduce carry-over effects between stimuli. Both males and females  
198 were tested using the same procedure.

199 In a given trial, we first placed a dim white light (LED, SPYLUX® LEDVANCE 3000K,  
200 0.3 W, 17 lm) on top of the enclosure. Lizards were used to this light as it was used during



201 feeding and generally during testing. Next, we located an individual in its' enclosure. If the  
202 individual was hiding we gently removed the refuge from the back to expose it. Next, a cotton  
203 swab was presented holding it in a pair of 20 cm long metal tweezers. This ensured that the  
204 hand of the experimenter was far enough away to prevent the experimenters' odour interfering  
205 with the experiment. The experimenter was visible during trials similar as during regular  
206 feeding. Trials from the first two test days were recorded with a GoPro (Hero 5). However,  
207 videos were too dark and we had issues scoring the lizards behaviour. For all other trials we  
208 switched to recording with a Samsung S20 smartphone (108 Megapixel, 8K-FUHD) which  
209 produced far better quality videos under the light conditions. Furthermore, the ability to switch  
210 between front and back camera enabled us to take videos even when lizards were sitting  
211 above the tank entrance. By the second week of testing we detected a large decrease in bites  
212 likely caused by lizards learning that the cotton swab was not edible. We, therefore, decided  
213 to repeat the first trial at the end of the testing period to ensure that our measurements were  
214 not confounded by changes in behaviour.

215

#### 216 Data collection

217 Videos were scored from the start of a trial, when the cotton swab was first presented within  
218 1 cm of the lizards snout. Trials lasted a maximum of 120 seconds (2 minutes). If a tongue  
219 flick (TF) or bite occurred, the behaviour was video recorded for 60s after the initial event  
220 following the procedure used in previous studies with squamates (e.g. Aragón et al., 2001;  
221 López et al., 1997; Martin et al. 2020). If the lizard showed a turn (whole body movement away  
222 from the swab, Table 1) and walked away from the swab the trial was terminated.

223 Videos were analysed blind as to which stimulus was presented but not to treatment  
224 which was visible in some videos. We used VLC media player (Version 3.0.7.1, Vetinari, Intel  
225 64 bit) to score behaviour (Table 1) shown during trials. We scored bites, TF, breaths if the  
226 ventral side of the individual was visible (i.e. gular pumping, Norris and Lopez, 2011), deep  
227 breaths, and turns. TFs were divided into flicks directed at the stimulus (tongue tip aimed at  
228 the swab) and flicks directed towards the ground (tip aimed at the ground). We also measured

229 the trial time in seconds starting from the time the stimulus was presented within 1 cm of the  
230 lizards' snout until either 120 seconds without a bite or TF elapsed, the lizard performed a turn  
231 or 60 seconds after the first bite or TF. Enclosure temperature was recoded automatically to  
232 an accuracy of 0.1 °C by the system responsible for regulating the environment within rooms.

233

234 **Table 1.** Ethogram of behaviours shown by tokay geckos in response to chemical stimuli.

Name of behaviour	Description
Breath	One up and down movement of the lizards' throat = 1 breath. Only visible from the ventral side. Recorded as counts.
Deep breath	One extension and retraction of the flanks behind the front legs. Visible from the dorsal and ventral side. Recorded as counts.
Tongue flick	Quick protrusion of the tongue forward away from the mouth. NOT licking of the lips which is also a protrusion of the tongue but along the skin of the mouth. Recorded as counts.
Bite	The tip of the swab is taken between the upper and lower jaw. May be accompanied by shaking of the head. Recorded as counts.
Turn	The lizards' moves away from the swab. The whole body moved either past the swab, backwards away or involved a turn away from the swab. Recoded as yes or no. A trial was terminated if this behaviour was shown.

235

236 Ethical note

237 The test reported in this study are strictly non-invasive observations of behaviour. Introducing  
238 odour of conspecifics is a practice used during enrichment in reptiles. We followed the  
239 guidelines provided by the Association for the Study of Animal Behaviour/ Animal Behaviour  
240 Society for the treatment of animals in behavioural research and Teaching (2018). All testing  
241 was approved by the Suisse Federal Food Safety and Veterinary Office (National No. 33232,  
242 Cantonal No. BE144/2020). Captive conditions were approved by the Suisse Federal Food  
243 Safety and Veterinary Office (Laboratory animal husbandry license: No. BE4/11).

244

245 Statistical analysis

246 *Power analysis*

247 Before data collection, we performed a power analysis using G\*power (Faul et al., 2007;  
248 2009). As our study was designed as a 2x2x3 factorial designed, we calculated power based

249 on a within factor repeated measures ANOVA. The literature on chemical discrimination in  
250 other lizard and worm lizard species (Alberts,1992; Cooper et al., 1999; López et al., 1997)  
251 generally suggested large effect sizes. We were, however, unsure what effect size to expect  
252 from our geckos and therefore calculated the minimal effect size that could be reliably detected  
253 at a power of 0.8. We specified an alpha level of 0.05, a power of 0.8, six groups with three  
254 measurements, a correlation among repeated measures of 0.5 and a correction of 1. With  
255 these settings and a sample size of 24 individuals we are able to detect an effect size of 0.3  
256 at an actual power of 0.99. The sample size used in our study was 22 individuals. We  
257 expected, however, only a slight reduction in the actual power to detect a small effect size.

258

#### 259 *Data analysis*

##### 260 General reaction

261 We were interested if the reaction towards the presented stimuli was affected by the treatment  
262 (scat or skin), stimulus (water control, own or unfamiliar odour), sex (male or female), the order  
263 in which stimuli were presented, trial and temperature. These were used as fixed effects in  
264 three models looking at all tongue flicks produced in 60 seconds, deep breaths per second  
265 and breaths per second. For TFs we used a generalised linear mixed zero-inflation Poisson  
266 model (GLMM, package glmmTMB, Brooks et al., 2017) because our dataset included a large  
267 amount of 0 TFs. The conditional model included the above mentioned fixed effects while the  
268 zero-inflation model only included treatment, stimulus and sex as fixed effects. We did not  
269 expect all fixed effects to cause zero-inflation. Both the models included a random effect of  
270 animal identity to account for repeated measures. We were also interested if the difference in  
271 size between the test subject and the unfamiliar individual (delta SVL) from which the odour  
272 was taken affected TFs. To this end, we looked at TFs produced in the unfamiliar condition  
273 only as the response variable in another zero-inflation Poisson model. Both the conditional  
274 model and zero-inflation model included delta SVL and treatment as fixed effects and trial and

275 animal identity as random effects. In both analyses we specified session for the over-  
276 dispersion component.

277           For the two measures of breathing, we first divided the number of breaths by the trial  
278 time to get a comparable measure for the breaths (breaths and deep breaths per second). We  
279 used breaths and deep breaths per second as the response variable in linear mixed effects  
280 models (LME, package lmerTest, Kuznetsova et al., 2017) with Gaussian family including the  
281 above mentioned fixed effects. Both models conformed to the assumption of residual normality  
282 (visual inspection of qqplots). Both models included a random effect of animal identity and  
283 session to account for repeated measures. We did not analyse bites because they were shown  
284 too infrequent to be analysed.

285

286 Differences between swab and ground directed tongue flicks

287 Across all trials, males only tongue flicked three times while females together produced 202  
288 TFs. We, therefore, based the following analysis on the data from females only. To identify if  
289 lizards compared their own odour to that of an unfamiliar individual we recorded TFs directed  
290 at the swab and those directed at the ground (on which their own odour was present). We  
291 analysed swab and ground directed TFs separately. We used generalised linear mixed zero-  
292 inflation Poisson models with ground or swab TFs as the response variable. The conditional  
293 models included stimulus as the only fixed effect as well as treatment, trial and animal identity  
294 as random effects. Treatment and trial were included as random effects because the general  
295 analysis revealed significant effects on TFs. In the zero-inflation models we used treatment  
296 and stimulus as fixed effects and animal identity as the random effect. We also specified  
297 session for the over-dispersion component. Finally, we also compared the two TFs within  
298 stimulus conditions using their average across trials and treatments (to avoid pseudo-  
299 replication) with Wilcoxon signed rank tests for paired data.

300

301 Data analysis was done in the free, open source software R (Version 4.0.3; R Core Team,  
302 2020). All data and code produced during this study are available on the Open Science

303 Framework (OSF; link for review purposes:

304 [https://osf.io/jp7h8/?view\\_only=b4c0eac3792f4adaaef2ff6745aebf45](https://osf.io/jp7h8/?view_only=b4c0eac3792f4adaaef2ff6745aebf45))

305

## 306 **Results**

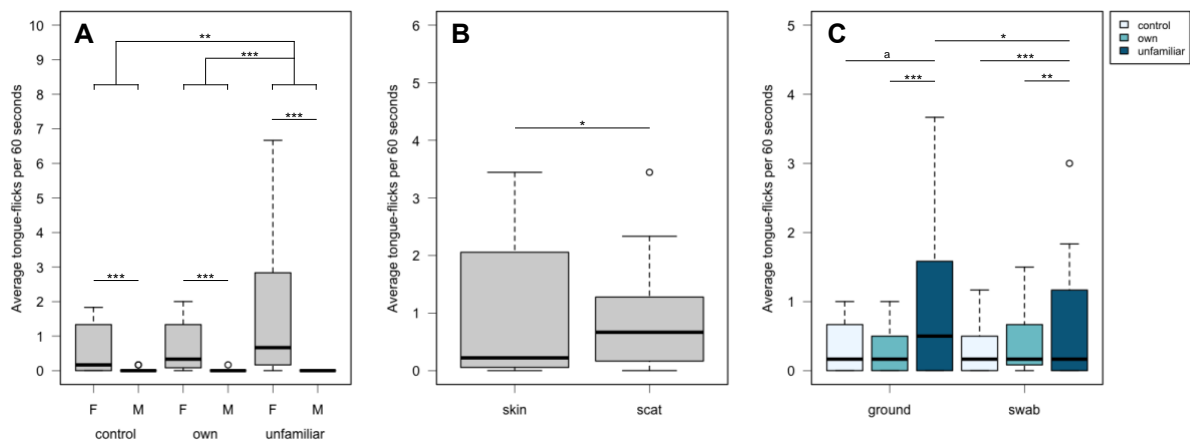
307 One female (G015) could not be tested as she was too anxious and was only used as a  
308 stimulus individual. All other geckos habituated fast to being rubbed on their back with a swab  
309 and did not flee during stimulus collection by the second week of testing (the first week of  
310 testing was not used for analysis).

311

312 General reaction to the presented stimuli

313 Our analysis revealed that males tongue flicked much less than females (GLMM, estimate = -  
314 4.249, z-value = -4.674,  $CI_{low}$  = -6.031,  $CI_{up}$  = -2.467,  $p$ -value < 0.001; Figure 2A) and that  
315 lizards tongue flicked less towards odour originating from scats than from skin (GLMM,  
316 estimate = -0.406, z-value = -2.413,  $CI_{low}$  = -0.736,  $CI_{up}$  = -0.076,  $p$ -value = 0.016, Figure 2B).  
317 Compared to swabs containing the odour of unfamiliar individuals, lizards directed less TFs  
318 towards tap water from a paper towel (GLMM, estimate = -0.556, z-value = -2.733,  $CI_{low}$  = -  
319 0.954,  $CI_{up}$  = -0.157,  $p$ -value = 0.006; Figure 2A) and their own odour (GLMM, estimate = -  
320 0.698, z-value = -3.562,  $CI_{low}$  = -1.083,  $CI_{up}$  = -0.314,  $p$ -value = 0.0004; Figure 2A). Overall,  
321 lizards decreased TFs over the course of the experiment (GLMM, estimate = -0.196, z-value  
322 = -2.099,  $CI_{low}$  = -0.378,  $CI_{up}$  = -0.013,  $p$ -value = 0.036). We detected no effect of stimulus  
323 order (GLMM, estimate = 0.043, z-value = 0.481,  $CI_{low}$  = -0.133,  $CI_{up}$  = 0.219,  $p$ -value = 0.631)  
324 and temperature (GLMM, estimate = 0.086, z-value = 0.277,  $CI_{low}$  = -0.524,  $CI_{up}$  = 0.697,  $p$ -  
325 value = 0.782) and the size of the stimulus individual had no effect on the number of TFs  
326 (GLMM, estimate = -0.123, z-value = -0.667,  $CI_{low}$  = -0.524,  $CI_{up}$  = 0.697,  $p$ -value = 0.505).  
327 The zero-inflation models did not produce any significant results (GLMM,  $p$ -value > 0.05; Table  
328 A1 and A2).

329 We found no significant effects of any of the fixed effects on deep breaths per second  
330 (LME,  $p$ -value > 0.05, Table A3) but geckos showed a higher breathing rate in response to  
331 stimuli originating from scats (when responses towards all stimuli were lumped together)  
332 indicating a stronger involvement of olfaction (LME, estimate = 0.106,  $t$ -value = 3.132,  $CI_{low}$  =  
333 0.039,  $CI_{up}$  = 0.170,  $p$ -value = 0.002, Table A4). None of the other fixed effects were significant  
334 (LME,  $p$ -value > 0.05, Table A4).  
335



336  
337 **Figure 2.** (A) Average tongue flicks produced within 60 seconds in the three stimulus  
338 conditions separated between males and females. Overall, lizards tongue flicked the most in  
339 the unfamiliar conditions and males tongue flicks less than females. (B) Average tongue flicks  
340 produced within 60 seconds across the skin and scat treatment. Lizards tongue flicked less in  
341 response to scats. (C) Average tongue flicks produced within 60 seconds directed towards the  
342 ground and the swab separated into stimulus conditions. Only data from females are shown.  
343 Females tongue flicked more when stimuli originated from unfamiliar individuals (dark blue)  
344 compared to the own (medium blue) and control condition (light blue). Females tongue flicked  
345 the ground more than the swab in the unfamiliar condition only. a  $p < 0.06$ , \*  $p < 0.05$ , \*\*  $p <$   
346 0.01, \*\*\*  $p < 0.001$ .

347

348 Differences between swab and ground directed tongue flicks  
349 Females directed less ground TFs towards their own odour compared to odour from unfamiliar  
350 individuals (GLMM, estimate = -1.133, z-value = -3.872,  $CI_{low}$  = -1.707,  $CI_{up}$  = -0.560,  $p$ -value  
351 = 0.00011, Figure 2C). Females also directed less swab TFs towards their own odour (GLMM,  
352 estimate = -0.927, z-value = -2.979,  $CI_{low}$  = -1.538,  $CI_{up}$  = -0.317,  $p$ -value = 0.003, Figure 2C)  
353 and even less towards the water control (GLMM, estimate = -1.405, z-value = -4.614,  $CI_{low}$  =  
354 -2.002,  $CI_{up}$  = -0.808,  $p$ -value < 0.001, Figure 2C). The zero-inflation models did not produce  
355 any significant results (GLMM,  $p$ -value > 0.05, Table A5 and A6). Within conditions females  
356 directed more TFs towards the ground in the unfamiliar condition (Wilcoxon signed rank tests,  
357  $V = 3$ ,  $N = 11$ ,  $p$ -value = 0.012, Figure 2C). We found no differences in the control (Wilcoxon  
358 signed rank tests,  $V = 18.5$ ,  $N = 11$ ,  $p$ -value = 0.801, Figure 2C) and own odour condition  
359 (Wilcoxon signed rank tests,  $V = 14.5$ ,  $N = 11$ ,  $p$ -value = 0.829, Figure 2C).

360

## 361 Discussion

362 Our experiment demonstrated that, at least female tokay geckos, discriminate between their  
363 own odour and that of an unfamiliar female using chemicals originating from the skin and scats  
364 but they show a weaker response to chemicals originating from scats. More TFs occurred  
365 towards the odour of unfamiliar individuals and females produced more ground directed TFs  
366 in response to the unfamiliar conspecific odour. In general, lizards sampled the stimulus most  
367 (swab directed TFs) in the unfamiliar condition and we found no differences in TFs directed  
368 towards their own odour and the water control.

369 Based on previous studies in other lizards (e.g. Alberts, 1992; Cooper et al., 1999;  
370 Graves and Halpern, 1991), we predicted that tokay geckos would show more TFs towards  
371 chemical stimuli originating from unfamiliar, same-sex conspecifics. Our results are in line with  
372 these studies but only in females. Males only tongue flicked a total of three times during the  
373 course of the experiment. Either, males do not rely as strongly on skin and scat chemicals for  
374 individual recognition or they show a delayed response which we did not record using our

375 methodology. Indeed, we observed an increase in activity including TFs in some males after  
376 trials had ended. Male tokay geckos are territorial (Grossmann, 2006) and their behaviour  
377 might be interpreted as searching for the intruder. It is, however, necessary to run additional  
378 test recording not just the immediate response of males within two minutes but record  
379 behaviour for a longer time such as 10-15 minutes after stimulus presentation. Furthermore,  
380 males might react stronger to femoral gland secretions similar to male amphisbaenians  
381 (*Blanus cinereus*; Cooper et al., 1994) which should be tested in the future.

382 We also predicted that lizards would show chemical self-recognition by producing more  
383 ground directed TFs in response to the unfamiliar odour compared to their own odour. Our  
384 results confirm our prediction. Testing individuals inside their own enclosure posed an  
385 experimental advantage. Their enclosures are saturated with their own odour which made it  
386 possible to detect “self-directed” behaviour which would not have been possible in a neutral  
387 environment. Although male desert iguanas showed self-directed TFs towards their femoral  
388 glands (Alberts, 1992), we did not expect to find such behaviour in our geckos. Tokay geckos  
389 are, however, territorial, show site fidelity and scat pile. We expected, therefore, that if any  
390 comparison between the presented stimuli and self-produced odour did take place, this would  
391 likely be shown by TFs towards the ground. These ground directed TFs were very pronounced  
392 and easy to score because animals would always turn their heads away from the swab before  
393 tongue flicking the ground. Our results point towards similar difficulty to recognise tap water  
394 and their own scent because ground and swab directed TFs did not differ across these test  
395 conditions. They did differ in the unfamiliar condition. We recorded higher rates of ground  
396 directed TFs compared to swab directed TFs demonstrating a need for increased comparison  
397 with their own odour. Interestingly, a study in male Iberian rock-lizards (*Lacerta monticola*)  
398 showed no differences in non-swab directed TF between males own and unfamiliar males  
399 femoral gland secretion (Aragón et al., 2001). This study tested wild caught males that were  
400 kept together with a second individual on their reaction to femoral gland secretions. We used  
401 chemical from skin and scats from captive bred individuals kept singly and mainly analysed  
402 the reaction from females to these stimuli. It is possible that the scent of the second individual



403 present in the enclosure interfered with “self-directed” TFs in rock-lizards. A comparison to our  
404 results is, however, difficult due to the many differences between studies.

405 A next step towards more conclusive evidence for true self-recognition would be to test  
406 geckos’ reaction towards a change in their own odour similar to what was done with dogs  
407 (Horowitz, 2017). Dogs are more interested in their own odour when it was marked but where  
408 less interested in the mark alone. If geckos similarly increase ground directed TFs towards  
409 their marked odour compared to the mark alone then this would further support our geckos’  
410 ability to show true self-recognition.

411 Previous studies have considered that an increased rate of TFs towards the odour of  
412 unfamiliar individuals could be caused by novelty of the stimulus (Bull et al., 1999a; 2000).  
413 Bull and colleagues (1999a; 2000) used chemical stimuli from heterospecific individuals that  
414 were unfamiliar to the test lizards as a control. If novelty was causing increased TF rates then  
415 lizards would also show an increased response towards the heterospecifics’ odour which they  
416 did not ruling out novelty as a cause for increased TF rates (Bull et al., 1999a; 2000). In our  
417 study, we used tap water from a paper towel as a control instead of odourless deionised water  
418 which elicited a lower rate of TFs compared to the unfamiliar odour. The fact that similar  
419 numbers of TFs (ground and swab directed) were directed towards their own odour and the  
420 odour of tap water and a paper towel shows that novelty was not solely responsible for our  
421 lizards’ reaction. As tap water and paper towels are not odourless, we would expect increased  
422 TF rates to inspect the novel odour which we did not find. We acknowledge, however, that an  
423 additional control similar to what was used in previous studies (Bull et al., 1999a; 2000) is  
424 needed to completely rule out novelty as a cause for the strong effect we found. Furthermore,  
425 we can also rule out that diet differences caused the difference in response towards own and  
426 unfamiliar odour because all our lizards were fed the same diet.

427 Finally, our results also point towards a social function of scat piling. Although geckos  
428 produced less TFs towards scats this difference was small. Additional research could  
429 determine if geckos inspect scat piles of other individuals when available, if they are more  
430 likely to defecate in locations with their own scat present (Carpenter and Duvall, 1995), and

431 could investigate if lipids are deposited on scats by glands (Bull et al., 1999b). Furthermore,  
432 scat piling might have a possible function related to predator avoidance when predators use  
433 the odour of scats to locate refuges (Bull et al., 1999a; Carpenter and Duvall, 1995; Norris and  
434 Lopez, 2011). Studies on wild lizards should document the location of scat piles to determine  
435 if scat piles have an anti-predator function as well. Scat piles in locations that are not frequently  
436 visited by geckos would point towards an anti-predator function.

437 In summary, we provide first evidence for chemical self-recognition in a gecko species  
438 and a possible social function of scat piles. Further investigations are, however, needed to  
439 confirm true self-recognition in tokay geckos and to better understand the communicative  
440 function of scats. Future studies could also look at other forms of recognition such as  
441 discrimination between familiar and unfamiliar individuals, mate recognition and kin  
442 recognition of skin, femoral gland and scat odours. Tokay geckos are a good model species  
443 to investigate recognition in general as they show biparental care and form temporary family  
444 groups with their offspring (Grossmann, 2006; Somma, 2003). Such studies can potentially  
445 demonstrate more sophisticated social cognitive abilities than have previously been attributed  
446 to reptiles (Doody et al., 2013).

447

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452

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- 558

559 **Appendix**

560

561 Results tables

562

563 **Table A1.** Parameter estimates and test statistics for the generalised linear mixed zero-  
 564 inflation Poisson model looking at all tongue flicks produced by all tested individuals. The  
 565 models included a random effect of animal identity and an over-dispersion parameter of  
 566 session. Significant results are highlighted in bold. CI – confidence interval.

<b>Conditional model</b>					
<b>Parameter</b>	<b>Estimate</b>	<b>z-value</b>	<b>CI<sub>low</sub></b>	<b>CI<sub>up</sub></b>	<b>p-value</b>
Intercept	-1.924	-0.239	-17.681	13.833	0.811
<b>Scat</b>	<b>-0.406</b>	<b>-2.413</b>	<b>-0.736</b>	<b>-0.076</b>	<b>0.016</b>
<b>Water control</b>	<b>-0.556</b>	<b>-2.733</b>	<b>-0.954</b>	<b>-0.157</b>	<b>0.006</b>
<b>Own odour</b>	<b>-0.698</b>	<b>-3.562</b>	<b>-1.083</b>	<b>-0.314</b>	<b>0.0004</b>
<b>Male</b>	<b>-4.249</b>	<b>-4.674</b>	<b>-6.031</b>	<b>-2.467</b>	<b>2.95*10<sup>-6</sup></b>
Stimulus order	0.043	0.481	-0.133	0.219	0.631
<b>Trial</b>	<b>-0.196</b>	<b>-2.099</b>	<b>-0.378</b>	<b>-0.013</b>	<b>0.036</b>
Temperature	0.086	0.277	-0.524	0.697	0.782
<b>Zero-inflation model</b>					
<b>Parameter</b>	<b>Estimate</b>	<b>z-value</b>	<b>CI<sub>low</sub></b>	<b>CI<sub>up</sub></b>	<b>p-value</b>
Intercept	-1.462	-1.083	-4.107	1.184	0.279
Scat	-1.959	-1.820	-4.069	0.151	0.069
Water control	1.393	1.282	-0.737	3.523	0.200
Own odour	0.469	0.450	-1.574	2.511	0.653
Male	-17.667	-0.003	0.554	5.785	0.998

567

568 **Table A2.** Parameter estimates and test statistics for the generalised linear mixed zero-  
569 inflation Poisson model looking at all tongue flicks produced in the unfamiliar condition by all  
570 tested individuals. The models included trial and animal identity as random effects. Significant  
571 results are highlighted in bold. CI – confidence interval.

<b>Conditional model</b>						
<b>Parameter</b>	<b>Estimate</b>	<b>z-value</b>	<b>CI<sub>low</sub></b>	<b>CI<sub>up</sub></b>	<b>p-value</b>	
<b>Intercept</b>	<b>-2.662</b>	<b>-2.233</b>	<b>-4.998</b>	<b>-0.325</b>	<b>0.026</b>	
Scat	-0.318	-1.405	-0.761	0.126	0.160	
Delta SVL	-0.123	-0.667	-0.485	0.239	0.505	
<b>Zero-inflation model</b>						
<b>Parameter</b>	<b>Estimate</b>	<b>z-value</b>	<b>CI<sub>low</sub></b>	<b>CI<sub>up</sub></b>	<b>p-value</b>	
Intercept	-1.518	-1.817	-3.155	0.119	0.069	
Scat	-0.158	-0.143	-2.314	1.998	0.886	
Delta SVL	-0.662	-1.490	-1.533	0.209	0.136	

572

573



574 **Table A3.** Parameter estimates and test statistics for the linear mixed model looking at deep  
575 breaths per second. The model included session and animal identity as random effects. CI –  
576 confidence interval.

Parameter	Estimate	<i>df</i>	<i>t</i> -value	CI <sub>low</sub>	CI <sub>up</sub>	<i>p</i> -value
Intercept	0.489	35.2	0.352	-2.142	3.112	0.727
Scat	0.015	315.8	0.559	-0.036	0.065	0.576
Water control	0.023	315.3	0.727	-0.038	0.085	0.468
Own odour	-0.005	315.5	-0.151	-0.066	0.057	0.880
Male	0.108	18.9	1.879	-0.004	0.219	0.076
Stimulus order	-0.019	315.4	-1.191	-0.050	0.012	0.235
Trial	-0.025	39.0	-1.117	-0.070	0.023	0.271
Temperature	-0.006	35.1	-0.118	-0.108	0.096	0.907

577

578

579 **Table A4.** Parameter estimates and test statistics for the linear mixed model looking at breaths  
580 per second. The model included a random intercept of animal identity and a random slope of  
581 session. Significant results are highlighted in bold. CI – confidence interval.

Parameter	Estimate	<i>df</i>	<i>t</i> -value	CI <sub>low</sub>	CI <sub>up</sub>	<i>p</i> -value
Intercept	0.124	111.9	0.099	-2.296	2.514	0.921
<b>Scat</b>	<b>0.106</b>	<b>154.7</b>	<b>2.132</b>	<b>0.039</b>	<b>0.170</b>	<b>0.002</b>
Water control	0.044	142.9	1.163	-0.030	0.116	0.247
Own odour	0.020	140.7	0.512	-0.055	0.096	0.610
Male	0.008	19.1	0.143	-0.094	0.113	0.888
Stimulus order	-0.013	137.8	-0.686	-0.050	0.024	0.494
Trial	-0.032	59.2	-1.418	-0.077	0.014	0.162
Temperature	0.033	112.2	0.684	-0.059	0.127	0.496

582

583

584 **Table A5.** Parameter estimates and test statistics for the generalised linear mixed zero-  
585 inflation Poisson model looking at all ground tongue flicks across stimulus conditions in  
586 females. The conditional model included treatment, trial and animal identity as random effects,  
587 the zero-inflation model included animal identity as the random effect. Significant results are  
588 highlighted in bold. CI – confidence interval.

<b>Conditional model</b>						
<b>Parameter</b>	<b>Estimate</b>	<b>z-value</b>	<b>CI<sub>low</sub></b>	<b>CI<sub>up</sub></b>	<b>p-value</b>	
Intercept	-1.064	-1.239	-2.746	0.618	0.215	
Water control	-0.637	-1.899	-1.294	0.021	0.058	
<b>Own odour</b>	<b>-1.133</b>	<b>-3.872</b>	<b>-1.707</b>	<b>-0.560</b>	<b>0.0001</b>	
<b>Zero-inflation model</b>						
<b>Parameter</b>	<b>Estimate</b>	<b>z-value</b>	<b>CI<sub>low</sub></b>	<b>CI<sub>up</sub></b>	<b>p-value</b>	
Intercept	-1.463	-1.157	-3.942	1.016	0.247	
Scat	-1.693	-1.621	-3.739	0.354	0.105	
Water control	1.998	1.680	-0.333	4.329	0.093	
Own odour	0.240	0.203	-2.069	2.548	0.839	

589

590

591 **Table A6.** Parameter estimates and test statistics for the generalised linear mixed zero-  
592 inflation Poisson model looking at all swab tongue flicks across stimulus conditions in females.  
593 The conditional model included treatment, trial and animal identity as random effects, the zero-  
594 inflation model included animal identity as the random effect. Significant results are highlighted  
595 in bold. CI – confidence interval.

<b>Conditional model</b>					
<b>Parameter</b>	<b>Estimate</b>	<b>z-value</b>	<b>CI<sub>low</sub></b>	<b>CI<sub>up</sub></b>	<b>p-value</b>
Intercept	-0.483	-0.838	-1.613	0.647	0.402
<b>Water control</b>	<b>-1.405</b>	<b>-4.614</b>	<b>-2.002</b>	<b>-0.808</b>	<b>3.96*10<sup>-6</sup></b>
<b>Own odour</b>	<b>-0.927</b>	<b>-2.979</b>	<b>-1.538</b>	<b>-0.317</b>	<b>0.003</b>
<b>Zero-inflation model</b>					
<b>Parameter</b>	<b>Estimate</b>	<b>z-value</b>	<b>CI<sub>low</sub></b>	<b>CI<sub>up</sub></b>	<b>p-value</b>
Intercept	-1.018	-0.895	-3.249	1.213	0.371
Scat	1.912	1.597	-0.435	4.259	0.110
Water control	-21.217	-0.002	-16347.2	16304.9	0.998
Own odour	-1.809	-1.445	-4.262	0.645	0.148

596