1 **Title:**

2 Aggressive interactions between smooth-coated otters and water monitor lizards in

3 Singapore

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5 **Running title:**

6 Aggressive otter-monitor interactions

7

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18

19 **Abstract:**

20

21 Smooth-coated otters (*Lutrogale perspicillata*) and Malayan water monitor lizards (*Varanus*

22 *salvator*) occupy similar habitats and and interact regularly in Singapore's waterways. These

23 interactions have a range of potential outcomes and are sometimes lethal. Few formal

24 behavioral studies exist for either species. We analyzed interactions between otters and

25 monitor lizards by gleaning data from publicly available videos from citizen scientists to

26 examine what factors influence aggressive and defensive behaviors, and what influences

27 vigilance in otters. Behavioral sequence analysis revealed no obvious monitor lizard

28 behavior that predicted otter aggression towards monitors. We found that the presence and

29 number of otter pups is positively associated with otter aggression. Otters also tended to be

30 more vigilant in groups with more pups, and more vigilant on land than water. Monitor

31 lizards displayed aggressive and defensive behaviors more frequently than did otters,

32 regardless of whether the otters were aggressive towards lizards. These observations

33 suggests that otters vary their aggression and vigilance levels depending on the context of

34 each interaction.

35

36 **Key words:**

37   Smooth-coated otters, monitor lizards, aggression, group defence, *Lutrogale perspicillata*,

38 *Varanus salvator*, citizen science

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43   **Elements:**

44   Text 5570 words

45   Nine figures (Figure 1 – Figure 9)

46   Four tables (Table 1 – Table 4)

47   Two Appendixes (Appendix 1 is a table; Appendix 2 is a figure)

48

49   **Introduction**

50   Smooth-coated otters are medium-sized aquatic carnivores (about 10 kg) that live

51   throughout South and Southeast Asia (see Hwang & Larivière 2005 for review). They live in

52   both freshwater and brackish environments where they feed on fish and other aquatic

53   organisms. Smooth-coated otters are cooperative breeders that live in family groups

54   ("romps") of up to 14 or more individuals (Hwang & Larivière 2005, Khoo & Sivasothi 2018a,

55   2018b, personal observation). They function as the apex predator in many ecosystems and

56   can be a sign of healthy waterways (Theng et al. 2016). In Singapore, otters had disappeared

57   by the 1970s, coinciding with increased urban development; partly due to an active

58   campaign to clean Singapore's waterways, smooth-coated otters have returned (Khoo &

59   Sivasothi 2018b), and sightings of smooth-coated otters surged around 2014, in part

60   because otter watchers in Singapore could easily share their sightings over social media,

61   along with the rapid increase in the otter population (Theng & Sivasothi 2016). Singapore's

62   otters have been extremely successful in their recolonization of local waterways (Khoo &

63   Lee 2020), and there are now at least 11 family groups across Singapore (Khoo & Sivasothi

64   2018b) as well as lone otters not attached to any romp.

65

66   Otters encounter other species, sometimes with negative consequences. Feral dogs can be

67   aggressive to otters and vice versa (Clements 2019), and social media includes reports of

68   otters harassing estuarine crocodiles (*Crocodylus porosus*; Toh 2018), a behavior similar to

69   that of giant otters (*Pteronua brasiliensis*), which sometime attack caimans (Ribas et

70   al. 2012). Smooth-coated otters also frequently encounter Malayan water monitor lizards

71   (*Varanus salvator*). These large lizards (up to 20 kg) inhabit a range of tropical environments

72   from the Molucca Islands to Sri Lanka (Twining & Koch 2018). Water monitors are

73 opportunistic, and like smooth-coated otters they prey on fish and other animals, but unlike

74 otters also frequently scavenge (Twining & Koch 2018). Monitors persisted in Singapore,

75 even as otters were driven out by a deterioration of suitable habitat. Today, they are

76 common in Singapore's waterways, whether concrete canals or natural riverbanks.

77

78 Interactions between otters and monitors can take several forms. Water monitors can be

79 commensalists that scavenge fish remains otters leave (personal observations),

80 kleptoparasites that steal fish from otters (e.g., Tan 2019), competitors for food resources,

81 or predators that attack young otters (e.g., Lee 2019; personal observations). Sometimes

82 otters and monitors interact aggressively (Figure 1), which can lead to otters attacking

83 monitors and to the injury or even death for the monitor lizard (e.g., Mitchell 2021). Otter-

84 monitor conflict has been noted before (Goldthorpe et al. 2010), albeit from a single

85 observation in Peninsular Malaysia.

86

87 Few formal studies have been conducted on either smooth-coated otter or monitor lizard

88 behaviors. The demographics of smooth coated otters in Singapore and elsewhere are well-

89 studied (e.g., Theng & Sivasothi 2016; Theng et al. 2016; Khoo & Sivasothi 2018a, 2018b),

90 but there is scant literature on their behavioral traits, especially those that may be unique to

91 urban otters. Urban environments change behaviors in other animals (e.g., Slabbekoorn &

92 den Boer-Visser 2006; Breck et al. 2019), and urban otters also adjust to their environments.

93 They construct unique holts in manmade structures (Khoo & Sivasothi 2018b) and use

94 manmade features like ladders in their movements (Lay 2021). The robust population of

95 otters in Singapore is notable because in other areas, smooth-coated otters are associated

96 with natural landscapes (Kamjing et al. 2017). Likewise, outside of a few ecological and

97   descriptive studies (e.g., Twining & Koch 2018; Uyeda 2009), very little is known about

98   water monitor behaviors, especially in urban environments.

99

100   These sometimes-violent encounters between otters and monitor lizards raise questions of

101   their causes. In other species, otter groups can be formidable. In one study, giant South

102   American otters (*Pteronura brasiliensis*) mobbed jaguars until the jaguars left the area, but a

103   lone otter did not engage the larger cat by itself (Leuchtenberger et al. 2016). Smooth-

104   coated otters live in family groups ("romps") like those of giant otters, and group dynamics

105   may play a role in their interactions with water monitors. Otter pups are particularly

106   vulnerable; the presence and number of pups may influence otters' responses. Likewise,

107   whether monitor lizards' are aggressive or defensive may depend on both otter behaviors

108   and the otter group composition. Otters are vigilant to potential threats, adopting a

109   characteristic upright posture and other behaviors in and out of water, but the relationship

110   between group size, the number of pups present, and how vigilant otters are to monitors or

111   other threats, has not been addressed. Here we examine encounters between otters and

112   monitor lizards to assess factors that lead to aggressive interactions, and specifically to

113   otters attacking monitor lizards.

114

115   Collecting behavioral data can be extraordinarily time consuming, especially data related to

116   uncommon events like otter-monitor interactions. However, the ease with which consumer-

117   grade technology like smart phones and relatively inexpensive cameras can record photos

118   and videos has led to an explosion of raw data on social media and other corners of the

119   internet. Crowd-sourced data has been used for citizen science studies related to

120   occupancy, ecology, and conservation for some time (see Cooper 2016 for review). Citizen

121   science can also be effective in animal behavior studies, and some studies glean data from

122   public sources (e.g., Boydston et al. 2018; Loong et al. 2021; Bungum et al. 2022). Gleaning

123   data from public repositories, such as social media or YouTube, can be particularly useful

124   when the behavior or species is rare or difficult to find (Nelson & Fijn 2013). Here we glean

125   data from publicly available sources of video to address otter-monitor interactions. Because

126   social media posts amount to *ad lib* sampling (Altmann 1974), there is a potential for bias.

127   We try to avoid that by narrowing the scope of our study to otter-monitor interactions.

128

129   **Materials and Methods**

130

131   Almost all data in this study came from online sources due in part to the restrictions

132   imposed by COVID-19 pandemic. Selected videos were obtained from YouTube

133   (www.YouTube.com) using search terms such as "Singapore otter monitor" and "Singapore

134   otter lizard" (Appendix 1). One YouTube channel had a large collection of videos,

135   "RandomSG" (Wong 2019; www.youtube.com/channel/UCLz7pIXxzaFzz_MN02kNzsQ), and

136   the videos posted on this channel were not edited. Otters in Singapore's waterways are

137   generally active early and late in the day (roughly 06:30 to 10:00 and 16:00 to 19:30), and

138   there was a nearly complete record of twice-daily videos spanning 2019-2021, ceasing only

139   during the mandated lockdowns due to COVID-19. The regular recordings were free of

140   obvious bias and allowed us to track pup age over time. We identified 160 videos with

141   potential interactions between otters and monitors; due to quality, duplications, and scoring

142   protocols, we scored 63 for the study, all taken between October 2018 and July 2019, of the

143   Pandan otter romp, which resided near the Ulu Pandan River in southwestern Singapore. (In

144   Singapore, people name otter romps after the first place they were observed; in 2019, after

145   the events in this study, the Pandan romp was forced out of the river by the Jurong Lake

146   Gardens romp.) The Pandan romp consisted of 9 adults and up to 9 pups at the time. Videos

147   provided were taken using a handheld, fixed-lens DSLR camera, generally positioned at the

148   bank opposite the otters' activities, 10-30 m away.

149

150   These 63 videos were chosen from a time of 70 days before the first emergence of the pups

151   in May 2019 until 40 days post-emergence. Pups remain in the holt for roughly six weeks

152   after birth (Khoo and Sivasothi 2018a). At this age, pups are not yet fully weaned, and so are

153   still heavily reliant on romp members' help to survive (Hwang & Larivière 2005). This

154   chronologically complete set of videos allowed us to compare behavior of adults before

155   pups were born, after pups were born but before they emerged from their holt, and after

156   the pups emerged and as they aged.

157

158   First we examined the association between otter and monitor aggression in all 63 videos

159   without distinguishing between potential aggression based on a minimum distance criteria.

160   If monitor lizards and otters came within one otter body length of each other (about 1m),

161   that encounter had the potential for direct aggressive. Videos with the potential for

162   aggressive encounters were then divided into "bouts", where each bout lasted up to one

163   minute before and after: 1) an aggressive behavior between otters and monitors; 2) the first

164   instance of otters and monitors coming within one otter body length of each other; or 3)

165   until the subjects left the frame and scoring ceased within the one-minute window. Videos

166   without the potential for aggression could not be separated into bouts because otters and

167   monitors were never close enough to physically interact, although monitors were free to

168   display a defensive posture. (It is difficult to disentangle monitor aggression and defense,

169   and here we group monitor aggressive and defensive behaviors.) We treated bouts within

170   videos as independent events. The bout ended if the lizards and otters turned away and

171   disengaged from each other; if they performed a "benign" rather than aggressive or

172   defensive behavior – typically something like "sit" or "groom" – or if a focal otter interacted

173   with another otter. By these criteria the average bout length was 53.24 + 35.78s (median

174   50.49s). Otters are extremely active and often engage in several behaviors per minute. In

175   the one incident in which there were back-to-back bouts between the same monitor and

176   otter, the behavior that ended one bout began the next. By these criteria we observed 234

177   bouts within the 63 videos. Each bout included 1 to 18 otters and f 1 to 3 lizards. All 234

178   bouts reached a conclusion before the videos cut off, and there were no recorded serious

179   injuries in any of the scored observations. There were also no edits or other post-production

180   cuts within videos, i.e., the videos accurately reflected interactions. (Many otter watchers in

181   Singapore edit their videos before posting them.)

182

183   We analyzed behavioral sequences in the 234 bouts to describe typical behavioral

184   exchanges between otters and monitor lizards, and to examine possible suites of behaviors

185   that might spur attacks. In our behavioral sequence analysis, we included behaviors from

186   both otters and monitors to address cause and effect between species. We used four pilot

187   videos, excluded from the final analysis, to generate an ethogram of otter and monitor

188   behaviors (Table 1; Figure 2). We scored the 63 videos using the Behavioral Observation

189   Research Interactive Software (BORIS; (Friard & Gamba 2016; http://www.boris.unito.it),

190   using an all-occurrences approach (Altmann's 1974). Smooth-coated otters usually lack

191   individual markings, which precluded our tracking individuals from one video to the next.

192   Within each video, we assigned each otter and each monitor lizard an identifier ("subject")

193   based on the animal's initial position at the start of the interaction. If either the otter or

194   lizard exited the frame, we ceased all scoring, i.e., both otter and monitor needed to be in

195   view for any scoring to occur. If both subjects returned to the frame, they retained their

196   subject designation only if we could be certain they were the same individuals. If there were

197   any doubt or lack of clarity, subjects were reassigned and we analyzed subsequent

198   behaviors as a new bout. We exported behavioral strings from BORIS to the BORIS tool

199   Behatrix (http://www.boris.unito.it/pages/behatrix), in which we conducted a 10,000

200   permutation test to limit the behavioral transitions to those that occurred more frequently

201   than chance ($p < 0.05$, transition occurring at least 1% of the time).

202

203   For each video and bout we also recorded: presence of pups, number of pups if present,

204   number of adults, number of monitors, age of pups, whether the events happened on land

205   or water, whether there was an aggressive interaction, location of interaction, time of day,

206   relative size of monitor to otter, minimum distance between otter and monitor, and general

207   activity of otters (Table 2). We then constructed generalized linear mixed models (GLMMs),

208   where we examined each bout as unique (n=234), unless it occurred both on land and in

209   water, for a total of 270 analyzable interactions. We considered general movement between

210   land and water benign behaviors, meaning the bout would end and a new one begin, should

211   this occur. We considered the presence or absence of otter aggression, per otter, per bout.

212   We examined otter vigilance with linear mixed models (LMMs), where we treated the

213   initiation of otter vigilance as a point event, and because bouts varied in length, we treated

214   vigilance as a continuous rate, per otter, per bout-minute. For consistency, we analyzed

215   vigilance using the same subset of potentially aggressive encounters, even though vigilance

216   could potentially occur when otters and monitors were further than one body length apart.

217

218   We generated GLMMs and LMMs with functions glmer and lmer, depending on whether the

219   dependent variable was binomial (otter aggression) or continuous (vigilance), using the R

220   package (R Core Team 2021; https://www.R-project.org/) lme4 (Bates et al. 2020). Fixed

221   and random effects are in Table 2. We visualized flow diagram scripts from BORIS using the

222   R package "DiagrammeR" (Iannone 2020), and we used the Tidyverse package (Wickham &

223   RStudio 2019) for data analysis and created figures with the ggplot2 and sjPlot packages.

224   Because this is a descriptive study, we present multiple linear models and then discuss their

225   common features.

226

227   **Results:**

228

229   Monitor lizards displayed aggressive behaviors in more videos than otters did. Monitors

230   displayed aggression in 79% (50/63) of videos, but otters were generally not overtly

231   aggressive, displaying aggressive behaviors in only 27% (17/63). We found a significant

232   association between otter and monitor aggression among videos (Fishers exact P = 0.013).

233   In all videos where otters displayed aggression, monitors also displayed aggression (17/17);

234   but otters were only aggressive in 34% of the videos where monitors were aggressive

235   (17/50). Monitors displayed aggression in 72% of videos where otters did not (33/46), and

236   otters never displayed aggression when monitors did not (0/13). Including only videos

237   where otters and monitors were within a body length, monitors almost always displayed

238   aggressive behaviors (33/34; 97%) while otters did only half the time (17/34).

239

240   To gain more insight into the causes of aggression, we examined the behavioral sequences

241   within bouts. Permutation tests on behavioral sequences revealed that otter aggression

242   typically led to monitor aggression, and not the other way around (Figures 3 & 4). For

243   example, otters floated near, dived, then attacked monitor lizards (Figure 3, arrow a).

244   Aggressive otter behaviors included biting or touching the head or tail of the monitor, which

245   often responded by either curling its tail and frilling its neck, or by whipping its tail (Figure

246   3, arrows b, c & d). Although monitors often whipped their tails when attacked, they did not

247   always hit; on land and in water (Figures 4A & 4B), monitors were about four times as likely

248   to whip their tails after otters touched them as to successfully connect (22.2% vs 5.6%).

249   Many aggressive behaviors by otters did not have any significant monitor precursors, but

250   rather were starting points for a sequence of aggressive behaviors (e.g., Figure 4A, arrow a).

251   In the water, otters often dived and emerged next to the lizard, which led to the lizard

252   escaping away (Figure 4B, arrow d). Some behaviors frequently led to one another, such as

253   lizards frilling and curling (Figure 4A, arrow b), or otters alternately displaying vigilance and

254   playing (Figure 4A, arrow c). (For the purpose of this study we did not distinguish among

255   play behaviors.)

256

257   We examined whether the composition of otter groups within bouts influenced whether

258   otters were aggressive. We found otters were more likely to display aggression towards

259   monitor lizards in otter romps with pups than in romps without pups (Figure 5; Fisher's

260   Exact test p = 0.0018). We further examined the effects of group composition on the

261   occurrence of otter aggression by fitting GLMMs to the number of pups, adults, pup age,

262   and the environment (land or water) (Table 2). In all models, the number of pups in a group

263   was a significant predictor of otter aggression (Table 3; Figure 6); groups with more pups

264   were more likely to be aggressive. In the best model (Model 1; AIC = 59.1), the number of

265   adults, the interaction between number of pups and adults, and pup age, were also

266   significant predictors of otter aggression (Figure 6). However, in the simplest model, Model

267   2 (AIC = 60.6) only pups predicted otter aggression (Figure 7A). In Models 3 and 4 the

268   number of adults also played a role in predicting otter aggression. In Model 3 (AIC = 62.3)

269   the coefficient estimates for the number of pups and adults suggests a sigmoidal equation,

270

271    $Z = - 11.58*Adults + 12.15*Pups$

272

273   which implies a line of inflection points for the binomial GLMM with a slope,

274

275    $adults = 1.05*pups$

276

277   This result suggests that if there were more pups than adults in a group, adults were likely

278   to display aggression towards monitor lizards (Figure 7B; Appendix 2), and therefore, groups

279   with more adults required more pups before becoming aggressive. Model 4 includes the

280   interaction between the number of pups and adults as a significant predictor of otter

281   aggression (Figure 7C). Although Model 4 (AIC 77.2) has less support than Models 1, 2, and

282   3, the effect of adults is qualitatively similar to that in Model 3: more adults in a group

283   shifted the inflection point for otter aggression (Figure 7C). Pseudo-R^2 values (Nakagawa

284   and Schielzeth 2013) for these models ranged from 0.031-0.064 (Table 3), but notice that

285   low pseudo-R^2 values are typical of logistic models (Hosmer et al. 2013).

286

Vigilance

288   We examined what influenced otter vigilance by fitting the same fixed and random effects

289   (Table 2) to LMMs explaining the rate of vigilance (Table 4). The first three vigilance models

290   performed similarly (AIC = 650.0 to 653.3; Table 4); and some combination of pups,

291   environment, and pup age were significant predictors in all four models. The number of

292   pups in a group was a significant predictor in 3 out of the 4 models (Figure 8). There was a

293   difference between vigilance rates on land and water (Figure 9A); adult otters displayed

294   higher vigilance levels on land. Pup age was a significant predictor of otter vigilance in

295   Model 4 (Figures 8, 9B). All four models have pseudo-R^2 values above 0.3, indicating

296   reasonable explanatory power, especially for an unmanipulated observational study (Table

297   4).

298

Discussion

300   In interactions between otters and monitor lizards, we found monitor lizards were

301   aggressive or defensive far more often than are otters. Monitors adopted defensive

302   postures, consisting primarily of a frilled neck and curled tail, even when otters were too far

303   away to cause any physical harm, and monitors were especially aggressive or defensive

304   when otters were within range of an attack (33/34 observations). The frequency of

305   defensive monitor lizards suggests that otters are not responding to monitors, usually, but

306   that monitors respond to the otters' presence and approach. In general monitors react to

307   otters as a threat.

308

309   Our behavioral sequence analysis supports this conclusion. Many of the monitors' defensive

310   and aggressive behaviors are preceded by an otter behavior, notably otters biting or

311   touching monitors' tails (Figures 3 & 4), and in water these behaviors are often preceded by

312   diving or floating nearby (Figure 4). Monitors nearly always frill their necks and curl their

313   tails when an otter is near them on land, even when the otter does not directly approach

314   the lizard. Behavioral sequence analysis revealed no single cue from lizards that caused

315   otters to react aggressively; nor was a cue obvious from our personal observations. Some

316   behaviors led to predictable outcomes, e.g., if a monitor whipped its tail at an otter, then

317   the otter retreated, but we found no behaviors that predicted why the otters first attacked

318   the lizard.

319

320   Adult and subadult otters are fast and extremely agile swimmers, much more so than

321   monitor lizards, even though monitors spend much of their day in water. Monitors

322   frequently exit waterways and head onto land when otters are near; we observed this in 20

323   of the 63 scored videos, while a monitor escaped into the water only once. Once on land,

324   monitors typically stay in place and adopt defensive postures. These behaviors suggest that

325   monitors are less vulnerable to otters on land than in water, even when otters have a

326   numerical advantage. Monitors can quickly scurry away on land, and their tail-whips are less

327   affected by water, possibly increasing their effectiveness on land. Monitors on land are also

328   likely able to better view the entire otter romp and avoid being attacked from below the

329   water surface, which occurred fairly often. Perhaps most importantly, otters cannot

330   submerge monitors on land and kill them, which was observed twice in interactions that

331   occurred after the study period (e.g., Mitchell 2021). In one of the fatal interactions

332   observed, a second, much larger lizard was in the water prior to the attack, and very slowly

333   swam away as more and more otters attacked the smaller lizard. The larger lizard may have

334   been just as vulnerable as the smaller lizard, despite its size, and took actions to leave the

335   scene.

336

337   Monitors generally reacted the same way to otters, especially when otters were within one

338   body length. The consistent defensive reaction of monitors suggests that the lizards do not

339   primarily use pups as a cue. However, anecdotal evidence suggests monitors can distinguish

340   pups from adults, including a monitor lizard attacking of a pup (Lee 2019) as well as one

341   chasing a pup in one of the 63 videos in our study. There, a medium-large lizard chased a

342   pup into the holt, with a few adult otters nearby. The pup had emerged from the holt about

343   one month earlier, suggesting it was around 10 weeks old, and it was able to outrun the

344   lizard. The monitor then moved away with no aggressive reaction from the adult otters.

345   Presumably the monitor's actions were predatory, and it is not clear why the adult otters

346   did not react in this case.

347

348   **Otter aggression**

349   Overall, we found that otters were only aggressive in encounters where monitors were also

350   aggressive. However, that included situations where the otters instigated an attack, and the

351   monitors responded, i.e., otters are not responding to monitor aggression *per se*. This

352   observation supports the notion that monitors are reacting to the presence of the otters,

353   rather than otters reacting to the behaviors of the lizards. Our sequential analysis did not

354   give a clear indication of a "trigger" for otter aggression, other than a monitor approaching

355   the otter head on, which was a rare occurrence (3.8% of transitions). Although otter

356   aggression towards monitor lizards can be lethal, in general otters are not especially

357   aggressive, displaying aggression half the time an attack was possible.

358

359   In all the models we examined, the number of otter pups in a group contributed to otter

360   aggression towards monitor lizards. Otters are less likely to be aggressive in the absence of

361   pups, and otter aggression is more likely as the number of pups increases, especially if there

362   are more than five pups. When more pups present, there is a greater chance that at least

363   one of them will encounter a threat. Otter pups are notoriously curious and active; they

364   show little hesitancy to approach or even touch a monitor lizard. We generally observed at

365   least one adult otter in the immediate vicinity of pups, but there were times when it seemed

366   as if the adults could not oversee all the pups at once. One pup might wander near a

367   monitor, and an adult would then attack the lizard; this was the case in one of the fatal

368   incidents we observed (below).

369

370   One observation that occurred after our study period was especially illustrative. A small

371   monitor was attacked and partly eaten by the romp of 20 otters at Ulu Pandan (this was the

372   Jurong Lake Gardens romp; they displaced the original Pandan romp in early 2020). Here, a

373   pup approached and contacted the lizard, which whipped its tail, leading to the ensuing

374   melee. Pups in the romp were very young, having only emerged from the holt about one

375   week prior. After a series of tail-whips kept the adult otters at bay, the lizard maintained its

376   defensive stance as the otters appeared to regroup nearby on the bank. Notably, one adult

377   otter began carrying the pups away from the lizard, towards the holt, with the pups

378   scurrying back down in between drop-offs. After a minute of attempting to shift pups and

379   milling around, one adult charged the monitor and the rest followed suit. The otters flipped

380   the monitor onto its back and dragged it into the river, where they continued to attack it for

381   over 30 minutes. They later appeared to begin eating the floating corpse. This occurrence

382   supports the idea that the lizards are vulnerable to large romps of otters, even romps with

383   young pups. It builds on Goldthorpe et al.'s (2010) observation, which speculated on but did

384   not confirm the death of the lizard and subsequent consumption by the otter.

385

386   Adult numbers play a role as well. In two of the five models predicting otter aggression, the

387   number of adults had a significant effect, and in three models the interaction between the

388   number of adults and pups had a significant effect (Table 3). The combined effects of adults

389   and pups were qualitatively similar across models (Figure 6, Appendix 2): if few adults are

390   present, having only a few pups in a group can lead to otter aggression; with more adults in

391   a group, more pups need to be present to lead to aggression. Small groups of adults can be

392   aggressive. Even lone otters sometimes attack monitors and even larger species, such as

393   estuarine crocodiles (Goldthorpe et al. 2010). One explanation for the relationship between

394   adults and aggression is that larger numbers of adults are a natural deterrent to monitor

395   attacks. Consequently, in groups with more adults, otters may be less prone to react to

396   monitors as threats. Another possibility is that, with larger numbers of adults, there are

397   fewer wayward pups. Larger groups may have more babysitters, effectively. We observed

398   groups with wide ranges of adult and pup numbers, including several adults with few pups,

399   so the pattern is unlikely to be an artefact of group size, per se.

400

401   Group composition itself could play a role, and which adults are present may determine

402   whether otters are aggressive or not. For example, if certain individuals such as the breeding

403   pair initiate attacks on monitor lizards, then additional adults may not increase the chance

404   of aggressive responses to monitors and may even dilute the breeding pair's ability to

405   respond to monitors. We cannot tease apart the effects of individual otters without being

406   able to identify individuals, which we could not do in this study. Some evidence suggests

407   that different otters have different tendencies to attack, however. In one bout, a large

408   monitor lizard chased an otter pup under a human-made structure while several adult

409   otters watched, but none reacted aggressively. Adult offspring may have been waiting for

410   another otter to respond to monitors or may not have known what to do.

411

412   Pup age may also play a role. We found pup age was positively related to otter aggression in

413   the best model (Figure 6) but negatively related to otter vigilance (Figure 8). Presumably at

414   some point pups become independent enough that adults do not need to watch over them,

415   but it is hard to reconcile these contrasting patterns in aggression vs vigilance. Pup age, like

416   other factors in this observational study, warrants further investigation.

417

418   **Vigilance**

419   In none of our models did the number of adults in a group have a significant effect on

420   vigilance rates. This differs from many other studies of vigilance, where group size often

421   decreases vigilance rates (see Quenette 1990, Fernández-Juricic E 2012). However we found

422   that vigilance rates generally increase as the number of pups in a group increase, which

423   supports the hypothesis that adult otters increase their vigilance rates to compensate for

424   unequal pup contribution. The effect was significant in 3 out of our 4 models. Pups are

425   curious and frequently venture near lizards; adults likely need to keep a better lookout.

426   Vigilance is typically interspersed with other stationary riverbank behaviors, such as

427   grooming and playing, but we found it did not by itself lead to aggression (Figures 3 & 4).

428   Pup age was a significant factor towards increased vigilance levels in one model (model 4,

429   Figures 3 & 4), but was either insignificant or marginal for the other three models. The

430   duration of this study may not have been long enough to measure a change in adult

431   behavior. At some point pups grow up, and presumably adults stop compensating for them

432   then.

433

434   Vigilance rates were also higher when the otters were on land than in water. There could be

435   several reasons for increased vigilance rates on land. One is that visibility is less obstructed

436   on land. Otters often go onto banks to groom, eat, or visit spraint sites, and the group

437   remains more stationary than in water, allowing otters to better "keep watch" over each

438   other. But predators can spot otters, too, and otters on land may be more vulnerable to

439   predators than swimming otters. The increased risk may compel otters to be more vigilant

440   on land. On land, they are likely more vulnerable not just to large monitors, but also to

441   packs of dogs and even crocodiles (Clements 2019), plus, of course, humans. Swimming

442   otters' agility seems to explain why lizards are reluctant to be in the water when otters are

443   around; there are few animals in Singapore's waterways that otters cannot outswim. The

444   difference between land and water was probably not an artefact of our criteria for vigilance;

445   we defined vigilance such that it could be observed on land and water.

446

447   Our study was not aimed at water monitor lizards, *per se*, but so little research exists on wild

448   monitor behavior that it provided some insights. Otter watchers and other scientists had

449   hunches that monitor lizards sometimes avoid smooth-coated otters, and our analyses bear

450   this out: monitors respond defensively to otters. We observed only one incident of what

451   was presumably a failed attempt by a monitor lizard to prey on an otter pup. Whether

452   monitors regularly prey on otter pups is something we cannot ascertain from this study.

453   Adult otters may respond aggressively to monitors, not specifically because they are a

454   threat to pups, but because the monitors are large and live in the same areas. Anecdotally,

455   groups of smooth-coated otters engage aggressively with larger species, such as dogs (e.g.,

456   Chua 2018), crocodiles (e.g., Choudhary 2019), and occasionally even tigers

457   (Narasimhamurthy 2021), and romps of giant otters engage with caimans (Ribas et al. 2012)

458   and jaguars (Leuchtenberger et al. 2016). Monitor lizards might simply do their best to avoid

459   romps of angry otters.

460

461   Our findings derive from a study of a single romp of otters living on a highly modified river in

462   Singapore, the Ulu Pandan River, where otters and monitors are both common. The extent

463   to which our conclusions are generalizable to other families within Singapore, and to

464   locations outside of Singapore, is not clear. Collecting animal behavior data is very time and

465   labor intensive by nature, and here we were able to glean information from videos collected

466   by local otter watchers. By crowdsourcing video recording, citizen science has the potential

467   to be an extremely powerful tool in animal behavior studies due to the "many eyes" effect:

468   if more people are recording animal behaviors, we can collect a more complete record of

469   what animals do. In this manner, this analysis of data gleaned from the internet can be

470   viewed as a form of "next-gen" natural history (Tosa et al. 2021). But this approach has

471   limitations. The current study gleaned information from videos collected in an *ad lib*

472   manner, albeit with impressive regularity. (The only gap in otherwise daily video recordings

473   of wildlife was about three weeks during the COVID-19 lockdown). Biases in *ad lib* data

474   collection can skew data towards rare, conspicuous behaviors. However, our videos were

475   taken at about the same time and place every day, which should reduce bias towards any

476   particular set of behaviors. Further, we limited which videos we included in the analysis to

477   those with otters and monitors. We make no claims about the overall frequency of otter-

478   monitor interactions (other than that they are surprisingly frequent) and limit our analysis

479   to what happens during otter-monitor interactions. We hope the regular, frequent, and

480   relatively unbiased collection of videos, combined with our filtering the videos to a

481   particular narrow topic, reduced unintentional biases.

482

483   **Conclusions**

484   While we did not discover a specific behavioral "trigger" that otters use as a cue to attack

485   monitor lizards, we did find several factors that affect the likelihood of aggression towards a

486   monitor. Otters were only aggressive in 50% of close-up interactions. Monitors, conversely,

487   displayed aggressive or defensive behaviors in almost all such encounters. Otters are faster

488   and more agile, especially in water, and combined with their group behaviors, can pose a

489   real threat to monitors. Monitors seem to be content to scavenge what the otters leave

490   behind and otherwise avoid them entirely if possible. The presence of young pups increases

491   the chance that otters act aggressively to monitors and increases the rate of vigilance within

492   the otter group. The increased vigilance rates could then lead to otters being more aware of

493   monitors' presence, with a greater chance of aggression resulting. To what extent the

494   growing population of large otter romps in Singapore's very urban environment contributes

495   to this is something we cannot ascertain from this study.

496

497

498

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662

663 **Figure legends**

664

665 **Figure 1.** Two smooth-coated otters approach a monitor lizard in Singapore. Notice that the

666 monitor lizard's neck frill is extended in an aggressive manner. The monitor whipped its tail

667 at the otters shortly after this photo was taken. Photo courtesy of Alicia Ellen Brierley.

668

669 **Figure 2**. Notable otter and monitor behaviors. Otter vigilance (A), monitor lizard curling its

670 tail (B), otter grooming (C), monitor with throat frill extended (D), otters playing (E), monitor

671 climbing (F). See Table 1 for ethogram describing behaviors.

672

673 **Figure 3.** Behavioral sequences of all otter-monitor interactions. Ovals represent otter

674 behaviors; rectangles represent monitor behaviors; colored symbols indicate aggression.

675 See Table 1 for ethogram. Numbers describe transitions between behaviors; only transitions

676 that occur more frequently than chance are shown. Letters indicate behaviors that precede

677 aggression (see text).

678

679 **Figure 4.** Behavioral sequences of otter-monitor interactions in water (A) and on land (B).

680 Ovals represent otter behaviors; rectangles represent monitor behaviors; colored symbols

681 indicate aggression. See Table 1 for ethogram. Numbers describe transitions between

682 behaviors; only transitions that occur more frequently than chance are shown. Letters

683 indicate behaviors that precede aggression or notable behavioral sequences (see text).

684

685   **Figure 5**. Occurrence of bouts with (y) and without (n) otter aggression in otter groups with

686   (Y) and without (N) pups.

687

688   **Figure 6.** Coefficients for GLMM models 1-5 explaining occurrence of otter aggression.

689

690   **Figure 7.** Models 2, 3, and 4 (panels A, B, C, respectively) predicting otter aggression on the

691   number of pups in a group (X-axis; see Figure 6). In panels A and C, Y-axis represents

692   probability of otter aggression; in panel B Y-axis represents the number of adults in a group,

693   with a line of inflection points, adults = 1.05*pups, to the right of which otters are more

694   likely to be aggressive (see text).

695

696   **Figure 8.** Coefficient estimates for LMMs, models 1-4, explaining the rate of vigilance, per

697   otter, per minute.

698

699   **Figure 9**. Models 2 and 4 (panels A and B, respectively) predicting rate of vigilance on the

700   number of pups in a group (see Figure 8). Panel A includes environment (land or water);

701   Panel B includes number of adults in a group (X-axis). Shaded areas are 95% confidence

702   intervals.

703

704 **Table legends**

705

706 **Table 1.** Ethogram used in scoring otter and monitor behaviors.

707

708 **Table 2.** List of variables used in GLMMs and LMMs.

709

710 **Table 3.** Generalized linear mixed models 1-5 predicting otter aggression towards water

711 monitors.

712

713 **Table 4.** Linear mixed modelss 1-4 predicting rate of otter vigilance in the presence of water

714 monitors.

715

716

717   **Appendix legends**

718

719   **Appendix 1.** List of search terms used on social media to find otter-monitor videos.

720

721   **Appendix 2.** Three-dimensional depiction of the function described by Model 3 (Figure 7)

722   predicting otter aggression towards monitors as a function of pups and adults. See text for

723   sigmoidal equation.

724

725

Data accessibility:

726

727

728   Raw data, BORIS files, and R code archived at FigShare,

729   https://figshare.com/articles/dataset/Bungum_Johns_Otter-MonitorLizard-Interaction-

730   Data/20188241 , https://doi.org/10.6084/m9.figshare.20188241

731

732

733   **Competing interests:**

734

735   The authors have no competing financial or non-financial interests that are directly or

736   indirectly related to this study.

737

738

748   College Centre for International and Professional Experience (CIPE), and by NParks permits

749   NP/RP20-073 and NP/RP20-075.
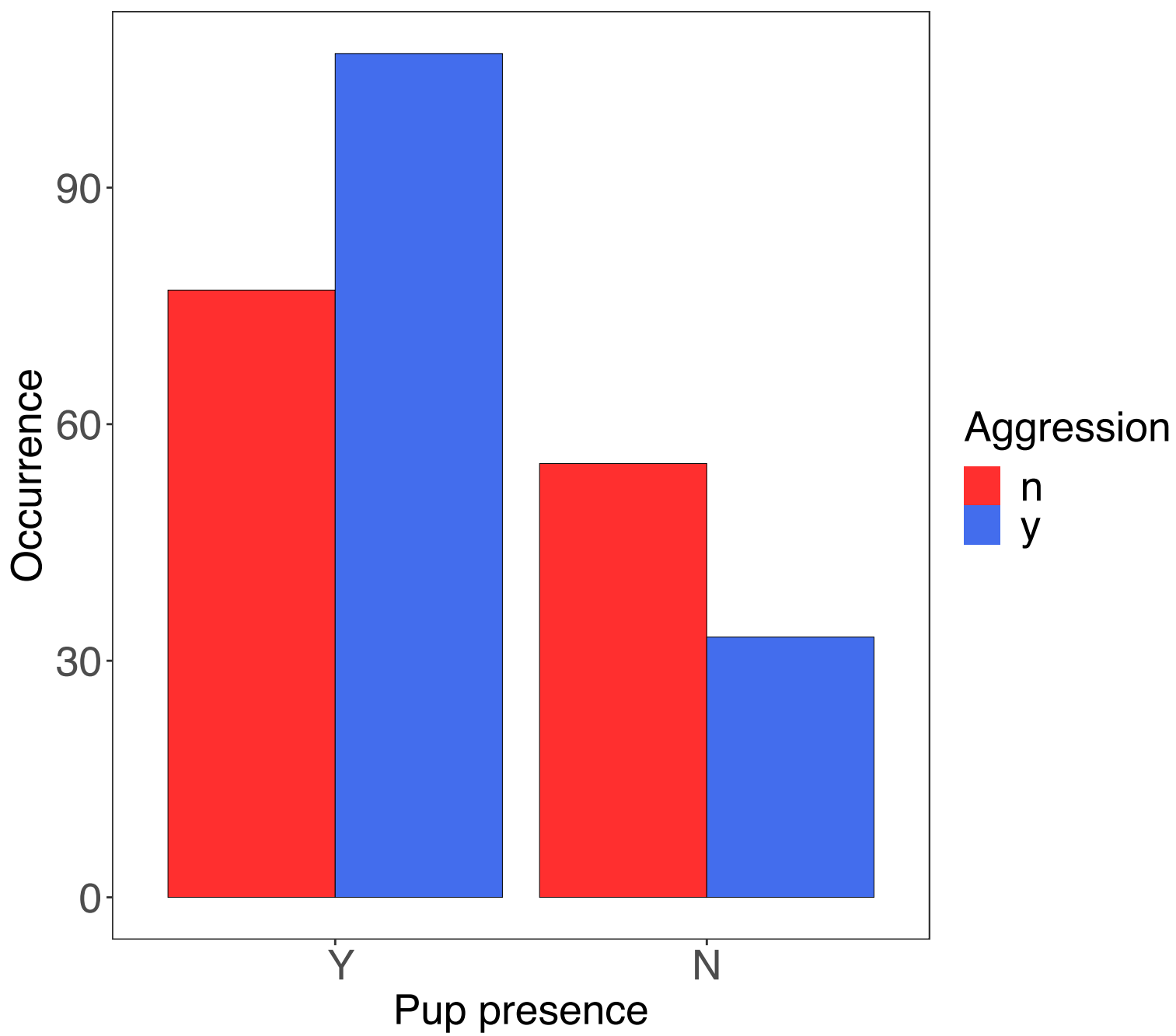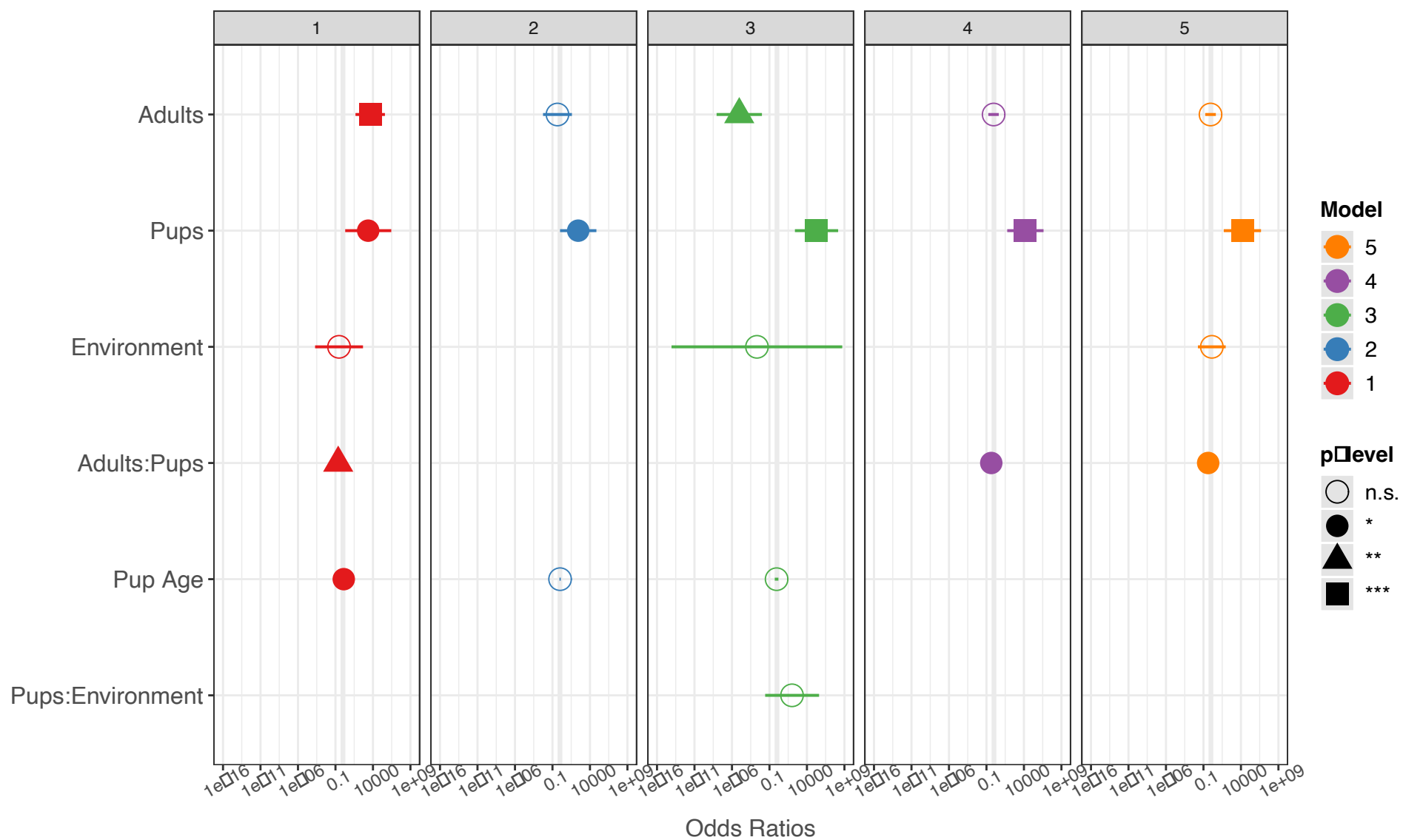
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Combined Behavioral Sequences
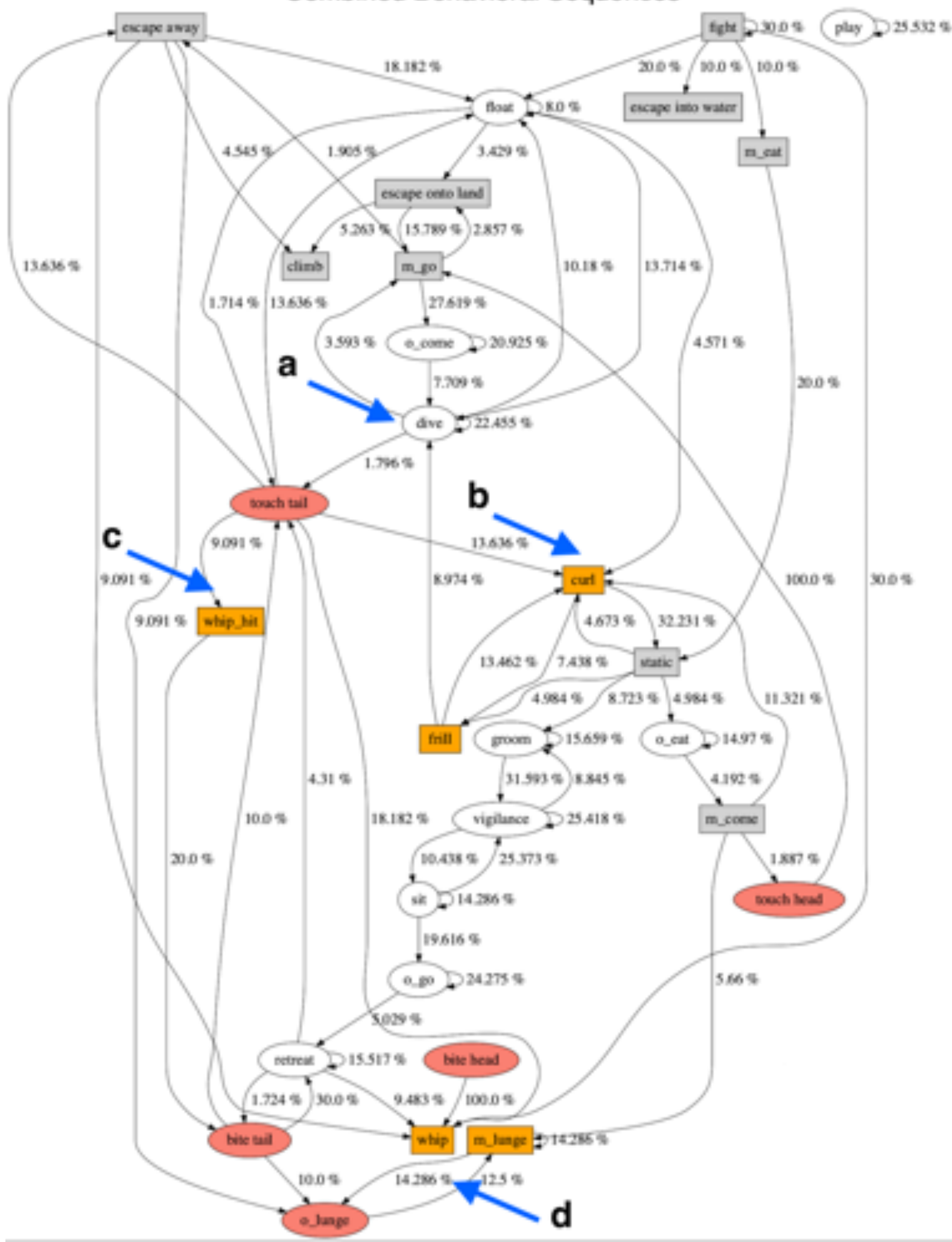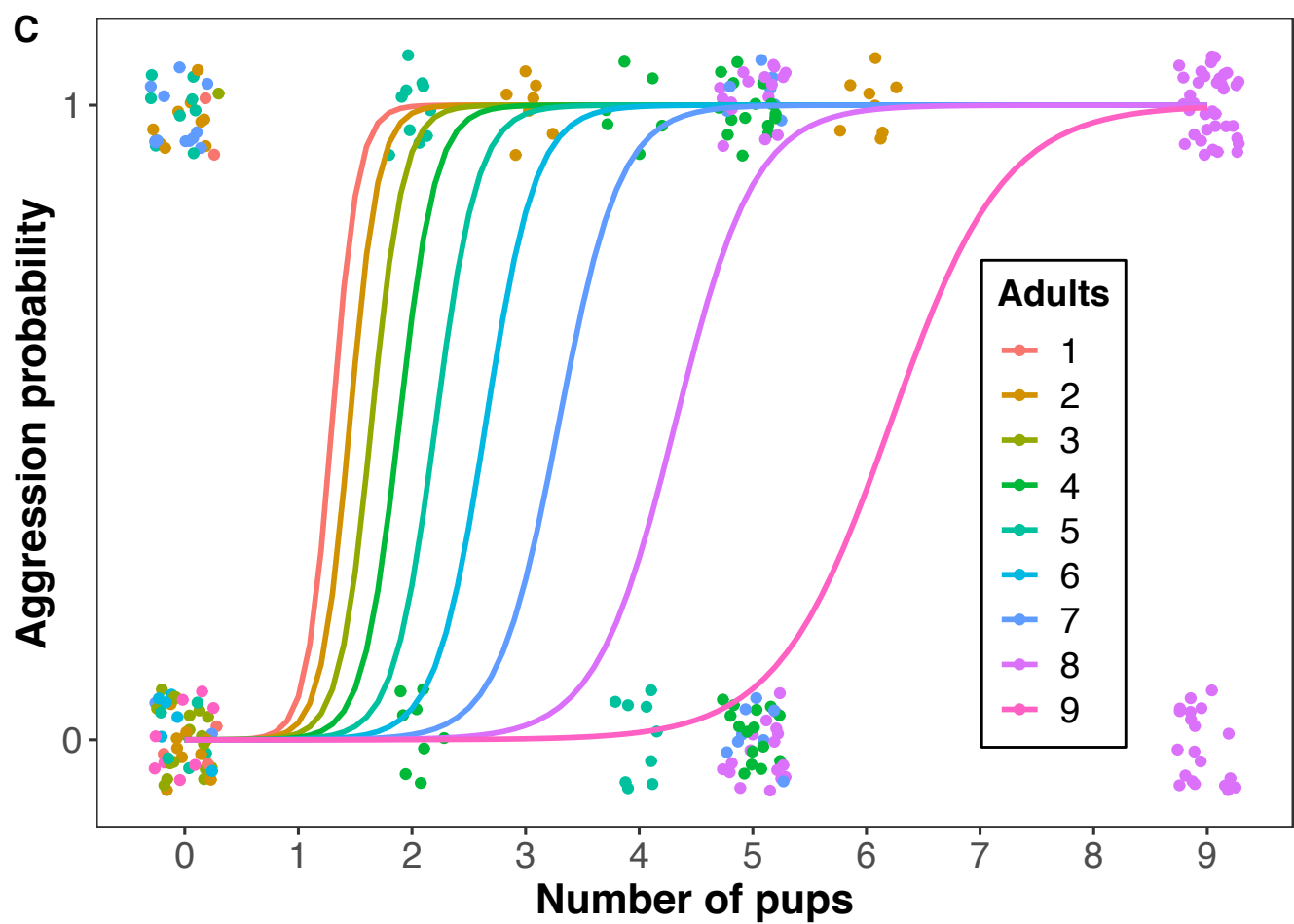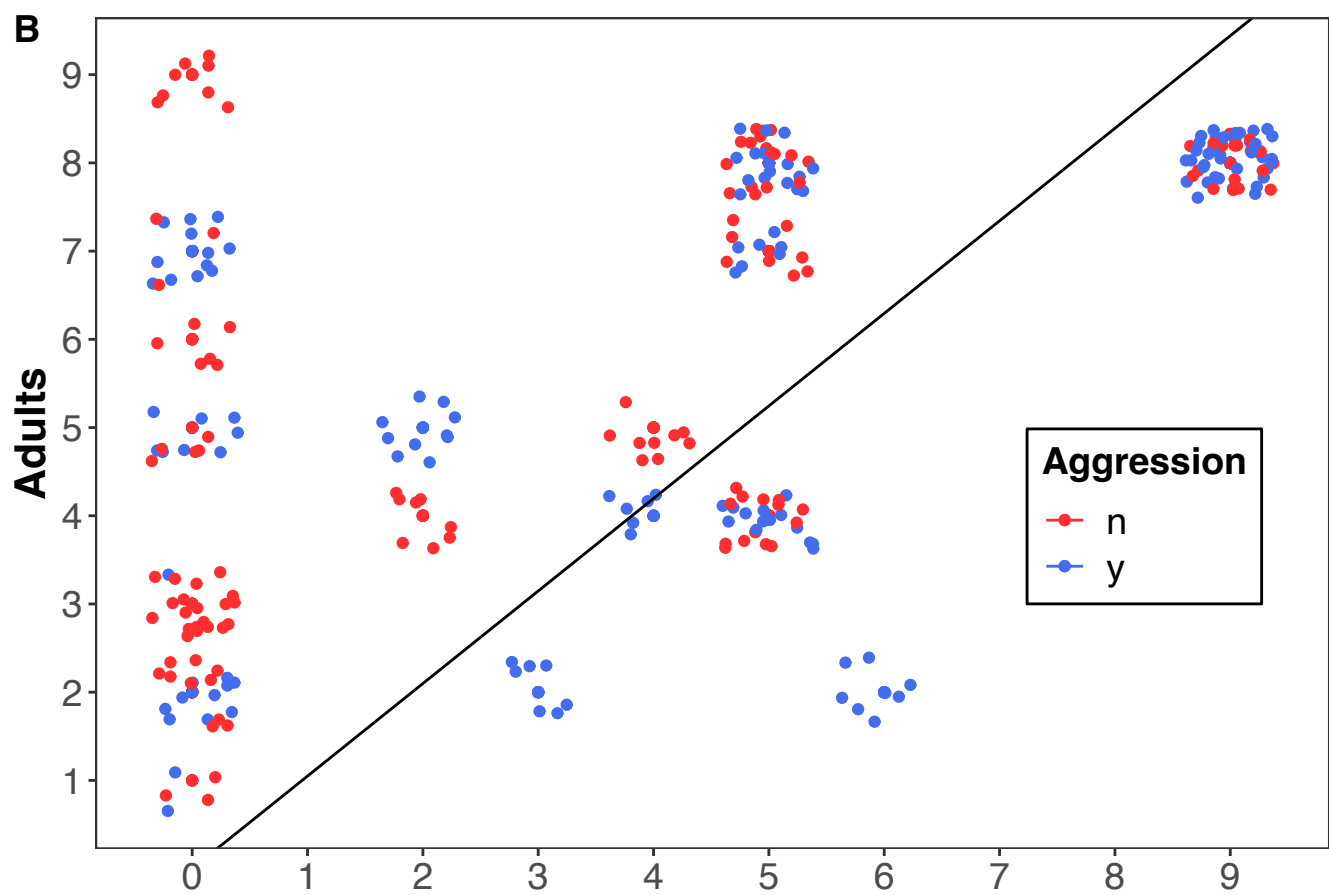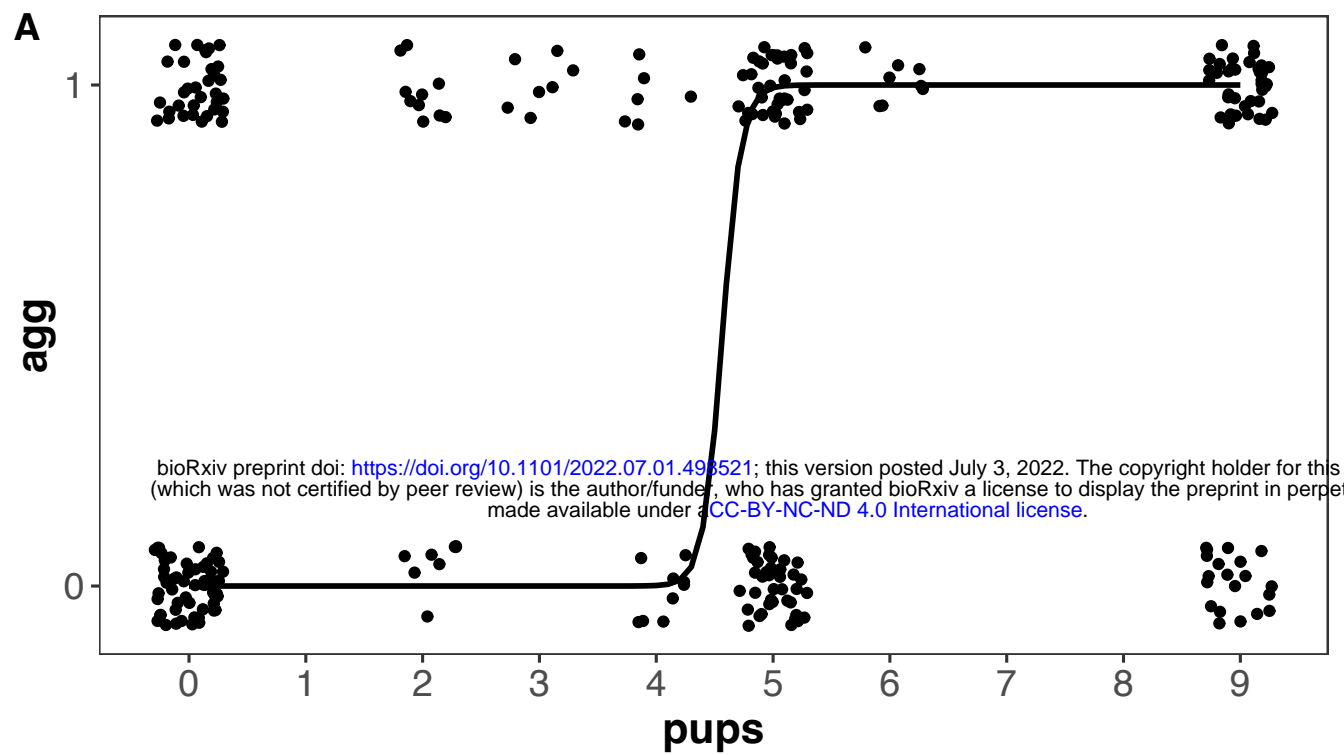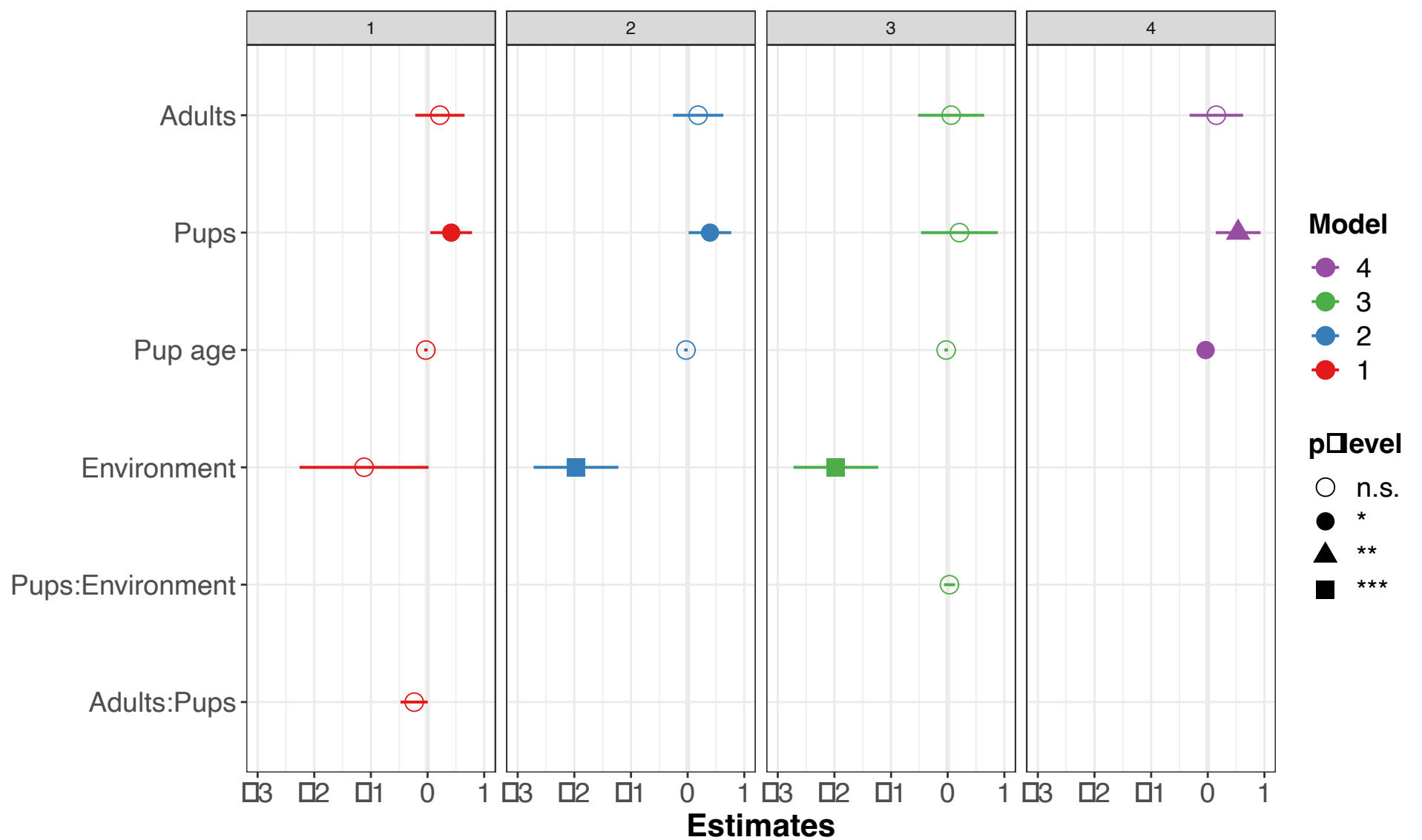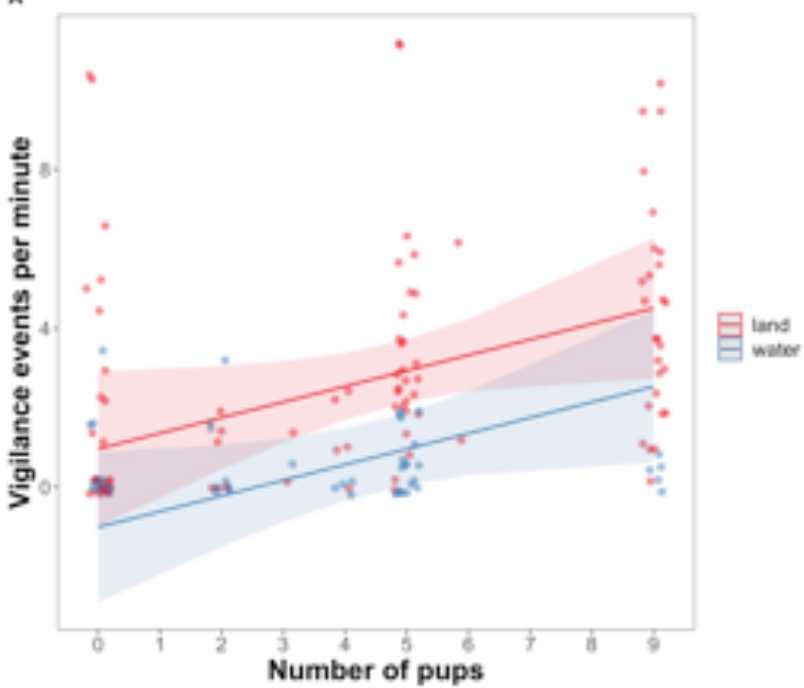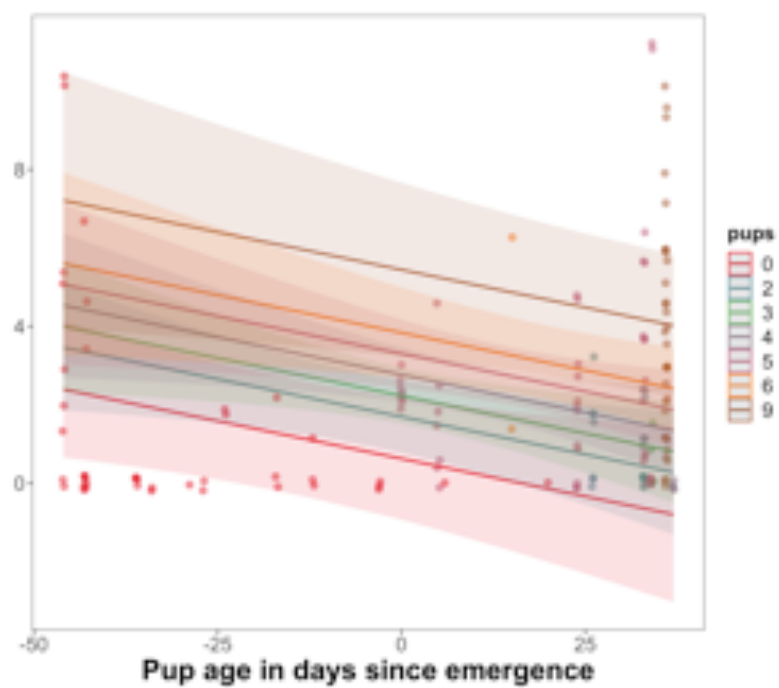
Behavior	Type	Description	Category
Fight	State	Monitor enga	aggression
Escape	Point	Monitor quic	locomotion
Climb	Point	Monitor clim	locomotion
Curl	State	Monitor curls	sound/sign
Bite	Point	Monitor bites	aggression
Static	State	Monitor is st	sound/sign
M_come	State	Monitor mov	locomotion
M_go	State	Monitor mov	locomotion
Whip	Point	Monitor whip	aggression
Whip hit	Point	Monitor whip	aggression
Frill	Point	Monitor frills	sound/sign
Mouth	State	Monitor oper	sound/sign
M_lunge	Poin	Monitor acce	aggression
M_eat	State	Monitor eatii	sound/sign
O_bite	Point	Otter bites n	aggression
O_come	State	Otter moves	locomotion
O_eat	State	Otter in act c	sound/sign
O_go	State	Otter moves	locomotion
O_lunge	Point	Otter quickly	aggression
Play	State	Otter playfig	sound/sign
Groom	State	Otters groom	sound/sign
Sit	State	Otter sits stil	sound/sign
Touch	Point	Otter contact	aggression
Vigilance	State	Otter strikes	sound/sign
Retreat	Point	Otter reacts	locomotion
Float	State	Otter is stati	sound/sign
Dive	Point	Otter dives u	sound/sign

Variable	Description	Type of Effect
Adults	Number of adults in observation	Fixed
Pups	Number of pups in observation	Fixed
Pup Age	Age of pups in days since first holt emergence	Fixed
Environment	Whether interaction occurred on land or in water	Fixed
Environment/Pups	Cross interaction of environment and number of pups	Interaction
Adults/Pups	Cross interaction of number adults and number of pups	Interaction
Bout ID	Unique bout ID	Random

Predictors	Model 1 Odds Ratios	CI	p	Model 2 Odds Ratios	CI	p	Model 3 Odds Ratios	CI
(Intercept)	0	0.000 – 0.000	<0.001	0	0.000 – 0.161	0.017	12.485	0.000 – 1862624
adults	4291.604	46.747 – 393993.913	<0.001	0.466	0.006 – 39.370	0.736	0	0.000 – 0.010
pups	2352.438	1.993 – 2777278.903	0.031	272.221	1.024 – 72386.12	0.049	189699.213	248.705 – 14469
pup age	1.293	1.005 – 1.665	0.046	1.051	0.851 – 1.298	0.646	0.894	0.509 – 1.570
environment [water]	0.299	0.000 – 467.951	0.747				0.002	0.000 – 5084478
adults * pups	0.231	0.095 – 0.564	0.001					
pups * environment							105.039	0.027 – 413172.2
Marginal R2 / Conditiona	0.030 / 1.000			0.050 / 0.999			0.034 / 1.000	
AIC	59.058			60.632			62.346	
BIC	83			77.7			86.3	

	Model 1			Model 2			Model 3	
Predictors	**Estimates**	**CI**	**p**	**Estimates**	**CI**	**p**	**Estimates**	**CI**
(Intercept)	0.473	-1.116 – 2.063	0.557	0.813	-0.773 – 2.399	0.313	1.285	-0.846 – 3.417
adults	0.218	-0.217 – 0.654	0.323	0.186	-0.259 – 0.631	0.41	0.06	-0.524 – 0.645
pups	0.418	0.050 – 0.786	0.026	0.394	0.018 – 0.770	0.04	0.207	-0.471 – 0.885
pup age	-0.028	-0.058 – 0.001	0.058	-0.03	-0.060 – 0.000	0.052	-0.027	-0.058 – 0.005
environment [water]	-1.121	-2.259 – 0.017	0.054	-1.971	-2.719 – -1.222	<0.001	-1.974	-2.722 – -1.226
pups * environment	-0.237	-0.478 – 0.004	0.054					
adults * pups							0.032	-0.065 – 0.128
Marginal R2 / Conditional	0.338 / 0.601			0.328 / 0.602			0.339 / 0.608	
AIC	649.962			651.692			653.267	
BIC	673.9			672.6			677.2	

	Model 4		
p	Estimates	CI	p
0.235	-0.13	-1.777 – 1.51	0.876
0.839	0.151	-0.322 – 0.62	0.529
0.548	0.536	0.141 – 0.93(	0.008
0.097	-0.038	-0.070 – -0.0	0.018
<0.001			
	0.515		
	0.232 / 0.529		
	674.506		
	692.4		

p	Model 4 Odds Ratios	CI	p	Model 5 Odds Ratios	CI	p
0.728	0	0.000 – 0.012	0.001	0	0.000 – 0.019	0.003
0.001	0.878	0.177 – 4.348	0.873	0.88	0.173 – 4.463	0.877
<0.001	15546.668	58.682 – 4118824.8C	0.001	15729.755	51.849 – 4772017.	0.001
0.696						
0.645				1.298	0.018 – 92.553	0.905
	0.428	0.210 – 0.871	0.019	0.428	0.207 – 0.883	0.022
0.27						
	0.064 / 0.999			0.063 / 0.999		
	77.187			79.173		
	95.2			100.8		

Search term	Platform	Remarks
singapore otter monitor	Facebook, YouTube	
singapore otter lizard	Facebook, YouTube	
otter monitor	YouTube	Randomsg
monitor	YouTube	Randomsg
lizard	YouTube	Randomsg
otter lizard	YouTube	Randomsg
interaction	YouTube	Common title by Randomsg
confrontation	YouTube	Playlist by Randomsg
encounter	YouTube	Another common title

No. adults

Pr(Aggression)

No. pups