

1 **Early life differences in behavioral predispositions in two Alligatoridae species**

2

3 Stephan A. Reber^{1,2,3*}, Jinook Oh^{2,4}, Judith Janisch^{2,5}, Colin Stevenson⁶, Shaun Foggett⁶ & Anna
4 Wilkinson^{1,*}

5

6 ¹School of Life Sciences, University of Lincoln, Lincoln, UK

7 ²Department of Cognitive Biology, University of Vienna, Vienna, Austria

8 ³Lund University Cognitive Sciences, Lund University, Lund, Sweden (current address)

9 ⁴Institute of Science and Technology Austria, Klosterneuburg, Austria

10 ⁵Department of Interdisciplinary Life Sciences, University of Veterinary Medicine Vienna, Austria

11 ⁶Crocodiles of the World, Brize Norton, UK

12 *Correspondence to: mail@stephanreber.com / awilkinson@lincoln.ac.uk

13

14 Stephan A. Reber ORCID ID: 0000-0001-8015-2538

15 Anna Wilkinson ORCID ID: 0000-0002-4500-0181

16

17

18

19

20 **Acknowledgements** We thank Jamie Gilks and Terry Miles for their support at Crocodiles of the
21 World. We are grateful to the Department of Cognitive Biology, University of Vienna for
22 provision of working space and hardware. Finally, we would like to thank Cliodhna Quigley,
23 Rachael Harrison and Urs A. Reber for discussion.

24 **Abstract**

25

26 Behavioral predispositions are innate tendencies of animals to behave in a given way without the
27 input of learning. They increase survival chances and, due to environmental and ecological
28 challenges, may vary substantially even between closely related taxa. These differences are likely
29 to be especially pronounced in long-lived species like crocodilians. This order is particularly
30 relevant for comparative cognition due to its phylogenetic proximity to birds. Here we compared
31 early life behavioral predispositions in two Alligatoridae species. We exposed American alligator
32 and spectacled caiman hatchlings to three different novel situations: a novel object, a novel
33 environment that was open and a novel environment with a shelter. This was then repeated a week
34 later. During exposure to the novel environments, alligators moved around more and explored a
35 larger range of the arena than the caimans. When exposed to the novel object, the alligators reduced
36 the mean distance to the novel object in the second phase while the caimans further increased it,
37 indicating diametrically opposite ontogenetic development in behavioral predispositions.
38 Although all crocodilian hatchlings face comparable challenges, e.g. high predation pressure, the
39 effectiveness of parental protection might explain the observed pattern. American alligators are
40 apex predators capable of protecting their offspring against most dangers, whereas adult spectacled
41 caimans are frequently predated themselves. Their distancing behavior might be related to
42 increased predator avoidance and also explain the success of invasive spectacled caimans in the
43 natural habitats of other crocodilians.

44

45 **Key words:** Behavioral predisposition, *Caiman crocodilus*, *Alligator mississippiensis*,
46 crocodilian, exploration, neophobia

47 **Introduction**

48

49 The comparative approach is one of the main methods used to study the evolution of cognition
50 (Tinbergen 1963). Cognitive capacities can be traced through time and their origins better
51 understood by examining similarities and differences between different species in various
52 positions in the tree of life. However, closely related species may also differ greatly in their
53 cognition. Factors that could be involved in producing such differences are the behavioral
54 predispositions of the species. A species that is more likely to explore novel stimuli in its
55 surroundings may learn more rapidly than one that is less likely to do so. Behavioral
56 predispositions may vary due to ecological differences rather than phylogenetic distance, resulting
57 in quite different cognitive abilities being observed in closely related species. It is therefore
58 important to consider such factors in order to draw lasting conclusions from comparisons of
59 cognition across different taxa (MacLean et al. 2012).

60

61 Behavioral predispositions, e.g. an innate tendency to freeze when facing a potentially dangerous
62 situation, may markedly increase an organism's chances of survival (Gray 1987; Vilhunen and
63 Hirvonen 2003). This could be particularly relevant very early in life, as behavioral predispositions
64 may decrease the risk of predation before an animal has had time to learn about the threats in its
65 environment (Tierney 1986; Hawkins et al. 2004). Such innate behavioral traits may subsequently
66 be shaped by life experience, the extent to which this occurs depending on the animal's behavioral
67 plasticity (Gumbert 2000; Kelley and Magurran 2003). For instance, neonate cottonmouths
68 (*Agkistrodon piscivorus*) do not habituate to a non-harmful predatory stimulus while adults,
69 exposed to the same stimulus, show a reduction in their tendency to strike over time (Glaudas et

70 al. 2006). Behavioral dispositions can also differ between animals of the same taxonomic order
71 (Fraser and Gilliam 1987), populations of the same species (Wilson et al. 1993; Bell and Stamps
72 2004) and even individuals from the same clutch when exposed to different conditions *in ovo*
73 (Rokka et al. 2014; Siviter et al. 2017). These differences are likely to reflect survival strategies
74 dictated by specific challenges in the environments they inhabit (Greenberg and Mettke-Hofmann
75 2001). Further, behavioral predispositions can also change drastically across an animal's life span
76 (Kendal et al. 2005; Miller et al. 2015). It is therefore likely that such differences would be most
77 pronounced in long-lived species that exhibit significant ontogenetic changes in their feeding and
78 social ecology. A great example are crocodylians, where some species increase their body size by
79 three to five orders of magnitude (Radloff et al. 2012), preferential prey species can shift from
80 insects to large ungulates throughout life (Cott 1961), and juveniles seek safety in numbers while
81 adults of several species are highly territorial (Grigg and Kirshner 2015).

82

83 Crocodylians are the closest living relatives of birds and both groups share a common ancestor with
84 all extinct dinosaurs (Hugall et al. 2007). Their brain structure is highly similar to birds but
85 physiologically they resemble other non-avian reptiles and mammals (Grigg and Kirshner 2015).
86 This makes them an interesting order for understanding the evolutionary origin of avian cognition
87 in particular (Vergne et al. 2009; Reber et al. 2017) and for the comparative approach in general.
88 Crocodylians are widespread across the globe but have relatively few surviving species (currently
89 28 are recognized; Stevenson 2019; Murray et al. 2019). They share a highly conserved body
90 plan, a semi-aquatic life history, and a seemingly identical call repertoire (Webb et al. 1987; Britton
91 2001; Reber 2018). It is therefore tempting to assume that crocodylian species do not differ greatly
92 in behavior. However, they face different challenges in their respective environments. This can

93 depend on the prey they hunt, the predators they are exposed to, and the seasonal changes they
94 have to cope with, e.g. the avoidance of drought in Nile crocodiles (*Crocodylus niloticus*; Kofron
95 1993); or the risks of hibernation in Chinese alligators (*Alligator sinensis*; Thorbjarnarson and
96 Wang 2010). Thus, crocodylians are likely to differ in their overall behavioral predispositions.
97 Observations in the wild and in captivity have revealed that different species behave differently
98 towards conspecifics and other entities in their environment (Garrick and Lang 1977; Trutnau and
99 Sommerland 2006). There are, however, only few experimental comparisons. For instance, in a
100 serial reversal learning study, American crocodiles (*Crocodylus acutus*) produced significantly
101 fewer errors than American alligators (*Alligator mississippiensis*) for each reversal (Gossette and
102 Hombach 1969). But the latter species showed consistently shorter latencies to make a choice in a
103 trial. The authors suggested that the alligators were more motivated to participate than the
104 crocodiles, which might have led to more errors. This difference is particularly interesting, because
105 the two species overlap in their geographical range and have no natural predators as adults; they
106 do, however, occupy different ecological niches. American crocodiles are commonly found in
107 coastal areas and frequently hunt in marine habitats, whereas American alligators predominantly
108 inhabit inland habitats and rarely swim in saltwater (Stevenson 2019). It is therefore conceivable
109 that their differing performances in cognitive tasks could be explained by the differences in
110 behavioral ecology between the two species.

111

112 All crocodylians are highly susceptible to predation in the first months of life by a large variety of
113 other animals, including large fish, snakes, monitor lizards, raptors, wading birds, small
114 mammalian carnivores, and also conspecifics (Somaweera et al. 2013). However, members of
115 certain species (e.g. saltwater crocodile *Corocodylus porosus*, American alligator *Alligator*

116 *mississippiensis*) become apex predators in their respective habitats when they reach maturity
117 (Grigg and Kirshner 2015), while others (e.g. Yacare caiman *Caiman yacare*) remain susceptible
118 to predation into adulthood (Azevedo and Verdade 2012). Because of the similar risks of predation
119 in early life, one might predict that hatchlings of any species would show similar responses to
120 novel stimuli, such as little exploration behavior in a novel environment and overall lower levels
121 of activity. After reaching a less vulnerable body size, crocodylians have a far smaller range of
122 potential predators (Somaweera et al. 2013) and could be expected to display higher levels of
123 activity and increased exploration behavior. Although this has, to our knowledge, not yet been
124 studied in crocodylians, similar dispositions have been described in their closest living relatives,
125 birds: species facing higher predation pressure are less explorative and more neophobic (Heinrich
126 1995; Greenberg and Mettke-Hofmann 2001), and growing evidence suggests that these traits
127 might vary more between age-classes than between species (O’Hara et al. 2017).

128

129 Some crocodylian species are critically endangered and reintroduction is either recommended or
130 ongoing (Wang et al. 2011; Kanwatanakid-Savini et al. 2012). To increase the potential success of
131 such conservation efforts, it is vital to determine whether crocodylians adapt their behavior in a
132 developmentally dependent manner. For instance, if a species shows high levels of exploratory
133 behaviors early in life despite still being vulnerable to a large spectrum of predators, it would be
134 advisable to raise the juveniles to a larger body size before their release, whereas that might not be
135 necessary for members of a species with stronger predispositions for anti-predator behaviors.
136 Conversely, some crocodylians have become successful invasive species in other crocodylians’
137 natural habitat, negatively affecting local populations (Ellis 1980). In such cases, population
138 management efforts could benefit from a better understanding of early life behavioral

139 predispositions and whether hatchlings of an invasive species might have an advantage due to
140 stronger intrinsic predator avoidance or superior competitive abilities (Hudina et al. 2015).

141

142 We investigated behavioral predispositions of American alligator (*Alligator mississippiensis*) and
143 spectacled caiman (*Caiman crocodilus*) hatchlings using well-established experimental methods
144 (Réale et al. 2007). We aimed to determine whether i) individuals from these two species display
145 consistent behavioral traits at a very young age and ii) whether there were differences between the
146 two species. All subjects in the present study were the same age and maintained under the same
147 conditions prior to and during the experiments. In an initial phase (Phase 1) all animals were
148 exposed to three conditions: Novel Object, Novel Environment: Open Field, and Novel
149 Environment: Shelter. The proximity to a novel object in a familiar environment, but in the absence
150 of an additional positive stimulus (e.g. food), can be used as a measure for exploration behavior
151 (Greggor et al. 2015). The range of movement in a novel environment serves as an assessment of
152 activity. Shelter usage served as a control, i.e. to determine whether high levels of movement in
153 the Novel Environment: Open Field trials were actually indicators of activity levels in unfamiliar
154 surroundings, and thereby possible exploration behavior, or whether animals primarily wanted to
155 escape open space. All conditions were then repeated a week later (Phase 2) to investigate whether
156 individual hatchlings showed behavioral consistency over time.

157

158 While adult American alligators have no natural enemies, adult spectacled caimans have a number
159 of predators, such as jaguar, cougar, and green anaconda (Calle et al. 1994; Scognamillo et al.
160 2003). Should juveniles of the two species already exhibit behavioral predispositions similar to
161 those of adults, we could expect them to show differential behaviors in our conditions; e.g.

162 alligators might be more explorative. In addition, spectacled caimans are a successful invasive
163 species in many areas, including the Everglades, a natural habitat of the much larger American
164 alligator (King and Krakauer 1966). In regions where these two species cohabit, spectacled
165 caiman juveniles are hence confronted with an additional predator against which a guarding parent
166 cannot provide effective protection. Predispositions for increased anti-predator behaviors, e.g.
167 reduced activity in novel environments, could consequently increase the caimans' survival
168 chances. Therefore, we could expect to observe differences in behavioral predispositions in young
169 members of these two Alligatoridae species.

170

171 **Methods**

172

173 **Subjects**

174

175 The experimental subjects were 11 American alligator and 11 spectacled caiman hatchlings. The
176 animals were too young to identify their sex. As crocodylians have temperature-dependent sex
177 determination (Grigg and Kirshner 2015), the presumed sex of the subjects is based on their
178 incubation temperature. The alligators hatched on the 8th September (5 individuals, 70 days of
179 incubation, average incubation temperature = 32.42 °C, presumed males) and 16th September (6
180 individuals, 79 days of incubation, average incubation temperature = 29.8 °C, presumed females).
181 The caimans all hatched on the 17th September (11 individuals, 75 days of incubation, average
182 incubation temperature = 31.8 °C, presumed males (Ferguson and Joanen 1982)). All subjects were
183 left in the incubator for two days to fully absorb the remaining yolk. Each incubation group was
184 then transferred into a transparent plastic enclosure (48 x 39 x 31 cm), filled with water which was

185 changed daily in order to let the nasal openings seal under hygienic conditions. Afterwards, the
186 hatchlings were kept in glass vivaria with 5-cm high depth water, a heat-lamp, and a brick as a dry
187 basking spot. All subjects could be individually recognized by their distinctive hide markings. The
188 animals were well habituated to human handling. At the start of the experiment the alligators were
189 between 26 and 32 days old, and the caimans between 27 and 28 days old.

190

191 **Experimental setup**

192

193 Two plastic arenas (70 x 55 x 37 cm) with lids were used to run the experiment. Five optically
194 different environments were created; two from the arena's original colors (black, blue) and three
195 in which the walls of the boxes were covered with colored wrapping paper (cyan with white dots,
196 rose with flower pattern, white with silver stars). The floor of each arena was fully lined with
197 corrugated cardboard to reduce light reflection. Each arena was covered with a lid upon which an
198 LED bulb was attached (light bulb: Philips Master LEDbulb 7W, 470 lumen). The animals'
199 behavior was recorded using a GoPro (Hero4 silver edition, <https://gopro.com>, 60 frames/sec,
200 image size: 1920x1080) through a small hole in the lid of the arena.

201

202 **Experimental procedure**

203

204 *Novel Object*

205 Two days before the start of the experiment, subjects were habituated to the Novel Object arena
206 (one of the two boxes without wrapping paper on the walls, environment counterbalanced across
207 animals). On the first day, they were allowed to explore the box with other animals (2-4

208 conspecifics in the arena simultaneously) for 20 minutes. Crickets and mealworms were offered
209 in the arena (8 alligators and 8 caimans showed hunting behavior). On the second day, each subject
210 spent 20 minutes alone in the arena. Again, food was offered. If the subject did not display hunting
211 behavior (chasing after or jumping towards food) in the first 20 minutes, they were given a break
212 and later on placed into the arena once more for 20 minutes (7 alligators, 10 caimans) to ensure
213 they were habituated to the environment.

214

215 During a Novel Object trial a small object was put in the middle of the arena, either a blue toy car
216 or a yellow spinning top (see Table S1, Online Resource 1 for details). The specific object
217 presented was counterbalanced across subjects and phases (subjects saw a different object in each
218 phase). At the onset of a trial the hatchling was placed in a starting area close to the center of one
219 of the longer sidewalls (Figure 1a).

220

221 *Novel Environment: Open Field*

222 This was identical to the previous condition but with some key changes. Instead of novel objects,
223 different novel environments were used. The environments were created by changing the walls of
224 the arena which could either be plain or covered with wrapping paper. This ensured an unfamiliar
225 environment for the subject. At the start of each trial a hatchling was placed in a starting area close
226 to the center of one of the longer sidewalls (Figure 1b).

227

228 *Novel Environment: Shelter*

229 This was identical to the Novel Environment: Open Field Condition except that animals had access
230 to a shelter. The shelter was a white tile laid onto two small bricks and was positioned at the center
231 of the arena. At the onset of the trial a hatchling was placed under the shelter (Figure 1c).

232

233 *Testing schedule across two phases*

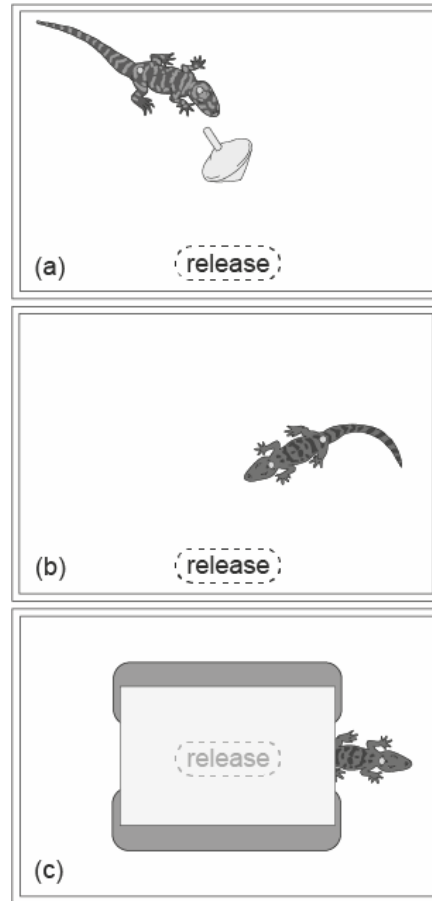
234 All trials took place either in the morning or the evening hours; this was consistent within a phase
235 but counterbalanced across phases for each individual. Each phase contained 3 trials (one for each
236 condition) with one 10-minute trial being run per day. On each day, an animal received a trial of a
237 different condition, with order of conditions counterbalanced across individuals. The second phase
238 commenced a week after the first and the order of conditions was the same for a given individual
239 in both phases. The different novel objects and environments were counterbalanced across
240 individuals for the two phases. For example, spectacled caiman #3 was always tested in the
241 morning hours in Phase 1. On the first day it participated in a ‘Novel Environment: Open Field’
242 trial, on the second in a ‘Novel Environment: Shelter’ trial, and in a ‘Novel Object’ trial on the
243 third. After four days without a trial, Phase 2 began. Now caiman #3 was always tested in the
244 evening hours. It again participated in one trial per day with the same order of the conditions as in
245 the first phase. However, the walls of the arena in the ‘Novel Environment: Open Field’ and ‘Novel
246 Environment: Shelter’ trials looked different than in the previous phase; and the novel object in
247 the ‘Novel Object’ trial was changed as well (see Table S1, Online Resource 1 for details).

248

249 Before each trial, the floor of the arena was wiped with a damp cloth, the subject was removed
250 from its home vivarium, dried off using paper towels, and two small round adhesive stickers (1 cm
251 diameter) were placed on its head (red or blue) and tail-base (green) to facilitate automated video

252 analysis. All trials were recorded and video recording was started immediately prior to the animal
253 being introduced into the arena. After the 10-minute trial time, recording was stopped, the subject
254 was removed from the arena, the stickers carefully removed and then it was returned to its home
255 vivarium.

256



257

258 **Fig. 1** The three conditions (not to scale). An American alligator during a Novel Object trial (a).
259 A spectacled caiman in a Novel Environment: Open Field trial (b). A spectacled caiman in a Novel
260 Environment: Shelter trial (c). For each condition the release location is indicated

261

262 Automated video analysis

263

264 Each frame (60 f/sec) was first exported as an image (jpg). A custom color tracking software
265 (“AMA”, Alligatoridae Motion Analyzer, available online: <https://github.com/jinook0707/AMA>),
266 used the color stickers on the head and tail-base to identify the positions of these body-parts and
267 recorded their coordinates in number of pixels (x-, y-axis of the entire video frame). If the animal
268 was fully or partially in the shelter, one or both color tags could not be detected. A pixel edge
269 length equaled roughly 1.278 mm for the chosen resolution (image size: 960x540, reduced from
270 original video to increase processing speed) and the distance from the arena floor was 37 cm. Both
271 were kept constant across trials. Additionally, the distance (again in pixels) between the head tag
272 and the center of the arena (location of the object in the Novel Object condition) was noted.
273 In order to obtain movement data, the software compared each individual frame (f_i) with a frame
274 (f_{i-30}) from half a second ago (30 frames). Only if the virtual “head line” (HL) connecting the head
275 tag’s (ht_i) position in the current f_i and the head tag’s (ht_{i-30}) position from the previous f_{i-30} had
276 changed in length by a minimum of 5 pixels (~6.39 mm), then the software recorded the distance
277 of this new position from the previously recorded position. Because of minute movements below
278 the threshold and small changes in the distance between the camera lens and the subject, this
279 recorded distance was usually larger than 5 pixels. The software also automatically recorded these
280 movement behaviors as ‘walking distance’ or as ‘head movements without walking’. To determine
281 which of the two behaviors had occurred, the program looked at the virtual “tail-base line” (TbL)
282 that, equivalent to HL, connects the position of the tail-base tags (tbt_i & tbt_{i-30}) of the two frames
283 (f_i & f_{i-30}). The angles of HL (AHL) and TbL (ATbL) relative to the whole frame were calculated
284 (e.g. straight to the right = 0° , straight up = 90° , straight down = -90°). If the absolute difference
285 between the two angles (AHL-ATbL) was smaller than 45° (a), the pixel difference was counted
286 as “walking distance”; if the difference exceeded the 45° -threshold (b), the pixel margin was

287 recorded as “head movements without walking” (see Fig. S2, Online Resource 1). These two
288 measures were mutually exclusive, because crocodylians have to keep their head stable during
289 locomotion on land; a head turn can only be performed from a stable position.

290

291 **Visual coding check**

292

293 To check the accuracy of the data, a researcher (JJ) screened the automated procedure using a
294 customizable program. All frames were displayed and automatically analyzed one after the other.
295 If tracking was correct then two digital tags (squares, edge length = 10 pixels ~ 1.28 cm) covered
296 the two color stickers. On rare occasions, the coding software could not accurately localize the
297 colored stickers, e.g. due to uneven light conditions. If the digital tag was not covering the color
298 sticker, the researcher could stop the analysis, rewind to specific frames and manually place the
299 tag onto the sticker. Also, if the subject moved the novel object, the researcher could adjust the
300 software to treat the new position of the object as the center of the arena (see supplementary video
301 “Video_1” in Online Resource 2; also accessible at [https://github.com/jinook0707/AMA:](https://github.com/jinook0707/AMA:ama_sample_video)
302 “ama_sample_video”).

303

304 **Statistics**

305

306 Three condition-specific variables were created. For Novel Object, the mean distance (in pixels)
307 of the head tag from the object across all frames per trial was recorded (‘mean dist. to object’). In
308 the case of Novel Environment: Open Field, the difference between the minimal and the maximal
309 distance of the head tag from the center of the arena across all frames was calculated per trial; this

310 'roaming range' variable served as an indication for roaming behavior. For Novel Environment:
311 Shelter, the number of frames the animals spent partially (only one tag detected) or fully (no tag
312 detected) in the shelter per trial were summed up and then transformed into seconds to measure
313 'shelter usage'. In order to warrant the planned comparisons between the two species and phases
314 (as outlined in the introduction) and to assess the influence of potentially confounding factors (e.g.
315 testing time, incubation temperature, etc.), the variables "walking distance" and "head movements
316 without walking" (sums of distances in pixels per trial) were investigated in a Generalized Linear
317 Mixed Model (GLMM), as they could be measured in each of the three conditions (number of
318 pixels served as the unit). They were united into a single variable, a 'movement component', by
319 conducting a Principal Component Analysis (PCA). The first component explained 95% of the
320 variance (eigenvalue = 1.91, rotation = varimax, see Table 1 for factor loadings) and was extracted
321 after conducting a factor analysis and a Bartlett's test on the correlation matrix ($df=1$, $\chi^2= 226.3$,
322 $P<0.001$). This movement component was used as the response variable in the GLMM together
323 with these coefficients: 'species' (alligator/caiman), 'phase' (1 or 2), 'condition' (Novel Object /
324 Novel Environment: Open Field / Novel Environment: Shelter), 'testing time' (morning/evening),
325 'incubation temperature' (male/female), and the three two-way interactions between 'species',
326 'phase', and 'condition'. Because the movement components contained negative values, the data
327 were transformed to be positive by adding the absolute value of the most negative data point
328 followed by taking the square root. The GLMM was run using a Gaussian distribution (with a log
329 link function) and contained subject identity as a random effect. The Akaike Information Criteria
330 (AIC) was used to reduce the full model to find the best fit. Degrees of freedom, the t-distribution,
331 and subsequently the two-tailed p-values were obtained by employing the Kenward-Roger
332 approximation (Halekoh and Højsgaard 2014). During post hoc analysis, pairwise comparisons

333 were conducted using exact Wilcoxon signed-rank tests within species and exact Wilcoxon rank-
 334 sum tests (Mann-Whitney-U tests) between species (Mundry and Fischer 1998). If the animals
 335 showed differential changes in behavior between the two phases, delta scores were calculated by
 336 subtracting the values from the second phase from those of the first phase for each individual and
 337 the scores were used to compare the two species. The *P*-values of all pairwise comparisons were
 338 checked with sequential Bonferroni-correction (Holm 1979), if the same data was used for more
 339 than one comparison. In order to evaluate individuals' behavioral consistency over time, the
 340 measurements for the two phases per subject were compared using interclass correlation
 341 coefficients (ICC). Statistical analysis was performed in R (version 3.0.2 GUI 1.62 for Mac, R
 342 packages: lme4, lmerTest, pbkrtest, coin, irr).

343

344 **Table 1** Component matrix of the principal component analysis for the movement component

	PC1
Total walking distance	0.98
Total head movements	0.98
Eigenvalue	1.91
% of variance explained	95

345 Standardized loadings (pattern matrix) based upon correlation matrix

346

347 **Results**

348

349 **Movement component**

350

351 The final GLMM with ‘movement component’ as response variable included main effects
 352 ‘species’, ‘phase’, and ‘testing time’, as well as the interaction between ‘species’ and ‘phase’.
 353 ‘Incubation temperature’, and hence presumed sex, did not explain any variance and was not part
 354 of the model with the best fit. With the exception of ‘testing time’, all contributing coefficients
 355 significantly affected movement behavior (Table 2). Consequently, in the post hoc analyses, the
 356 two species and the two phases were compared for each condition-specific measurement. Overall,
 357 animals of either species moved less in the second phase of the same condition (Fig. 2). These
 358 differences were significant for both species in Novel Environment: Open Field and Novel
 359 Environment: Shelter (‘movement component’, exact Wilcoxon signed-rank test, $N_{ind/species}=11$, Z
 360 ≥ 2.092 , $P \leq 0.037$), but not for the Novel Object trials ($N_{ind/species}=11$, $Z \leq 1.778$, $P \geq 0.083$). The
 361 alligators moved more in each phase of every condition than the caimans (‘movement component’,
 362 exact Wilcoxon rank sum test, $N_{ind/species}=11$, $Z \geq -3.090$, $P \leq 0.002$, Table 3).

363

364 **Table 2** Values of the final generalized linear mixed model

response variable	coefficients	estimate	SE	<i>t</i>	<i>P</i>	
movement component	(intercept)	1.616	0.036	44.856	<0.001	***
	species (caiman)	-0.531	0.046	-11.467	<0.001	***
	phase (2)	-0.188	0.03	-6.239	<0.001	***
	testing time (morning)	0.043	0.03	1.44	0.161	
	species (caiman)*phase (2)	0.114	0.043	2.68	0.013	*

365 SE=standard error, *** $P \leq 0.001$, * $P \leq 0.05$

366

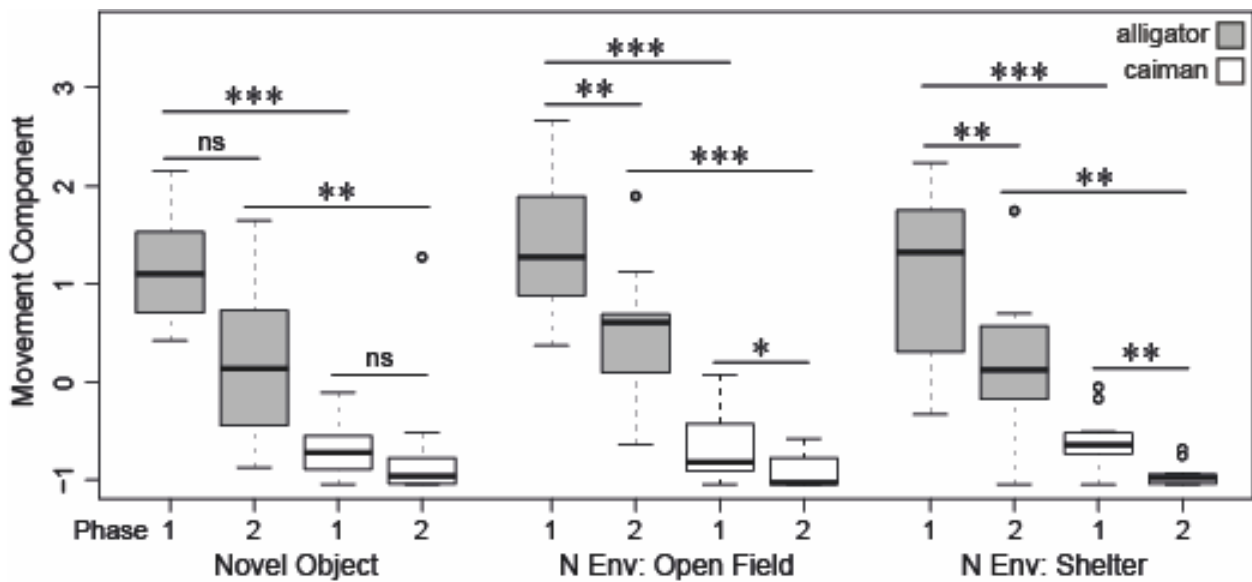
367

368 **Table 3** Testing matrix for the movement component across species (Alligator/Caiman) and
 369 phase (1/2)

	Novel Object		N Env: Open Field		N Env: Shelter	
	Alligator 2	Caiman 1	Alligator 2	Caiman 1	Alligator 2	Caiman 1
Alligator 1	Z=1.778	Z=-4.682	Z=2.845	Z=-4.682	Z=2.490	Z=-4.145
	P=0.083	P<0.001	P=0.002	P<0.001	P=0.010	P<0.001
Caiman 2	Z=-3.090	Z=0.889	Z=-3.879	Z=2.092	Z=-3.287	Z=2.893
	P=0.002	P=0.413	P<0.001	P=0.037	P=0.001	P=0.002

370 N Env=Novel Environment, N=11; number behind species name=Phase (1 or 2); in bold font are

371 $P \leq 0.05$



372
 373 **Fig. 2** The amount of overall movement by the two species (American “alligator”, spectacled
 374 “caiman”) in the three treatments (Novel Object, Novel Environment: Open Field, Novel
 375 Environment: Shelter) of the two phases (1-2). Data are represented by the principal component
 376 “movement component” comprised of “walking distance” and “head movements without walking”
 377 measured in pixels per frame. Box plots represent the 25th and 75th percentiles, the line in the box
 378 indicates the median, whiskers represent the non-outlier range and dots are outliers ($>Q_3+1.5*IQR$)

379 or $<Q_1 - 1.5 * IQR$). N Env=Novel Environment, $***P \leq 0.001$, $**P \leq 0.01$, $*P \leq 0.05$, ns = not
380 significant

381

382 **Condition-specific variables**

383

384 *Novel Object*

385 The two species did not differ in mean distance from the object in the first phase ('mean dist. to
386 object', exact Wilcoxon rank sum test, $N_{ind/species}=11$, $Z=-0.953$, $P=0.341$), but the alligators
387 significantly reduced that distance in the second phase (exact Wilcoxon signed-rank test, $N_{ind}=11$,
388 $Z=2.491$, $P=0.008$). The caimans showed a non-significant trend to increase the mean distance in
389 the second phase (exact Wilcoxon signed-rank test, $N_{ind}=11$, $Z=-1.868$, $P=0.064$) and the distance
390 clearly differed between the two species in the second phase (exact Wilcoxon rank sum test,
391 $N_{ind/species}=11$, $Z=-2.726$, $P=0.006$, Fig. 3a). A closer examination using delta scores (distance in
392 phase 1 minus distance in phase 2) indicated a diametrical ontogenetic development in exploration
393 behavior in the two species (see Fig. S1, Online Resource 1): Nine alligators were on average
394 closer to the novel object in the second phase and nine caimans increased the mean distance to the
395 novel object in the second phase. Overall, the delta scores significantly differed between the two
396 species (Novel Object-delta scores, exact Wilcoxon rank sum test, $N_{ind/species}=11$, $Z=-2.759$,
397 $P=0.006$).

398

399 *Novel Environment: Open Field*

400 The alligator hatchlings explored a wider area of the arena than the caimans in both phases
401 ('roaming range', exact Wilcoxon rank sum test, $N_{ind/species}=11$, $Z \geq -3.548$, $P < 0.001$) but neither

402 species differed between phases (exact Wilcoxon signed-rank test, $N_{ind} = 11$, $Z \leq 1.689$, $P \geq 0.102$,
 403 Fig. 3b).

404

405 *Novel Environment: Shelter*

406 Neither species really used the shelter in either phase (Fig. 3c). No differences were observed for
 407 ‘shelter usage’ between species (exact Wilcoxon rank sum test, $N_{ind/species} = 11$, $Z \leq -1.228$, $P \geq 0.219$)
 408 or phases (exact Wilcoxon signed-rank test, $N_{ind} = 11$, $Z \leq -1.206$, $P \geq 0.258$, see Table 4).

409

410 **Table 4** Testing matrix for the three condition-specific variables across species

411 (Alligator/Caiman) and phase (1/2)

	mean dist. to object [pixels]		roaming range [pixels]		shelter usage [sec]	
	Alligator 2	Caiman 1	Alligator 2	Caiman 1	Alligator 2	Caiman 1
Alligator 1	$Z=2.491$	$Z=-0.953$	$Z=1.334$	$Z=-3.678$	$Z=-1.206$	$Z=-0.572$
	$P=0.008$	$P=0.341$	$P=0.206$	$P<0.001$	$P=0.258$	$P=0.567$
Caiman 2	$Z=-2.726$	$Z=-1.868$	$Z=-3.548$	$Z=1.689$	$Z=-1.228$	$Z=0.361$
	$P=0.006$	$P=0.064$	$P<0.001$	$P=0.102$	$P=0.219$	$P=0.766$

412 $N=11$; in bold font are $P \leq 0.05$

413

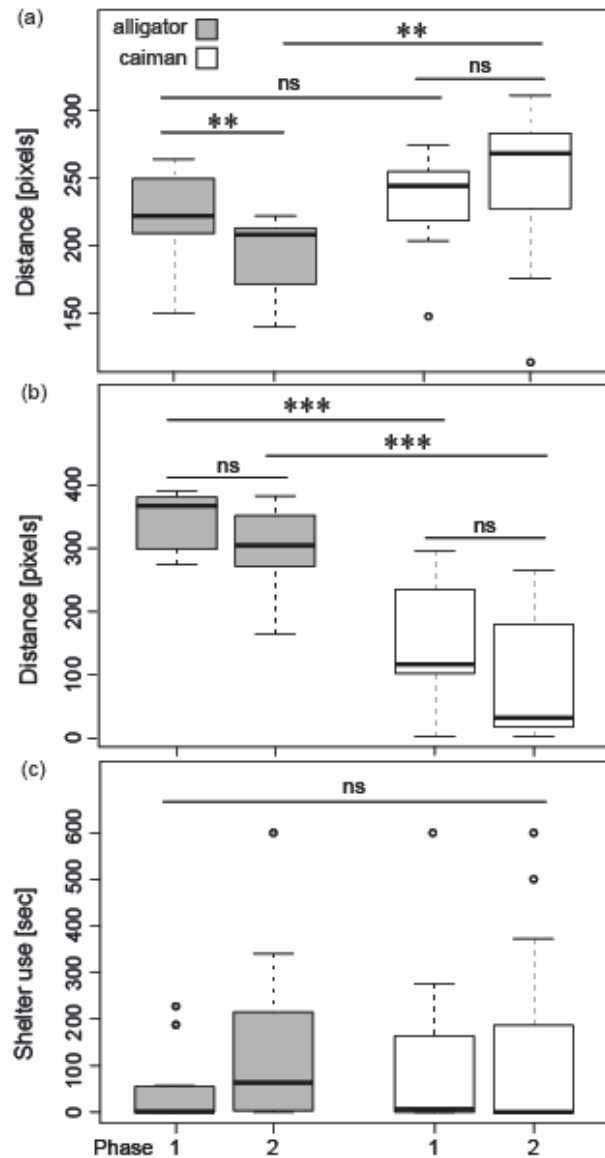
414 **Checking for individual behavioral consistency**

415

416 Neither species was consistent in its behaviors between the two phases for any of the
 417 measurements, with the exception of the caimans showing mediocre consistency in ‘roaming
 418 range’ (ICC=0.489, $F=3.39$, $P=0.035$). The alligators showed no consistency in ‘roaming range’
 419 for *Novel Environment: Open Field* (ICC=0.136, $F=1.37$, $P=0.307$). Both, alligators and caimans,

420 were not consistent across the two experimental phases with regards to the two other condition-
421 specific variables, the ‘mean dist. to object’ (alligators: $ICC=0.257$, $F=2.08$, $P=0.14$ / caimans:
422 $ICC=0.212$, $F=1.51$, $P=0.259$) or ‘shelter usage’ (alligators: $ICC=0.171$, $F=1.49$, $P=0.261$ /
423 caimans: $ICC=-0.199$, $F=0.806$, $P=0.63$). Neither species showed consistency for the ‘movement
424 component’; this held true for the overall comparison between the two phases (alligators: $ICC=0.2$,
425 $F=2.01$, $P=0.102$ / caimans: $ICC=0.152$, $F=1.42$, $P=0.162$) and the comparisons between the
426 phases for each of the three conditions, Novel Object (alligators: $ICC=-0.304$, $F=0.333$, $P=0.89$ /
427 caimans: $ICC=-0.216$, $F=1.5$, $P=0.266$), Novel Environment: Open Field (alligators: $ICC=0.412$,
428 $F=7.39$, $P=0.121$ / caimans: $ICC=-0.18$, $F=1.6$, $P=0.227$), and Novel Environment: Shelter
429 (alligators: $ICC=0.432$, $F=4.26$, $P=0.075$ / caimans: $ICC=0.13$, $F=1.96$, $P=0.211$).

430



431

432 **Fig. 3** Condition specific variables for the two species (American “alligator”, spectacled “caiman”)

433 in the three conditions (a-c) of the two phases. Novel Object (a): the mean distance of the head-

434 tag from the novel object. Novel Environment: Open Field (b): data represent the roaming range

435 (maximal - minimal distance of head-tag from the arena center). Novel Environment: Shelter (c):

436 time spent partially (one tag detected) or fully (no tags detected) in the shelter. Box plots represent

437 the 25th and 75th percentiles, the line in the box indicates the median, whiskers represent the non-

438 outlier range and dots are outliers ($>Q_3+1.5*IQR$ or $<Q_1-1.5*IQR$). $***P \leq 0.001$, $**P \leq 0.01$, ns
439 = not significant

440

441 **Discussion**

442

443 Our findings reveal consistent differences in behavioral predispositions of hatchling American
444 alligators and spectacled caimans across all experimental contexts. The alligators displayed more
445 movement behavior; they covered wider ranges of the novel environments and went closer to novel
446 objects. In contrast, the caimans moved less, covered a smaller proportion of the arena, and stayed
447 further away from the novel objects. The negligible use of the shelter shown by both species
448 indicates that the measured activity across conditions was not motivated by a need to leave the
449 open space; rather suggesting that the alligators indeed showed more exploration behavior than the
450 caimans. In the Novel Object trials, the alligators consistently decreased the mean distance to the
451 novel object in the second phase while the caimans even further increased it, indicating that the
452 alligators became more explorative while the caimans further reduced their activity level. Previous
453 to the experiment, all subjects were exposed to highly comparable surroundings and stimuli in
454 their husbandry, and thus the observed behavioral predispositions are unlikely to be the result of
455 differences in experience. It is in principle possible that American alligator and spectacled caiman
456 juveniles to some extent differ in their husbandry needs, and that the species activity levels were
457 affected by the chosen procedures. However, both species come from comparable habitats and
458 spectacled caimans are invasive in the natural habitat of American alligators. Hence, they were
459 kept under the same conditions after hatching. Interestingly, we found no individual behavioral
460 consistency over the course of the two phases, which further strengthens the hypothesis that the

461 predispositions of American alligators and spectacled caimans are indeed developed during early
462 ontogeny and can be quite different in even closely related crocodylian species.

463

464 Crocodylians are an interesting taxonomic order for comparative cognition due to their
465 phylogenetic proximity to birds. The relatively few studies to date taking advantage of this
466 potential usually focused on hatchlings and juveniles (Northcutt and Heath 1971; Sneddon et al.
467 2000; Somaweera et al. 2011; Vergne et al. 2012) due to the lack of availability of adult subjects
468 and the risks associated with handling them. It is therefore important to know whether general
469 conclusions, applicable to the entire order Crocodylia, can be drawn from such studies. We found
470 consistent early-life behavioral differences between two Alligatoridae species. These findings have
471 important implications for comparative cognition. First, even closely related crocodylian species
472 can have substantially varied behavioral predispositions during early ontogeny, and different
473 species might therefore not be interchangeable in large scale comparisons. Second, early-life
474 behavioral predispositions appear to be in line with species differences in adult crocodylians, e.g.
475 higher levels of activity in larger species (Grigg and Kirshner 2015), indicating that phylogenetic
476 comparisons can rely on studies focusing on juveniles. The present results add to earlier work,
477 which has shown that crocodylians exhibit species-typical visual signals during social interactions
478 already at the hatchling stage, e.g. raising the head with the snout tip upwards as a sign of
479 submission in several crocodile species (Brien et al. 2013).

480

481 As American alligators and spectacled caimans have similar habitats, these early life differences
482 are surprising from an ecological perspective. Both species have a similar range of predators as
483 hatchlings (Somaweera et al. 2013), to which individuals with increased levels of activity could

484 be expected to be more susceptible (Greenberg and Mettke-Hofmann 2001). On the other hand,
485 both species are food generalists (Dodson 1975; Magnusson et al. 1987) and would profit from
486 learning early on about different food sources by means of increased exploration behavior.
487 Differences in innate exploratory tendencies could indicate that two species originate from habitats
488 of different complexity (Mettke-Hofmann et al. 2002). However, the two subject species are native
489 to highly comparable geographical regions (Grigg and Kirshner 2015). Thus, the differences
490 observed are likely due to other factors. In crocodylians, hatchlings are guarded by their mothers
491 (Hunt and Watanabe 1982; Ferguson 1985; Vergne et al. 2009), and in some species by both
492 parents (Lang 1986; Brazaitis and Watanabe 2011), for the first months and up to three years after
493 hatching (Trutnau and Sommerland 2006; Thorbjarnarson and Wang 2010; Campos et al. 2012).
494 While an alligator mother can protect her offspring against virtually any natural danger, the
495 protection of a caiman mother might be far from absolute. Thus, it is possible that, as a result of
496 maternal care, alligator hatchlings can afford to be more active and explorative. Future studies
497 investigating this relationship should incorporate additional controls to determine whether parental
498 protection can indeed explain more neophilic tendencies.

499

500 Although the effectiveness of parental protection is certainly not the sole aspect influencing the
501 early life behavioral predispositions in crocodylians, it could help explain the success of spectacled
502 caimans as an invasive species. This species has been introduced to the natural habitat of the
503 American alligator, American crocodile (*Crocodylus acutus*), and Cuban crocodile (*Crocodylus*
504 *rhombifer*), and has established viable populations (Global Invasive Species Database,
505 iucngisd.org: <http://www.iucngisd.org/gisd/species.php?sc=1206>). All native species are larger
506 than, and probably behaviorally dominant over, the spectacled caiman. Nevertheless, it

507 successfully competes for resources, e.g. small prey items for hatchlings, putting additional
508 pressure on already critically endangered species (Ellis 1980; Powell et al. 2011). If an invasive
509 species such as the spectacled caiman evolved a less active behavioral predisposition due to high
510 predation risk in its natural range, and if such a species were introduced into a habitat where
511 crocodilians are the apex predators, its hatchlings might have an increased survival rate. It might
512 even be able to outcompete the local crocodilian species, at least in the short term. Over a longer
513 period of time, a species with an innate predisposition for heightened exploration behavior could,
514 however, hold advantages, e.g. because it might explore more potential food sources earlier during
515 ontogeny. Investigating more hatchlings of the same and different species is crucial to gain a full
516 picture of early life behavioral traits in crocodilians.

517

518 One limitation of our study is that our subjects were from few broods (two for American alligators,
519 one for spectacled caimans), which makes it possible that a genetic behavioral predisposition was
520 linked to the individual broods rather than the species. This is a general problem for studies
521 investigating young crocodilians; the availability of study subjects of the same age, particularly
522 from more than one species, is usually low (Brien et al. 2013). We are, however, confident that
523 our results indeed reflect behavioral predispositions of the two study species. The incubation
524 conditions differed within the alligators (5 presumably hatched as males, 6 as females) but not in
525 the caimans (11 presumably hatched as males). Incubation conditions, temperature and others,
526 have been demonstrated to significantly impact phenotype and behavior, including the tendency
527 to explore later in life in crocodilians and other non-avian reptiles, independent of kinship (Burger
528 1991; Sneddon et al. 2000; Deeming 2004; Yowell 2011; Siviter et al. 2017). We controlled for
529 the impact of the two different incubation temperatures and this factor was the first to be excluded

530 during model reduction, indicating that the presumed differences in activity levels originate from
531 an innate predisposition rather than environmental impact. Additionally, the observed plasticity in
532 the Novel Object trials further suggests that the subjects kept developing the described behavioral
533 traits. Future studies should ideally focus on animals from a larger number of broods and include
534 both sexes for each species.

535

536 The discovery that species-typical behavioral predispositions are probably innate in crocodylians
537 provides important implications for conservation efforts intending to release captive-bred
538 individuals into their natural habitat. If juveniles are to be repatriated without the protection of a
539 parent, their initial survival chances could be increased by selecting those with less active
540 behavioral predispositions during early ontogeny. This would particularly be the case for local
541 apex predators (e.g. *Crocodylus siamensis*, *Crocodylus intermedius*), which might naturally show
542 more exploration behavior than smaller species (e.g. *Crocodylus mindorensis*). It appears evident
543 that a better understanding of crocodylian innate behavior, learning capacities, and ecology will
544 play an important role in supporting conservation and management efforts.

545

546 **Declarations**

547

548 **Funding** This project was funded by the Marietta Blau grant (BMFWF) to S. A. R.

549

550 **Conflicts of interest** The authors declare that they have no conflict of interest.

551

552 **Compliance with ethical standards**

553

554 **Ethical statement** The research was approved by the University of Lincoln's ethics committee
555 (number CoSREC36). All applicable national guidelines for the care and use of animals were
556 followed.

557

558 **Consent to participate** Not applicable

559

560 **Consent for publication** Not applicable

561

562 **Availability of data and material** Original videos are stored on the server of the School of Life
563 Sciences, University of Lincoln, Lincoln, UK. For size and owner privacy reasons the videos are
564 not publicly available; for access by interested scientists please contact A. W. at
565 awilkinson@lincoln.ac.uk

566

567 **Code availability** The custom software used for the analysis is available under
568 <https://github.com/jinook0707/AMA>

569

570 **Author contributions** S. A. R. designed the study, built the devices, conducted the experiments,
571 analyzed the data, created the figures, and wrote the manuscript; J. O. designed and created the
572 software, and extracted data for analysis; J. J. conducted and checked the video coding; C. S.
573 helped conceive the study and write the manuscript; S. F. helped conceive the study, and provided
574 and habituated the subjects; A. W. helped conceive and design the study, and write the manuscript.
575 All authors gave final approval for publication.

576

577 **References**

578

579 Azevedo FCC, Verdade LM (2012) Predator-prey interactions: Jaguar predation on caiman in a
580 floodplain forest. *J Zool* 286:200–207. doi: 10.1111/j.1469-7998.2011.00867.x

581 Bell AM, Stamps JA (2004) Development of behavioural differences between individuals and
582 populations of sticklebacks, *Gasterosteus aculeatus*. *Anim Behav* 68:1339–1348. doi:

583 10.1016/j.anbehav.2004.05.007

584 Brazaitis P, Watanabe ME (2011) Crocodylian behaviour: A window to dinosaur behaviour? *Hist*
585 *Biol* 23:73–90. doi: 10.1080/08912963.2011.560723

586 Brien ML, Lang JW, Webb GJ, et al (2013) The good, the bad, and the ugly: Agonistic

587 behaviour in juvenile crocodylians. *PLoS One* 8:. doi: 10.1371/journal.pone.0080872

588 Britton ARC (2001) Review and classification of call types of juvenile crocodylians and factors
589 affecting distress calls. In: *Crocodylian biology and evolution*. Surrey Beatty & Sons,

590 Chipping Norton, pp 364–377

591 Burger J (1991) Effects of incubation temperature on behavior of hatchling pine snakes:

592 implications for reptilian distribution. *Behav Ecol Sociobiol* 28:297–303. doi:

593 10.1007/BF00175103

594 Calle PP, Rivas J, Muñoz M, et al (1994) Health assessment of free-ranging anacondas (*Eunectes*
595 *murinus*) in Venezuela. *J Zoo Wildl Med* 25:53–62

596 Campos Z, Sanaiotti T, Muniz F, et al (2012) Parental care in the dwarf caiman, *Paleosuchus*
597 *palpebrosus* Cuvier, 1807 (Reptilia: Crocodylia: Alligatoridae). *J Nat Hist* 46:2979–2984.

598 doi: 10.1080/00222933.2012.724723

599 Cott HB (1961) Scientific results of an inquiry into the ecology and economic status of the Nile
600 Crocodile (*Crocodilus niloticus*) in Uganda and Northern Rhodesia. Trans Zool Soc London
601 29:211–356. doi: 10.1111/j.1096-3642.1961.tb00220.x

602 Deeming DC (2004) Post-hatching phenotypic effects of incubation in reptiles. In: Reptilian
603 incubation: behaviour and environment. Nottingham University Press, Nottingham, pp 229–
604 252

605 Dodson P (1975) Functional and ecological significance of relative growth in Alligator. J Zool
606 175:315–355. doi: 10.1111/j.1469-7998.1975.tb01405.x

607 Ellis TM (1980) *Caiman crocodilus*: An established exotic in South Florida. Copeia 1980:152–
608 154. doi: 10.2307/1444148

609 Ferguson MWJ (1985) Reproductive biology and embryology of the crocodylians. In: Gans C,
610 Billett F, Maderson PFA (eds) Biology of the Reptilia, Volume 14. John Wiley and Sons,
611 New York, pp 451–460

612 Ferguson MWJ, Joanen T (1982) Temperature of egg incubation determines sex in *Alligator*
613 *mississippiensis*. Nature 296:850–853. doi: 10.1038/296850a0

614 Fraser DF, Gilliam JF (1987) Feeding under predation hazard: Response of the guppy and Hart’s
615 rivulus from sites with contrasting predation hazard. Behav Ecol Sociobiol 21:203–209

616 Garrick LD, Lang JW (1977) Social signals and behaviors of adult alligators and crocodiles. Am
617 Zool 17:225–239

618 Glaudas X, Winne CT, Fedewa LA (2006) Ontogeny of anti-predator behavioral habituation in
619 cottonmouths (*Agkistrodon piscivorus*). Ethology 112:608–615. doi:
620 <https://doi.org/10.1111/j.1439-0310.2005.01183.x>

621 Gossette RL, Hombach A (1969) Successive discrimination reversal (SDR) performances of

622 American alligators and American crocodiles on a spatial task. *Percept Mot Skills* 28:63–
623 67. doi: 10.2466/pms.1969.28.1.63

624 Gray JA (1987) The neuropsychology of emotion and personality. In: Stahl SM, S. D. Iversen
625 SD, Goodman EC (eds) *Cognitive neurochemistry*. Oxford University Press, New York,
626 NY, pp 171–190

627 Greenberg R, Mettke-Hofmann C (2001) Ecological aspects of neophobia and neophilia in birds.
628 In: Nolan V, Thompson CF (eds) *Current Ornithology*, vol 16. Springer US, Boston, MA,
629 pp 119–178

630 Greggor AL, Thornton A, Clayton NS (2015) Neophobia is not only avoidance: improving
631 neophobia tests by combining cognition and ecology. *Curr Opin Behav Sci* 6:82–89. doi:
632 <https://doi.org/10.1016/j.cobeha.2015.10.007>

633 Grigg GC, Kirshner D (2015) *Biology and evolution of crocodylians*. Cornell University Press,
634 ISBN: 9780801454103, Ithaca, New York, United States

635 Gumbert A (2000) Color choices by bumble bees (*Bombus terrestris*): innate preferences and
636 generalization after learning. *Behav Ecol Sociobiol* 48:36–43. doi: 10.1007/s002650000213

637 Halekoh U, Højsgaard S (2014) A Kenward-Roger Approximation and parametric bootstrap
638 methods for tests in linear mixed models - The R package pbrtest. *J Stat Softw* 59:. doi:
639 10.18637/jss.v059.i09

640 Hawkins LA, Magurran AE, Armstrong JD (2004) Innate predator recognition in newly-hatched
641 Atlantic salmon. *Behaviour* 141:1249–1262. doi: 10.1163/1568539042729694

642 Heinrich B (1995) Neophilia and exploration in juvenile common ravens, *Corvus corax*. *Anim*
643 *Behav* 50:695–704. doi: [https://doi.org/10.1016/0003-3472\(95\)80130-8](https://doi.org/10.1016/0003-3472(95)80130-8)

644 Holm S (1979) A simple sequentially rejective multiple test procedure. *Scand J Stat* 6:65–70

645 Hudina S, Hock K, žganec K (2015) The role of aggression in range expansion and biological
646 invasions. *Curr Zool* 60:401–409. doi: 10.1093/czoolo/60.3.401

647 Hugall AF, Foster R, Lee MSY (2007) Calibration choice, rate smoothing, and the pattern of
648 tetrapod diversification according to the long nuclear gene RAG-1. *Syst Biol* 56:543–563

649 Hunt RH, Watanabe ME (1982) Observations on maternal behavior of the American alligator,
650 *Alligator mississippiensis*. *J Herpetol* 16:235–239

651 Kanwatanakid-Savini C, Pliosungnoen M, Pattanavibool A, et al (2012) A survey to determine
652 the conservation status of Siamese crocodiles in Kaeng Krachan National Park, Thailand.
653 *Herpetol Conserv Biol* 7:157–168

654 Kelley JL, Magurran AE (2003) Effects of relaxed predation pressure on visual predator
655 recognition in the guppy. *Behav Ecol Sociobiol* 54:225–232. doi: 10.1007/s00265-003-
656 0621-4

657 Kendal RL, Coe RL, Laland KN (2005) Age differences in neophilia, exploration, and
658 innovation in family groups of callitrichid monkeys. *Am J Primatol* 66:167–188. doi:
659 10.1002/ajp.20136

660 King W, Krakauer T (1966) The exotic herpetofauna of Southeast Florida. *Q J Florida Acad Sci*
661 29:144–154

662 Kofron CP (1993) Behavior of Nile crocodiles in a seasonal river in Zimbabwe. *Copeia*
663 1993:463–469. doi: 10.2307/1447146

664 Lang J (1986) Male parental care in mugger crocodiles. *Natl Geogr Res* 2:519–525

665 MacLean EL, Matthews LJ, Hare BA, et al (2012) How does cognition evolve? Phylogenetic
666 comparative psychology. *Anim Cogn* 15:223–238. doi: 10.1007/s10071-011-0448-8

667 Magnusson WE, da Silva EV, Lima AP (1987) Diets of Amazonian crocodilians. *J Herpetol*

668 21:85–95. doi: 10.2307/1564468

669 Mettke-Hofmann C, Winkler H, Leisler B (2002) The significance of ecological factors for
670 exploration and neophobia in parrots. *Ethology* 108:249–272. doi: 10.1046/j.1439-
671 0310.2002.00773.x

672 Miller R, Bugnyar T, Pölzl K, Schwab C (2015) Differences in exploration behaviour in
673 common ravens and carrion crows during development and across social context. *Behav*
674 *Ecol Sociobiol* 69:1209–1220. doi: 10.1007/s00265-015-1935-8

675 Mundry R, Fischer J (1998) Use of statistical programs for nonparametric tests of small samples
676 often leads to incorrect P values: examples from *Animal Behaviour*. *Anim Behav* 56:256–
677 259. doi: <https://doi.org/10.1006/anbe.1998.0756>

678 Murray CM, Russo P, Zorrilla A, McMahan CD (2019) Divergent morphology among
679 populations of the New Guinea crocodile, *Crocodylus novaeguineae* (Schmidt, 1928):
680 Diagnosis of an independent lineage and description of a new species. *Copeia* 107:517–523.
681 doi: 10.1643/CG-19-240

682 Northcutt RG, Heath JE (1971) Performance of caimans in a T-Maze. *Copeia* 1971:557–560.
683 doi: 10.2307/1442459

684 O’Hara M, Mioduszewska B, von Bayern A, et al (2017) The temporal dependence of
685 exploration on neotic style in birds. *Sci Rep* 7:4742. doi: 10.1038/s41598-017-04751-0

686 Powell R, Henderson R, Farmer M, et al (2011) Introduced amphibians and reptiles in the greater
687 Caribbean: Patterns and conservation implications. In: Hailey A, Wilson BS, Horrocks JA
688 (eds) *Conservation of Caribbean Island Herpetofaunas Volume 1: Conservation Biology*
689 *and the Wider Caribbean*. Brill, Leiden, NL, pp 63–143

690 Radloff FGT, Hobson KA, Leslie AJ (2012) Characterising ontogenetic niche shifts in Nile

691 crocodile using stable isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) analyses of scute keratin. *Isotopes Environ*
692 *Health Stud* 48:439–456. doi: 10.1080/10256016.2012.667808

693 Réale D, Reader SM, Sol D, et al (2007) Integrating animal temperament within ecology and
694 evolution. *Biol Rev* 82:291–318. doi: 10.1111/j.1469-185X.2007.00010.x

695 Reber SA (2018) Crocodilia Communication. In: Vonk J, Shackelford T (eds) *Encyclopedia of*
696 *Animal Cognition and Behavior*. Springer International Publishing, Cham, pp 1–10

697 Reber SA, Janisch J, Torregrosa K, et al (2017) Formants provide honest acoustic cues to body
698 size in American alligators. *Sci Rep* 7:1–11. doi: 10.1038/s41598-017-01948-1

699 Rokka K, Pihlaja M, Siitari H, Soulsbury CD (2014) Sex-specific differences in offspring
700 personalities across the laying order in magpies *Pica pica*. *Behav Processes* 107:79–87. doi:
701 <https://doi.org/10.1016/j.beproc.2014.07.019>

702 Scognamillo D, Maxit IE, Sunquist M, Polisar J (2003) Coexistence of jaguar (*Panthera onca*)
703 and puma (*Puma concolor*) in a mosaic landscape in the Venezuelan llanos. *J Zool*
704 259:269–279. doi: 10.1017/S0952836902003230

705 Siviter H, Charles Deeming D, Rosenberger J, et al (2017) The impact of egg incubation
706 temperature on the personality of oviparous reptiles. *Anim Cogn* 20:109–116. doi:
707 10.1007/s10071-016-1030-1

708 Sneddon H, Hepper PG, Manolis C (2000) Embryonic chemosensory learning in the saltwater
709 crocodile *Crocodylus porosus*. In: Grigg GC, Seebacher F, Franklin CE (eds) *Crocodilian*
710 *Biology and Evolution*. Surrey Beatty & Sons, Chipping Norton NSW, pp 378–382

711 Somaweera R, Brien M, Shine R (2013) The role of predation in shaping crocodilian natural
712 history. *Herpetol Monogr* 27:23–51

713 Somaweera R, Webb JK, Brown GP, Shine RP (2011) Hatchling Australian freshwater

714 crocodiles rapidly learn to avoid toxic invasive cane toads. *Behaviour* 148:501–517. doi:
715 10.1163/000579511X565763

716 Stevenson C (2019) *Crocodiles of the world*. New Holland Publishers, London

717 Thorbjarnarson J, Wang X (2010) *The Chinese alligator: ecology, behavior, conservation, and*
718 *culture*. Johns Hopkins University Press, Baltimore, MD, United States

719 Tierney AJ (1986) The evolution of learned and innate behavior: Contributions from genetics
720 and neurobiology to a theory of behavioral evolution. *Anim Learn Behav* 14:339–348. doi:
721 10.3758/BF03200077

722 Tinbergen N (1963) On aims and methods of ethology. *Z Tierpsychol* 20:410–433. doi:
723 10.1111/j.1439-0310.1963.tb01161.x

724 Trutnau L, Sommerland R (2006) *Crocodylians: their natural history & captive husbandry*.
725 Edition Chimaira, Frankfurt am Main

726 Vergne AL, Aubin T, Martin S, Mathevon N (2012) Acoustic communication in crocodylians:
727 Information encoding and species specificity of juvenile calls. *Anim Cogn* 15:1095–1109.
728 doi: 10.1007/s10071-012-0533-7

729 Vergne AL, Pritz MB, Mathevon N (2009) Acoustic communication in crocodylians: From
730 behaviour to brain. *Biol. Rev.* 84:391–411

731 Vilhunen S, Hirvonen H (2003) Innate antipredator responses of Arctic charr (*Salvelinus*
732 *alpinus*) depend on predator species and their diet. *Behav Ecol Sociobiol* 55:1–10. doi:
733 10.1007/s00265-003-0670-8

734 Wang Z, Yao H, Ding Y, et al (2011) Testing reintroduction as a conservation strategy for the
735 critically endangered Chinese alligator: Movements and home range of released captive
736 individuals. *Chinese Sci Bull* 56:2586–2593. doi: 10.1007/s11434-011-4615-8

- 737 Webb GJW, Manolis SC, Whitehead PJ (1987) Wildlife management: crocodiles and alligators.
738 S. Beatty & Sons, Chipping Norton, NSW, Australia
- 739 Wilson DS, Coleman K, Clark A, Biederman L (1993) Shy-bold continuum in pumpkinseed
740 sunfish (*Lepomis gibbosus*): An ecological study of a psychological trait. J Comp Psychol -
741 J COMP PSYCHOL 107:250–260. doi: 10.1037//0735-7036.107.3.250
- 742 Yowell JL (2011) Aptitude in American alligators: Ecological factors affecting cognition and
743 behavior. Ph.D. dissertation. The University of Utah
- 744