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# Cloacal scent gland secretions are effective in a breeding season but not sex-specific in Japanese rat snake (*Elaphe climacophora*) (Chordata, Reptilia, Squamata, Colubridae)

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1 **Title**

2 Cloacal scent gland secretions are effective in a breeding season but not s  
3 ex-specific in Japanese rat snake (*Elaphe climacophora*) (Chordata, Reptili  
4 a, Squamata, Colubridae) [Scent gland secretions in *Elaphe climacophora*]

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12

13

14 **Abstract**

15 Although the odor of cloacal secretions in snakes is obvious, their functio  
16 n remains unclear. We tested whether these secretions are involved in sexua  
17 l communication and evaluated the seasonality of their effects. Using T-maz  
18 e assays across breeding and non-breeding seasons, we found that choices we  
19 re biased away from the scented arm in the breeding season, whereas choices  
20 were random in the non-breeding season. However, no clear sex-specific resp

21 onses were observed. Our findings emphasize that behavioral responses to cl  
22 oacal secretions are modulated by seasonality. Future studies are needed to  
23 decouple changes in signal chemistry from shifts in receiver sensitivity.

24 Keywords

25 chemical communication, cloacal scent glands, Colubridae, musk, seasonalit  
26 y, T-maze assay

27

## 28 Introduction

29 Chemical communication is a major facet of reptilian life that mediates soc  
30 ial and reproductive behaviors (Mason and Parker 2010). Snakes, in particul  
31 ar, rely heavily on chemical cues for sex recognition, trail-following, and  
32 courtship; for example, male snakes often follow chemical trails deposited  
33 by females during the breeding season to locate mates (Kroll et al. 1971; H  
34 eller and Halpern 1981; Ford 1986; Wilmes et al. 2012). Some chemical cues  
35 originate from sources such as skin lipids and secretions from cloacal scen  
36 t glands (cloacal secretions) (Mason and Parker 2010). Cloacal secretions h  
37 ave been hypothesized to mediate intraspecific chemical communication in sn  
38 akes (Darwin 1874; Brisbin 1968; Graves and Duvall 1988). Greene and Mason  
39 (2000, 2003) reported that female cloacal secretions modulate reproductive  
40 interactions through pheromonal inhibition of male courtship in *Boiga irreg  
41 ularis* (Colubridae). However, this function has only been tested in one spe  
42 cies. Moreover, although the conditions of the senders and receivers of sex

43 ual signals change between the breeding and non-breeding seasons (Mason et  
44 al. 1987; Lemaster et al. 2001), direct seasonal comparisons of cloacal sec  
45 retion effects remain scarce.

46

47 Here, we tested the seasonal responses of male and female snakes to female  
48 cloacal secretions in the Japanese rat snake *Elaphe climacophora* (Colubrida  
49 e). Using a standardized T-maze protocol during the breeding and non-breedi  
50 ng seasons, we aimed to examine the seasonal dependence of the potential se  
51 xual effects of cloacal secretions. Following Greene and Mason (2000, 200  
52 3), we predicted that males would show clear avoidance of female secretions  
53 during the breeding season, whereas females, not being the target of courts  
54 hip inhibition, would show no such avoidance. In the non-breeding season, t  
55 he responses of both sexes were expected to be weak or absent.

56

## 57 **Materials and methods**

### 58 *Study animals*

59 Between 2022 and 2025, we collected 30 adults (13 males and 17 females) of  
60 *E. climacophora* on Honshu Island, Japan. All snakes were housed at 22 ° C u  
61 nder a daily 12-h light/dark cycle. Snakes were fed once a week with thawed  
62 frozen mice or quails, and water was provided ad libitum. To standardize th  
63 eir starvation states, the snakes were food-deprived for at least three day  
64 s before each trial. Individuals in premolt or those refusing food were exc

65 luded a priori from behavioral testing. All experiments were performed at t  
66 he Center for Advanced Biomedical Sciences, TWIns, Waseda University.

67

### 68 *T-maze apparatus and odor stimuli*

69 We assessed behavioral responses to cloacal secretions using a binary-choic  
70 e T-maze. The apparatus consisted of a base arm and two choice arms made of  
71 transparent cylindrical acrylic tubes (60 mm inner diameter for all arms).  
72 The base arm was 300 mm long. Each choice arm was first extended 300 mm fro  
73 m the junction, then turned 90° and extended for an additional 300 mm. The  
74 odor stimulus was placed at either distal end of the second segment. The 60  
75 -mm inner diameter allowed unobstructed forward movement of the snakes with  
76 out excessive lateral freedom, the 300-mm base arm provided a short neutral  
77 sampling zone before the junction, and the 600-mm total distance from the j  
78 unction to each odor source reduced immediate visual or contact-based influ  
79 ences and allowed the test snakes to orient themselves using airborne odor  
80 cues. To further eliminate potential visual cues, an approximately 600-mm o  
81 paque screen obscured the view of the initial segments of the choice arms u  
82 ntil the test snake reached the junction. An electronic pump delivered gent  
83 le airflow equally to both distal ends of the choice arms, minimizing odor  
84 mixing and backflow. As an odor stimulus, we placed a Kimwipe tissue with f  
85 reshly collected cloacal gland secretion at the end of one choice arm and a  
86 tissue with distilled water at the end of the other arm as a control (Fukud

87 a et al. 2022). Cloacal secretions were collected from female donor snakes  
88 immediately before each trial by gently pressing around the donor's cloaca  
89 l region and dabbing the secretion onto the Kimwipe. Given that previous st  
90 udies suggest that cloacal secretions change over time (Greene and Mason 20  
91 06), all collected samples were used within 10 min of collection. The amoun  
92 t of secretions was visually standardized on the tissue (i.e., covering an  
93 area of approximately 1 cm in diameter). To eliminate potential confounds o  
94 f self-recognition, all test snakes were exclusively exposed to secretions  
95 from female donors other than themselves.

96

#### 97 *Experimental procedure*

98 For each trial, a single test snake was placed at the base arm of the T-maz  
99 e. The experimenter left the room and monitored the trial remotely via vide  
100 o (FDR-AX30; Sony Corporation, Tokyo, Japan) to reduce the cues associated  
101 with the experimenter's presence. A "choice" was defined as the head cro  
102 ssing a landmark 300 mm from the junction into a choice arm. Before the T-m  
103 aze experiment, the test snakes were left undisturbed for 10 min to settle.  
104 The trials were conducted under housing temperature and humidity condition  
105 s. The apparatus was washed with unscented soap and air-dried between the t  
106 rials. Captive females consistently oviposited in early August (2022-2025),  
107 confirming that they retained natural reproductive cycles under our housing  
108 conditions. Thus, we defined June-July as the breeding season and August-De

109 cember (strictly post-oviposition) as the non-breeding season (Fukada 197  
110 8). All odor donors were female snakes ( $n = 17$ ), and male and female test s  
111 nakes were tested in separate trials. The trials were conducted during the  
112 light phase of the daily cycle under standard fluorescent room lighting. Ea  
113 ch test snake was tested up to three times per season, with at least one da  
114 y between trials. In total, 34 valid choice trials were conducted using 23  
115 unique test snakes (13 males and 10 females). The majority of test snakes  
116 ( $n = 15$ ) were tested only once, while five were tested twice and three were  
117 tested three times. The complete dataset, including the individual trial hi  
118 stories, is presented in Supplementary Table S1. Trials were terminated and  
119 excluded if no arm was chosen within 90 min, a duration sufficient for all  
120 motivated individuals to reach the junction, based on our pilot observation  
121 s ( $n = 2$  excluded). The scented arm (left or right) was randomized across a  
122 ll trials and was approximately balanced within each season and sex group.

123

#### 124 *Statistical analysis*

125 We tested whether behavioral responses to female cloacal secretions depende  
126 d on the season and sex of the test snakes using a likelihood-ratio test be  
127 tween binomial generalized linear models (GLMs) with a logit link function.  
128 We incorporated the test snakes' choices of T-maze arms as a response vari  
129 able (1 = scented, 0 = control) into the models, including sex and season a  
130 s explanatory variables. To adjust for potential confounders, we included t

131 he side of scent presentation as a covariate. Our primary hypothesis was th  
132 at the effect of season on scent-arm choice would differ between males and  
133 females. Therefore, we tested it using a likelihood ratio test between mode  
134 ls, where the effect of the season-by-sex interaction was incorporated or n  
135 ot into the models.

136 To complement the confirmatory likelihood ratio test, we compared five cand  
137 idate models (Table 1) based on the corrected Akaike Information Criterion  
138 (AICc). This model comparison was not used to select variables for hypothes  
139 is testing but to quantify the weight of evidence for each predictor combin  
140 ation. The five models were a null model including only scent-arm side (M0)  
141 and models adding season (M1), the sex of the test snake (M2), both main ef  
142 fects (M3), or both main effects plus their interaction (M4). For M1, we re  
143 ported odds ratios (ORs) with Wald 95% CIs. To ensure that our results were  
144 not driven by pseudoreplication due to the repeated testing of eight test s  
145 nakes, we conducted a sensitivity analysis.

146

147 We created a subset of data containing only the first trial from each uniqu  
148 e test snake ( $N = 23$ ). We then refitted the candidate GLMs to this subset t  
149 o verify whether the seasonal effect remained consistent.

150

151 All statistical analyses were conducted in R 4.5.2 (R Core Team 2025) using  
152 “stats”, “lme4” (Bates et al. 2015), and “MuMIn” (Bartoń 2026) packag  
153 es.

154 We used Claude (Anthropic, San Francisco, CA, USA) to review the R scripts  
155 used for the statistical analyses.

156

### 157 *Ethics statement*

158 All procedures involving animals were reviewed and approved by the Waseda U  
159 niversity Committee for Animal Experiment (protocol nos. A22-020, A23-022,  
160 A24-035, and A25-028) and were conducted in accordance with the relevant in  
161 stitutional guidelines and regulations.

### 162 **Results**

163 We analyzed 34 valid trials after excluding two no-choice trials. These com  
164 prised 17 breeding season trials and 17 non-breeding season trials, with 10  
165 male and 7 female trials in each season. In the breeding season, test snake  
166 s chose the scented arm in 4 of 17 trials (24%), whereas in the non-breedin  
167 g season, they chose it in 10 of 17 trials (59%) (Fig. 1).

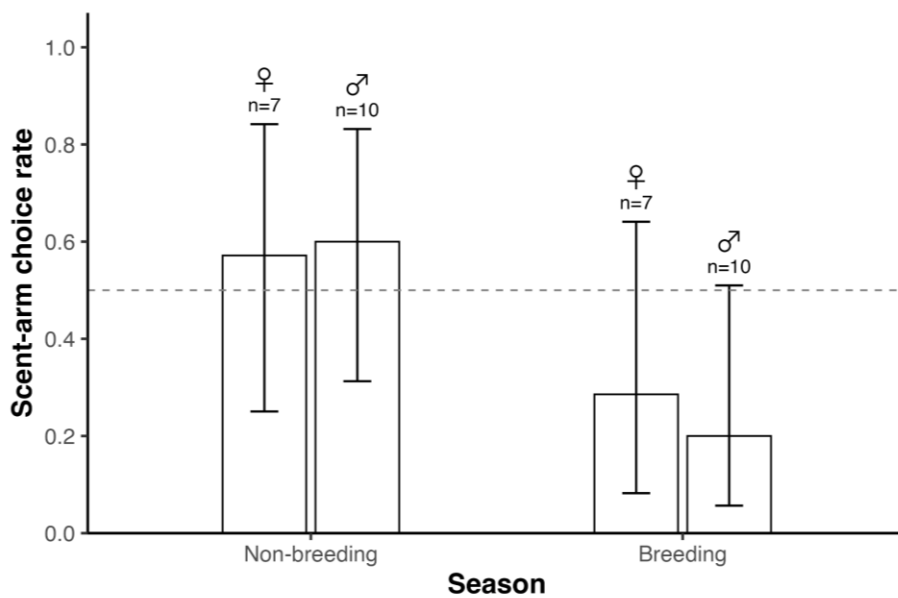
168

169 Our primary hypothesis was that the effect of the season on scent-arm choic  
170 e would differ between males and females; however, this interaction was not  
171 supported (likelihood-ratio test:  $\chi^2(1) = 0.385$ ,  $p = 0.535$ ). The sex of the  
172 test snake also had no detectable effect ( $\chi^2(1) = 0.011$ ,  $p = 0.915$ ).

173

174 In contrast, season had a significant effect on scent-arm choice ( $\chi^2(1) =$   
 175 4.893,  $p=0.027$ ). The odds of choosing the scented arm were lower in the br  
 176 eeding season than in the non-breeding season (OR = 0.18, 95%CI: 0.04-0.9  
 177 0). Model-based probabilities with the side of scent presentation fixed at  
 178 the reference level indicated that choices in the non-breeding season were  
 179 close to chance ( $\approx 0.46$ ), whereas the probability dropped to  $\approx 0.14$  in the b  
 180 reeding season, indicating marked avoidance of the female scent.

181



182

183 Figure 1.

184

185 Table 1.

186 Generalized linear models (GLMs) for scent-arm choice in T-maze trials.

Models	Variables	AICc	$\Delta$ AICc
M1	Side + Season	45.46	–
M0	Side	47.94	2.48
M3	Side + Season + Sex	48.03	2.57
M2	Side + Sex	50.35	4.89
M4	Side + Season + Sex + Season $\times$ Sex	50.41	4.95

187

188 All models include scent-arm side (left/right) as a covariate. Models were  
 189 ranked using the corrected Akaike Information Criterion (AICc).  $\Delta$ AICc indi  
 190 cates the difference from the best model.

191

192 The AICc-based model selection favored the model including seasons and scen  
 193 t-arm sides (M1; Akaike weight:  $w=0.576$ ), followed by the scent-arm side on  
 194 ly model (M0;  $w=0.167$ ) and the model with both season and sex (M3;  $w=0.15$   
 195 9) (Table 1). Models incorporating sex alone or the season-by-sex interacti  
 196 on had little support ( $w \leq 0.050$ ).

197

198 Eight test snakes were tested more than once, potentially causing pseudorep  
 199 lication. To address this concern, we conducted a sensitivity analysis usin  
 200 g only the first trial of each unique individual ( $N = 23$ ). In this subset,  
 201 the direction of the seasonal effect remained consistent (OR = 0.28, 95% C

202 I: 0.04-1.97), although the confidence interval included unity owing to the  
203 reduced sample size. This consistency in the effect direction suggests that  
204 the observed seasonal shift in behavior is not an artifact of repeated test  
205 ing.

206

## 207 Discussion

208 Our study revealed that behavioral responses to female cloacal secretions i  
209 n *E. climacophora* vary seasonally. Snakes chose scented arms less often dur  
210 ing the breeding season than during the non-breeding season. This result su  
211 ggests that female cloacal secretions elicit avoidance during the breeding  
212 season. However, this seasonal change was observed regardless of sex. The a  
213 bsence of a sex difference in *E. climacophora* contrasts with the patterns r  
214 eported for *Boiga irregularis* (Greene and Mason 2000, 2003). Greene and Mas  
215 on (2003) showed inhibition of male courtship behavior using direct behavio  
216 ral observation of courting pairs in a large arena. Given that our maze vis  
217 ually isolated the odor source, the present results reflect responses only  
218 to chemical cues. This difference in the experimental design might be the r  
219 eason why our findings differ from those of earlier studies in which cloaca  
220 l secretions were presented together with visual displays such as tail rais  
221 ing (Greene and Mason 2000, 2003). Thus, a standardized methodology is requ  
222 ired for effective comparison, although our study casts doubt on the primar

223 y function of secretions in sexual communication.

224

225 An alternative explanation consistent with our observations is that these s  
226 ecretions serve a defensive function (Weldon and Vander Meer 2025). Their o  
227 dor has reportedly been interpreted as an alarm cue by conspecifics (Brisbi  
228 n 1968; Graves and Duvall 1988). The fact that both male and female snakes  
229 produce cloacal secretions also supports this alternative hypothesis. The p  
230 ronounced avoidance observed exclusively during the breeding season may ref  
231 lect a seasonally gated risk aversion mechanism. During the breeding seaso  
232 n, extensive mate searching by males and oviposition site selection by fema  
233 les significantly increase their mobility and exposure to predators. Given  
234 that the baseline predation risk is higher during this active period, indiv  
235 iduals may become more responsive to alarm cues, resulting in a strong avoi  
236 dance of areas bearing the odor of defensive musk. Indeed, mammalian predat  
237 ion pressure on a congeneric snake (*Elaphe taeniura schmackeri*) is signific  
238 antly higher in summer than in winter (Tobe et al. 2024). Thus, these secre  
239 tions may serve dual defensive and communicative functions, with behavioral  
240 responses prioritized based on seasonal risk.

241

242 A limitation of our experimental design is the inherent confounding between  
243 the seasonal state of the odor donors and that of the test snakes. As we us  
244 ed freshly collected secretions in all trials, breeding-season trials neces

245 sarily used odors from breeding-season females, whereas non-breeding-season  
246 trials used odors from non-breeding-season females. Consequently, we cannot  
247 determine whether the observed behavioral shift arose from seasonal changes  
248 in the secretions or in the receiver state, as the chemical composition or  
249 absolute concentration of the secretions may change seasonally. Thus, the e  
250 cological context and olfactory sensitivity of the receivers may not be con  
251 stant. Future cross-seasonal bioassays and comparative chemical analyses ar  
252 e required to decouple signal chemistry from the receiver state.

253

## 254 **Conclusions**

255 By explicitly contrasting responses across seasons under a single controlle  
256 d paradigm, our study indicates that responses to female cloacal secretions  
257 are season-dependent in *E. climacophora*. Therefore, recognizing seasonality  
258 is important for interpreting the functions of cloacal secretions in this s  
259 pecies and possibly in snakes more broadly. Rather than a fixed “pheromona  
260 l” signal, these secretions appear to be a seasonally modulated cue whose  
261 behavioral meaning emerges from both the chemistry of the signal and the in  
262 ternal state of the receiver.

263

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### 333 Figure legends

#### 334 Figure 1.

335 Scent-arm choice rate of *Elaphe climacophora* in T-maze trials during the n  
336 on-breeding and breeding seasons in response to the scent of cloacal secre  
337 tions of conspecific females. White and gray bars represent female and mal  
338 e test snakes, respectively. Error bars indicate 95% Wilson confidence int  
339 ervals. The dashed horizontal line indicates the chance level (0.5). Numbe  
340 rs above bars denote sample sizes.

341