

1 **TITLE: Juvenile socio-ecological environment shapes material technology in**
2 **nest-building birds**

3
4 **RUNNING TITLE: Developing technological know-how**

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29

30 Data accessibility

31 Analyses reported in this article can be reproduced using the data provided by Breen
32 et al. (2020). Data and corresponding R script are also available as Supplementary
33 material.

34

35 Authors' contributions

36 A.J.B. and L.M.G. conceptualized and designed the experiment. A.J.B. performed
37 the experiment and extracted the data, with help on video scoring (K.E.L.; C.G.; J.C.)
38 and animal husbandry (S.C.E.). A.J.B. analyzed and visually presented the data.
39 A.J.B. wrote the manuscript, which was edited by S.D.H. and L.M.G. and approved
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41

42 Competing interests

43 The authors declare no competing interests.

44

45 Ethics approval

46 All research was conducted with the approval of the University of St Andrews Animal
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48 ABSTRACT

49 Variation in animal material technology, such as tool use and nest construction, is
50 thought to be caused, in part, by differences in the early-life socio-ecological
51 environment—that is, *who* and *what* is around—but this developmental hypothesis
52 remains unconfirmed. We used a tightly controlled developmental paradigm to
53 determine whether adult and/or raw-material access in early life shape first-time nest
54 construction in laboratory-bred zebra finches *Taeniopygia guttata* at sexual maturity.
55 We found that juvenile access to both an unrelated adult and raw material of one
56 color led to a majority preference (75%) by novice builders for this color of material
57 over that for either natal-nest or novel colored material, whereas a lack of juvenile
58 access to both an unrelated adult and raw material led to a four- and nearly three-
59 fold reduction in the speed at which novice builders initiated and completed nest
60 construction, respectively. Contrary to expectation, neither the amount of time
61 juveniles nor their adult group-mate spent handling the raw material appear to drive
62 these early-life effects on zebra finches' first-time nest construction, suggesting that
63 adult presence might be sufficient to drive the development of animal material
64 technology. Together these data show that the juvenile socio-ecological environment
65 can trigger variation in at least two critical aspects of animal material technology
66 (material preference and construction speed), revealing a potentially powerful
67 developmental window for technological advancement. Thus, to understand
68 selection on animal material technology, the early-life environment must be
69 considered.

70 KEY WORDS

71 Animal material technology, Nest construction, Early-life environment, Material
72 preference, Construction speed, Technological evolution

73 INTRODUCTION

74 The utilization of raw material from the surrounding environment for foraging,
75 protection, and reproduction—hereafter, material technology—is widespread in
76 animals (Hansell 2005; Lill and Marquis 2007; Shumaker et al. 2011). Examples of
77 animal material technology include bower building, dam design, nest construction,
78 tool manufacture and/or use, trap assembly, and shelter set-up. In these examples
79 an animal must exhibit sufficient skill in, first, selection of appropriate raw material
80 and, second, the technique(s) for successful construction of the technology (Hansell
81 2005). Adverse consequences of variation in animal material technology range from
82 loss of time (e.g., St Clair et al. 2018) and energy (e.g., Withers 1977), to missed
83 foraging or mating opportunities (e.g., Farji-Brener 2003; Östlund-Nilsson and
84 Holmlund 2003; respectively), and even, death (e.g., Damman 1987). Acquiring
85 technological competence, then, is undoubtedly crucial in the life history of these
86 animals (Bateson 1988). As developmental plasticity plays a ubiquitous role in
87 shaping organismal phenotype (reviews in Taborsky 2017; Langenhof and Komdeur
88 2018), one relatively untested driver of technological competence may be the early-
89 life environment in which an animal develops.

90 Rich observational data suggest the early-life socio-ecological environment—
91 *who* and *what* is around—interactively shapes material technology in animals
92 (reviews of bird and primate data: Biro et al. 2006; Frigaszy 2011; Frigaszy et al.
93 2013; Meulman et al. 2013; Breen et al. 2016; Rutz et al. 2018), with the
94 presence/behavior of experienced adults appearing to aid youngsters' learning of
95 'what to do'. For example, juvenile New Caledonian crows *Corvus moneduloides* are
96 more likely to handle abandoned extractive foraging tools made by their parents than
97 they are to handle tools made and abandoned by other adult crows (Holzhaider et al.

98 2010a); unweaned chimpanzees *Pan troglodytes* craft and use ant-dipping stick-
99 tools exclusively in the presence of their foraging, ant-dipping mother (Humble et al.
100 2009); and young Sumatran orang-utans *Pongo pygmaeus abelii* construct their first
101 weight-bearing nest only after three years of adolescent exposure to nests
102 constructed every night by their mother (van Noordwijk and van Schaik 2005).
103 Together these data imply that animals combine relevant social and ecological cues
104 from early life when developing their technological competence.

105 Owing to ethical and logistical constraints on field experiments, however, it
106 has remained difficult to determine experimentally whether adults and/or raw
107 material affect the development of material technology in animals. And the majority
108 of laboratory experiments to date—where the typical method has been to human-
109 rear a group of subjects in isolation from adult conspecifics (Scott 1902; Scott 1904;
110 Verlaine 1934; Collias and Collias 1964; Kenward et al. 2005; Kenward et al. 2006;
111 Videan 2006; Morimura and Mori 2010; but see Tebbich et al. 2001)—confound
112 possible effects of early learning opportunity with possible developmental effects of
113 rearing experience (e.g., developmental differences in brain morphology caused by
114 parental isolation; Bogart et al. 2014). To examine the effects of the socio-ecological
115 environment in early life on material technology in animals, then, a more tractable
116 study system and approach would be useful.

117 For decades, the zebra finch *Taeniopygia guttata* has played a key role in
118 illuminating how the environment in early life shapes mate choice and song
119 production in adults under laboratory conditions (reviews in Slater et al. 1988; Griffith
120 and Buchanan 2010). The zebra finch is also becoming a useful model system to
121 examine the effects of experience on construction behavior (Breen et al. 2016).
122 Indeed, laboratory work has identified social and ecological factors such as,

123 respectively, conspecific familiarity (Guillette et al. 2016) and raw-material properties
124 (e.g., color, Bailey et al. 2015; length, Muth and Healy 2014; rigidity, Bailey et al.
125 2014) involved in shaping adult zebra finches' nest constructions. The links between
126 the early-life environment and phenotypic development in zebra finches suggest,
127 then, that study on socio-ecological effects in early life on nest construction in zebra
128 finches should not only be feasible—but also profitable. Consistent with the idea that
129 the early-life socio-ecological environment plays a role in shaping zebra finches' nest
130 construction, observational data show that wild juvenile (i.e., fledged) zebra finches
131 remain near to their parents for at least 30 days post-fledging (Zann 1996),
132 potentially learning something of these experienced adults' choice/effective handling
133 of material if they breed again (wild pairs of zebra finches re-breed often, up to six
134 times, back-to-back in a single breeding period; Zann 1996). That the *juvenile* socio-
135 ecological environment may influence zebra finches' early learning of nest
136 construction is further suggested from experimental data showing that they appear
137 not to imprint on natal-nest material (Sargent 1965; Muth and Healy 2012). Without
138 appropriate controls, however, these imprinting results require verification.

139 The aim of the current study was twofold: to determine whether the early-life
140 social and ecological environment shape (I) material preference for, and (II) speed at
141 first-time nest construction (defined here as how quickly nest construction is initiated
142 and completed) by captive zebra finches. In this species, both the choice of material
143 for, and speediness at nest construction are particularly relevant breeding behaviors
144 because, in the wild, zebra finches are nomadic and breed opportunistically; they
145 need to readily identify suitable material and capitalize on a potential breeding
146 opportunity (Zann 1996). To test the hypothesis that the early-life socio-ecological
147 environment plays a role in the development of nest construction in zebra finches,

148 we conducted a 2 × 2 factorial developmental experiment (Figure 1) in which we
149 manipulated the social (provided access to an experienced nest-constructing adult
150 conspecific: yes or no; A+ or A-) and ecological (provided access to non-natal nest
151 material across 12 one-hour material experience sessions: yes or no; M+ or M-)
152 environment of 32 juvenile (60 – 90 days post-hatch) non-sibling same-aged male-
153 male pairs (because males are the builders in this species). At sexual maturity (90
154 days post-hatch), we then provided each of these males with a mate, a nest box, and
155 three materials for first-time nest construction: material that matched in color (I) to
156 their natal nest, (II) to their juvenile environment (where applicable), or (III) was
157 novel. Inclusion of a novel material prevented forced binary choices—for males in
158 the M+ treatments—between natal-nest material and colored material from the
159 juvenile environment. To enable meaningful comparisons between experimental
160 treatments, two of the raw-material options were novel for the males that had not had
161 access to material during the juvenile environment experimental phase (M-
162 treatments). The first-time nest-construction behavior of all males—material
163 preference and construction speed—was subsequently assayed from video
164 recordings (see Methods for details).

165 Our experimental design thus allowed us to test the following non-exclusive
166 hypotheses and predictions: (I) males imprint on natal-nest material irrespective of
167 the juvenile environment (if so, for construction of their first nest all males should
168 prefer material of the same color as that of the nest into which each hatched); (II)
169 juvenile experience of material alone is sufficient to shape a male's material
170 preference (if so, males provided access to material when juvenile—M+
171 treatments—should prefer this same color of material for first-time nest construction);
172 (III) males integrate both juvenile social and ecological cues when developing their

173 material preference (if so, then only those males provided with juvenile access to
174 both an adult and material—A+/M+ treatment—should prefer this same color of
175 material when they construct their first nest); finally, (IV) speed at first-time nest
176 construction is a result of an interaction between the juvenile social and ecological
177 environment (if so, then those males that have had juvenile access to both an adult
178 and material—A+/M+ treatment—should be the quickest to initiate and complete
179 their first nest)

180

181 **METHODS**

182 **Participants and husbandry**

183 Participants in the current study were 148 zebra finches (78 males; 70 females) bred
184 at the University of St Andrews or obtained from a local breeder. Of the 148 zebra
185 finch participants, 76 birds (38 males; 38 females) served as breeding pairs; 32 male
186 offspring of the breeding pairs served as experimental subjects; 32 female offspring
187 of the breeding pairs served as partners to the male subjects; and 8 additional males
188 served as companions to half of the male subjects. Breeding pairs and companion
189 males had all previously constructed at least one nest, whereas the male subjects
190 and their female partners were naïve to nest construction.

191 All birds were provided *ad libitum* access to food (Johnson & Jeff seed,
192 oystershell grit, calcium and vitamin block), egg mix for breeding pairs and young (up
193 to 35 days post-hatch; Haith's egg biscuit food) plus spinach three times per week
194 and water (supplemented with vitamin D3 three times per week) and kept on a 14:10
195 light:dark light cycle, with humidity and temperature levels at approximately 50% and
196 20° C, respectively. Prior to and following this study, birds were housed in same-sex
197 colony cages (140 × 71 × 122 cm).

198

199 Experimental apparatus and set-up

200 Twelve identical test cages (50 × 50 × 50 cm) were used to test all birds. Attached to
201 the left and right front of each test cage were, respectively, a food and water hopper,
202 in addition to two perches. On the floor of each test cage the following items were
203 placed: cuttlefish bone, oystershell grit, vitamin block, and a food and water bowl.
204 Two 2.4 GHZ Bird Box cameras (Spy Camera CCTV) were wired to the roof of each
205 test cage. One camera was focused on the cage floor and the second camera was
206 focused on the nestbox (when one was present—see Experimental protocol). Both
207 cameras were connected to one of four desktop computers or one of two laptop
208 computers used to record birds' behavior during testing as detailed below. Birds
209 could hear but not see their neighbors as we placed an opaque white barrier
210 between each test cage. See Supplementary material Figure S1 for an image of the
211 experimental apparatus and set-up.

212

213 Experimental protocol

214 The experiment consisted of three phases (Figure 1): (i) natal environment; (ii)
215 juvenile environment; and (iii) first-time nest construction. In each of these three
216 phases we used at least one of three different types of colored material: pink, orange
217 and white string (jute craft twine from James Lever Co., London, UK). All material
218 was cut to 15 cm lengths. These materials fall within the range of zebra finch color
219 vision (Hart 2001) and were chosen based on our previous work (Bailey et al. 2014;
220 Guillette et al. 2016; Breen et al. 2019), which shows that male zebra finches can
221 discriminate between each of them. We used the in-cage cameras described above
222 to record experimental phase (ii) and (iii).

223

224 **(i) Natal environment**

225 Breeding pairs were each placed in a breeding cage (50 × 50 × 50 cm) for six days
226 in order to form pair bonds. On the morning of the seventh day, pairs were provided
227 with a wooden nestbox (11 × 12 × 4.5 cm) and material (either 400 pieces of pink or
228 orange string cut to 15 cm lengths; $n = 19$ per string-type) with which to construct
229 their nest (males can construct a species-typical domed nest with this length and
230 amount of material—see Figure 2 in Breen et al. 2019). Nests were checked for eggs
231 once per day until the first egg, after which, we removed any remaining material not
232 in the nest (to prevent males from adding more material, which can result in the eggs
233 being buried; Zann 1996). The nests plus nestboxes were removed five days after
234 the first individual in a brood fledged (~23 days post-hatch). As zebra finch chicks do
235 not necessarily fledge all at once (Zann 1996), this time window allowed for all young
236 to leave the nest before we removed it. Fledglings remained with their parents until
237 nutritional independence (~35 days post-hatch; Zann 1996), after which, we returned
238 parents and any female offspring to the same-sex group housing conditions
239 described above. Nutritionally-independent subject males remained housed with
240 brothers until the start of the next experimental phase. Where this was not possible
241 (because parents produced a single male offspring), we added these single males to
242 a family group of same-aged males and, when later paired (see Juvenile
243 environment), treated these birds as if they were full brothers to prevent the pairing
244 of two familiar individuals. None of the offspring hatched in the natal environment
245 phase were able to observe nest construction as they did not have visual access of
246 other birds outside their cage (because we placed an opaque barrier between each

247 breeding cage). Throughout the natal environment experiment phase, we checked
248 pairs once per day in order to gauge breeding progress.

249

250 **(ii) Juvenile environment**

251 Approximately 56 days post-hatch, juvenile subject males were placed in non-sibling
252 same-aged male-male pairs matched for natal environment (i.e., pink or orange natal
253 nest) in a test cage and assigned to one of four treatments (Figure 1): (I) no access
254 to an adult or material (A-/M-); (II) access to an adult but no access to material
255 (A+/M-); (III) no access to an adult but access to material (A-/M+); and (IV) access to
256 both an adult and material (A+/M+). No juvenile birds were related to the adult males
257 or had a brother in the same treatment. Considering genetic as well as other
258 constraints (e.g., time, facility space, and equipment availability) in tandem with
259 statistical power (Taborsky 2010), the sample size for each of the four treatments
260 was thus eight birds (i.e., four juvenile pairs). Before we placed birds in their
261 respective cages, we marked the top of their head (using a non-toxic and non-
262 permanent marker pen; Jiffy Eco-marker Ink) with a unique mark so that we could
263 later readily identify (from videos) and score each bird's material-handling time (see
264 below) in this second experimental phase. Once in their cages, birds were given
265 three days to adjust to their new environment.

266 On day four in their testing environment, each bird experienced their first (of
267 12) material experience sessions (three sessions per week) at either four or five
268 hours (pseudo-randomized across sessions) post-light onset. During each material
269 experience session, birds in M+ treatments were provided colored (pink or orange)
270 material in two piles ($n = 20$ pieces in each pile) for one hour, after which, we
271 removed all of the material, whereas birds in the M- treatments were sham treated—

272 that is, the experimenter (AJB) briefly placed their hand without material in the
273 respective cages at the start and end of the hour to match the actions performed in
274 the M+ treatments. The material during the material experience sessions for birds in
275 the M+ treatments was always of an alternative color—either pink or orange—to their
276 natal-nest material. Note that we did not know if/how the juveniles or the adults in the
277 M+ treatments would interact with the material we provided, except that, as a female
278 was not present, we did not expect the adults to construct a nest (subsequent video
279 scoring confirmed this expectation). We returned adult males in both A+ treatments
280 to group housing (see above) after the 12th and final material experience session.
281 The juveniles remained in pairs for four days after completing the juvenile
282 environment experimental phase. The purpose of this was to ensure that each
283 subject reached sexual maturity (90 days of age) before being provided a mate and
284 moving onto the third phase of the experiment.

285

286 **(iii) First-time nest construction**

287 Approximately 90 days post-hatch, we moved each of the 32 (previously juvenile)
288 subject males into a new test cage and paired each with an unrelated, same-age
289 female (matched for natal-nest material). Pairs were then left for five additional days
290 to form pair bonds. On the sixth day, we attached a wooden nestbox (11 × 12 × 4.5
291 cm) midway along the back wall of each pair's cage (Figure S1). We then provided
292 pairs with three different types of material for constructing their first nest: material
293 that matched their (I) natal environment, (II) juvenile environment (for males in M+
294 treatments) or (III) was novel (an opt-out option to not assume a role for early
295 learning). Thus, for males in M+ treatments the novel material was always the white

296 string, whereas for males in M- treatments the novel material was always the white
297 string as well as a non-white string type—either pink or orange string.

298 We placed the three different types of colored material in three distinct piles (*n*
299 = 20 pieces in each pile, that is, 60 pieces in total—this amount is sufficient to yield
300 insight into experiential drivers of avian nest construction; Guillette et al. 2016;
301 Guillette and Healy 2018; Breen et al. 2019) centrally on the cage floor and
302 equidistant from one another. Material-color order was randomized across pairs.
303 After placing the material, we did not disturb pairs for three hours. Thereafter we
304 visually checked the nestbox three times per day, beginning at light on-set and
305 continuing at four-hour intervals until the end of this final experimental phase. The
306 first-time nest construction experimental phase began at six hours post-light onset
307 and ended once a male had moved all colored material into his nestbox, after which,
308 we removed the nestbox plus material, and we returned pairs to their respective
309 colony cages as described above.

310

311 **Data extraction and statistical analyses**

312 **General**

313 We used Solomon coder (www.solomoncoder.com) set at a time resolution of 0.2
314 seconds for all behavioral scoring of video recordings in the current study, and we
315 performed all statistical analyses in R (R Core Team 2017). We confirmed the
316 goodness-of-fit (all $p > 0.05$) of our statistical models using the ‘testUniformity’
317 function from the ‘DHARMA’ package (Hartig 2017) on the scaled model residuals.
318 Model significance was always assessed using Type II likelihood-ratio chi-square
319 tests (Langsrud 2003) from the ‘car’ package (Fox and Weisberg 2011).

320

321 Video scoring of first-time nest construction

322 To assay the first-time nest-construction behavior of males, we scored (blind to
323 treatment) the recorded 32 videos from the first-time nest construction experimental
324 phase. Specifically, we scored the following behaviors for each male: (I) latency (in
325 seconds; here and elsewhere) to first handle material (by making initial bill-to-
326 material contact); and (II) latency to initiate (by depositing a piece of material within
327 the nestbox) and (III) complete first-time nest construction (by depositing the 60th
328 piece of material within the nestbox). We were unable to score behavior (I) for five
329 males because (a) the female deposited all of the material in the nestbox (one male
330 in treatment A-/M+) or (b) the subject died after completing the juvenile environment
331 experimental phase (one male in treatment A-/M-) or (c) the video prematurely
332 stopped recording before first-time nest construction, rendering latency measures
333 inaccurate (one male in treatment A+/M- and one male in treatment A-/M-) or (d) the
334 camera was initially angled incorrectly, obscuring one of the piles of material from
335 view (one male in treatment A+/M+). We were also unable to score behaviors (II)
336 and (III) for reasons (a – c) for these same corresponding males. The final dataset
337 thus contained a sample size of 27 (A-/M-, $n = 6$; A+/M-, $n = 7$; A-/M+, $n = 7$; A+/M+,
338 $n = 7$) for behavior (I) and a sample size of 28 (A-/M-, $n = 6$; A+/M-, $n = 7$; A-/M+, $n =$
339 7 ; A+/M+, $n = 8$) for behaviors (II) and (III).

340 We also scored the color of the first 20 pieces of material a male deposited in
341 his nestbox to determine, as detailed below, each male's preferred color of material
342 for constructing his first nest. However, as explained above, we were unable to
343 determine the material-color preference for two males, and for a third male in
344 treatment A+/M-, because his video recording cut-out during first-time nest
345 construction. The final dataset thus contained the material-color preference of 29

346 males (sample size per treatment: A-/M-, $n = 7$; A+/M-, $n = 7$; A-/M+, $n = 7$; A+/M+, n
347 = 8).

348 To determine males' material color preference, we ran a Monte Carlo
349 simulation to create a distribution curve of the likelihood of depositing the same color
350 of material (e.g., pink) across 20 trials in an environment where three colored raw-
351 material options (pink, orange, and white) always exist. From this simulation, we
352 established that any one of the three colored materials deposited >10 times (out of
353 the first 20) within the nestbox is significantly different from chance ($p = 0.038$)—in
354 other words, preferred. We then applied this material-preference criterion (as we
355 have done elsewhere; Breen et al. 2019) to the first 20 pieces deposited by each
356 male in his nestbox when he constructed his first nest. Where this criterion was not
357 met ($n = 1$), we assigned material-color preference based on which colored material
358 a male first used in entirety (by depositing all 20 pieces of the colored material in his
359 nestbox; which this bird did in 43 deposits). A post-hoc Monte Carlo simulation
360 confirmed that depositing all 20 pieces of one colored material across 43 trials in a
361 three-material-option environment is significantly different from chance ($p = 0.026$).
362 For details on each male's material-color choices and preference, see Figure S2.

363

364 **Early-life effects on first-time nest construction**

365 **Material-color preference**

366 To determine the effect of the early-life environment on zebra finches' preferred color
367 of material for first-time nest construction, we first classified the material-color
368 preference of each male into one of three categories: (I) preferred material that
369 matched in color to the natal environment; (II) preferred material that matched in
370 color to the one provided during the juvenile environment (where applicable i.e., M+

371 treatments); or (III) preferred material of a novel color. We then analyzed these
372 preference data using binomial generalized linear models (GLMs), as exhibiting a
373 preference for a particular category of material effectively produces binary (i.e., yes
374 or no) outcomes. Because the true probability of expressing a preference for any one
375 of the three colored materials made available to each male was 0.33 (and not 0.5 as
376 specified by the binomial error structure of our models), Model 1 – 3, detailed below,
377 should be considered *conservative*.

378 Our first model (Model 1) tested if novice builder zebra finches prefer material
379 of the color of their natal nest irrespective of their juvenile experience. The response
380 variable for Model 1 was whether (yes or no) males in each of the four treatments
381 exhibited a preference for natal-nest material; the predictor variables included
382 juvenile adult presence (yes or no), juvenile material access (yes or no), and their
383 interaction. Our second model (Model 2) tested if juvenile material access is
384 sufficient experience to shape material preference or if an adult also needs to be
385 present, for experimental subjects in the M+ treatments. The response variable for
386 Model 2 was whether (yes or no) a male subject preferred material from their juvenile
387 environment; the predictor variable was whether (yes or no) they were, as a juvenile,
388 housed with an adult. Our third model (Model 3) interrogated, for scope, if the early-
389 life socio-ecological environment influenced whether (yes or no) males in each of the
390 four treatments exhibited a preference for a novel material—the dependent variable;
391 the predictor variables for Model 3 were identical to those of Model 1 described
392 above.

393 Ideally we would have included juvenile test cage as a mixed effect in the
394 above models to account for repeated sampling within each juvenile rearing
395 environment, but this was not possible because adding this additional term would

396 result in model overfitting (that is, too many model terms given the number of
397 observations). Nevertheless we are confident that our tightly controlled experimental
398 setting (in terms of food/water availability, temperature, and so on) minimized any
399 between-cage environmental variation in this juvenile, and in all other, experimental
400 phases.

401

402 **Construction speed**

403 We specified Cox proportional hazards models (CPHMs) using the 'coxph' function
404 from the 'survival' package (Therneau 2015) to determine whether juvenile access to
405 an adult and/or material influenced the speed at which males (Model 4) initiated and
406 (Model 5) completed the construction of their first nest, as survival models explicitly
407 consider time-to-event data. The response variable for Model 4 was the time taken
408 by males to make their first material deposit within their nestbox once the material
409 was made available. We used this measure in Model 4 because (I) males did not
410 differ in how quickly they first touched the material provided with their bill for first-time
411 nest construction (i.e., there was no confounding effect of material neophobia on
412 males' latency to initiate nest construction; Figure S3) and (II) the alternative
413 measure available for testing (i.e., latency to initiate nest construction as measured
414 from the initial handling of material by males) reduced the sample size in the A+/M+
415 treatment by one due to an initially incorrect camera recording angle (see above).
416 The response variable for Model 5 was the time taken by males to make their final
417 (60th) material deposit within their nestbox as measured from their first material
418 deposit. We used this measure in Model 5 to ensure any effect of treatment detected
419 on the speed of first-time nest construction by males was not driven by variation in
420 the time taken to initiate first-time nest construction. The response variable for both

421 Model 4 and 5 excluded the time elapsed due to the lights being turned off i.e., when
422 birds were asleep. The fixed-effects structure (i.e., predictor variables) for both
423 CPHMs included juvenile adult presence (yes or no), juvenile material access (yes or
424 no), and their interaction. The proportional hazards assumption (that the relative
425 probability of an event is constant across time) was satisfied ($p > 0.05$) by both
426 global CPHMs, which we tested using the 'cox.zph' function from the 'survival'
427 package.

428

429 **RESULTS**

430 A full output from each model can be found in the Supplementary material.

431

432 **Early-life effects on first-time nest construction**

433 **Material-color preference**

434 The early-life environment influenced males' material-color preference for first-time
435 nest construction, an effect that was specific to the juvenile period of development.
436 Specifically, if a male had had juvenile access to both an adult and material (A+/M+
437 treatment) the likelihood that he preferred to use material of the color of his natal
438 nest—no male in the A+/M+ treatment did (Figure 2a left panel)—decreased
439 significantly (preference for natal-nest versus other material across all treatments:
440 adult access*material access term, $\chi^2 = 4.90$, $n = 29$, $p = 0.027$; Model 1).
441 Furthermore, the majority (75%) of males in the A+/M+ treatment preferred, for their
442 first nest, to use material that matched in color to that which they experienced in their
443 juvenile environment, whereas only one male in the A-/M+ treatment (juvenile
444 material access only) preferred to do so (Figure 2a middle panel)—a significant
445 between-treatment difference (preference for juvenile versus other material across

446 M+ treatments: adult access*material access term, $\chi^2 = 5.99$, $n = 15$, $p = 0.014$;
447 Model 2). Collectively these data thus support the hypothesis that juvenile male
448 zebra finches integrate both early-life social and ecological cues concerning raw-
449 material 'suitability' (here, color) when developing their material preference.

450 Whether a male preferred to construct his first nest with a novel material did
451 not depend on the socio-ecological environment he experienced as a juvenile
452 (preference for novel material versus other material across all treatments: adult
453 access term, $\chi^2 = 0.83$, $n = 29$, $p = 0.360$; material access term, $\chi^2 = 2.80$, $n = 29$, p
454 $= 0.094$; adult access*material access term, $\chi^2 = 0.01$, $n = 29$, $p = 0.909$; Model 3;
455 Figure 2a right panel).

456

457 **Construction speed**

458 The juvenile social and ecological environment together also affected the speed with
459 which zebra finches initiated (adult access*material access term, $\chi^2 = 6.08$, $n = 28$, p
460 $= 0.014$; Model 4), and completed (adult access*material access term, $\chi^2 = 6.53$, $n =$
461 28 , $p = 0.011$; Model 5), their first nest. Males without juvenile access to both an
462 adult and material (A-/M- treatment; dashed red lines in Figure 2b) were more than
463 four times slower to make their first material deposit (Hazard ratio (HR) = 4.15, lower
464 and upper 95% confidence interval (CI) = 1.38 – 12.48, $n = 28$, $p = 0.011$), and close
465 to three times slower to deposit the remaining material into their nest (HR = 2.72,
466 95% CI = 1.00 – 7.40, $n = 28$, $p = 0.049$), compared to the males in the other three
467 treatments. These data, taken together, support the hypothesis predicting interactive
468 effects of the juvenile socio-ecological environment on first-time nest-construction
469 speed.

470

471 Follow-up analyses: Potential mechanistic explanations

472 Causal mechanisms underlying early-life social effects are often hard to test
473 (Taborsky 2016). Because we filmed the juvenile early-life environment, however, we
474 were able to examine potential links between juvenile and adult birds' amount of
475 material handling (defined here as bill-to-material contact) in the material experience
476 sessions, and how the juveniles then went on to construct their first nest (video
477 scoring and statistical details on how we did this are reported in the Supplementary
478 material). We focused on the material they preferred for, and not their speed at first-
479 time nest construction, as our results, reported above, showed that juvenile material
480 access is not essential to shaping first-time nest-construction speed (for example,
481 the males in the A+/M- treatment were just as quick to construct their first nest as
482 were the males in the M+ treatments; Figure 2b).

483 How might the early social environment bias animals towards preference for
484 using one particular kind of raw material? Firstly, corvid and primate field data
485 suggest that adults increase youngsters' engagement with raw material (because
486 youngsters will interact more with raw material/material artefacts in the presence of
487 adults; e.g., Humle et al. 2009; Holzhaider et al. 2010a). Contrary to these field data,
488 however, our juvenile zebra finches with an adult group-mate tended to spend *less*
489 time in each material experience session handling the material than did the juveniles
490 without an adult group-mate (mean \pm SE seconds spent handling material across the
491 12 material experience sessions: 208.58 ± 21.58 versus 417.11 ± 26.85 ,
492 respectively; Figure 3c left panel), although this between-treatment difference in
493 juveniles' material-handling time remained non-significant (adult access*material
494 session term, $\chi^2 = 18.42$, $n = 167$ from the 16 juveniles, $p = 0.072$; Model 6).
495 Secondly, social learning is considered to play a potent role in the development of

496 animal material technology, as exemplified by the considerable number of studies
497 wherein researchers report on how much time juveniles seem to spend watching
498 adults' material-use behavior (e.g., Ottoni et al. 2005; Humle et al. 2009; Holzhaider
499 et al. 2010a; Holzhaider et al. 2010b; Coelho et al. 2015). Although we do not know,
500 for our birds at least, how much time adults might need to engage with material
501 before juvenile group-mates prefer to use that material in adulthood, we can rule out
502 one possibility: adults need to engage with material more than juvenile group-mates.
503 In each of the material experience sessions, adults spent markedly *less* time than
504 their juvenile group-mates handling the material (mean \pm SE seconds spent handling
505 material across the 12 material experience sessions: 37.07 ± 5.74 versus $208.58 \pm$
506 21.58 , respectively; Figure 3c right panel), a significant within-treatment difference
507 that increased as juveniles gained material-handling experience (age*material
508 session term, $\chi^2 = 29.80$, $n = 127$ from the eight juveniles and four adults, $p = 0.002$;
509 Model 7). In summary, these data suggest that adult presence, rather than individual
510 or observational experience of raw-material handling, plays a more important role in
511 the development of material preference than has been previously considered.

512

513 **DISCUSSION**

514 In the wild, experienced adults probably aid the acquisition of material technology in
515 developing animals by increasing the salience of particular raw materials and, thus,
516 the constituent physical properties; this in turn might explain apparent within- or
517 between-species preferences for particular raw materials (or technological traditions;
518 Fragaszy 2011; Fragaszy et al. 2013). The current data provide compelling
519 experimental evidence to support this view: they show that material preference in
520 male zebra finches that is based on a physical property (color) is shaped by juvenile

521 experience of this material but only in the presence of an adult. There is more to
522 technological competence, however, than simply the choice of a suitable material—
523 effective execution of the task is key to the adaptive value of skilled behavior
524 (Bateson 1988). Here, too, our study unveils early-life social and ecological drivers of
525 construction ability in male zebra finches: adult presence and access to raw material.
526 Indeed, juvenile social and material impoverishment together led these males, as
527 adults, to be both slower to initiate and complete first-time nest construction, than
528 were males provided with juvenile access to an adult, material, or both.

529 The above results, taken together, show the early-life socio-ecological
530 environment shaped zebra finches' first-time nest construction, and crucially, reveal
531 that these early-life effects prevailed upon individuals during the juvenile, and not the
532 natal, developmental phase. The juvenile period of development in zebra finches is
533 also critical to their early learning of appropriate mate choice and vocal production.
534 To develop species-typical mate preference and song, recently fledged, juvenile
535 zebra finches require, respectively, exposure to (e.g., Immelmann 1972), or guided
536 feedback from (Carouso-Peck and Goldstein 2019), an adult conspecific before
537 reaching sexual maturity, whereafter both behaviors become fixed. As adult birds will
538 modify their construction behavior based on previous breeding experience (see
539 Table 3 in Breen et al. 2016), we do not suppose that such fixation occurs with
540 respect to avian nest construction. But our data reveal hitherto unknown parallels, in
541 terms of timing and environmental cues, between the development of song, mate
542 choice, and nest construction in zebra finches. It seems likely that the juvenile socio-
543 ecological environment plays a more dominant role in the development of animal
544 material technology in general.

545 In the wild, both the amount of individual material-use practice and social
546 material-use guidance (where ‘guidance’ is defined as the opportunity to observe
547 proficient adults, without implying any active process such as teaching) experienced
548 by juveniles are thought to relate to technical skill-competence in later life (Biro et al.
549 2006; Fragaszy 2011; Fragaszy et al. 2013; Meulman et al. 2013; Breen et al. 2016;
550 Rutz et al. 2018). Our findings that neither the amount of time juveniles spent
551 handling material nor that spent by their adult group-mate appear related to how they
552 construct their first nest, were, thus, fairly surprising. Indeed, juvenile exposure to an
553 adult conspecific seems sufficient experience (Figure 2b) to ensure that speed at
554 first-time nest construction is comparable to that of males that had had juvenile
555 material-handling experience. These data imply that juvenile adult access and
556 juvenile raw-material access had similar but nonadditive effects on first-time nest-
557 construction speed. These effects may be buffering or enhancing in nature as, on
558 one hand, adult presence in early life can safeguard developing builders against later
559 behavioral inefficiency (e.g., prolonged contest resolution over resources; Taborsky
560 et al. 2012), while on the other hand, mandibulation of material in early life can lead
561 to faster nest construction in adulthood (Collias and Collias 1964). In any case, the
562 current study reveals the convergent effect that early-life social and ecological
563 factors can have on the development of technological competence. It is less clear,
564 however, to what extent, if at all, juvenile and/or adult males living together need to
565 handle material in order for developing males to acquire a preference for, or to learn,
566 this stimulus. Variation in behavior can be generated by a multitude (Hoppitt and
567 Laland 2008) of social processes such as social facilitation—a clear candidate for
568 future testing—as well as social factors such as differences in sex, age, and genetic
569 relatedness (Lonsdorf and Bonnie 2010). And we note that our data do *not* exclude a

570 role for these social dynamics in the development of zebra finches' nest construction,
571 and animal material technology more generally; rather, they both encourage
572 discussion of, and invite much-needed (Taborsky 2016) study on the causality of
573 candidate causal mechanisms in developmental experiments.

574 It is also worth noting that the experimental approach applied here revealed
575 clear effects of the early-life environment on adult phenotype, despite our modest
576 sample size. For example, the interactive effect of the juvenile social and ecological
577 environment on first-time construction speed—that is, a four- and nearly three-fold
578 reduction in the speed at which novice builders in the A-/M- treatment initiated and
579 completed their nest, respectively—was considerable, given that a reduction in
580 speed of a 2.8 magnitude or greater constitutes a large effect size (Azuero 2016).
581 We anticipate that our experimental approach applied to other study systems with
582 shorter (and, therefore, less experimentally time-consuming) developmental periods,
583 coupled with the implementation of automated tracking technology, will facilitate
584 faster collection of larger and richer datasets, from both laboratory and natural
585 environments. Rodents, for example, may be one such study system, as there is
586 tantalizing evidence of early-life socio-ecological effects on nest construction in
587 adults (Van Loo and Baumans 2004; Margulis et al. 2005), and methods available for
588 successful automatic recording of behavior (e.g., social interactions and movement
589 patterns) among individuals living together either in the laboratory (e.g., Freund et al.
590 2013) or in the wild (e.g., König et al. 2015). As we have shown, this type of
591 approach should illuminate whether, and, if so, when different early-life
592 environmental factors, in isolation or in combination, shape animal material
593 technology.

594 For nest construction in zebra finches, future study could now focus on
595 whether material preference follows a two-stage developmental process—the
596 consolidation or modification of initial preference—akin to that which underpins their
597 choice of mate (Immelmann et al. 1991; Kruijt and Meeuwissen 1991; Kruijt and
598 Meeuwissen 1993). Indeed, as wild zebra finches breed colonially (Zann 1996) and
599 prospect on neighbors' nests (Brandl et al. 2019), and nests themselves can
600 influence laboratory-bred zebra finches' material preference (Breen et al. 2019), it
601 seems plausible that they may 'double-check' early-life information on material
602 suitability. Alternatively, future study could examine whether variation in nest-
603 construction speed as a consequence of variation in the early-life environment leads
604 to differences in birds' reproductive success. Females of other bird species appear to
605 lay sooner in response to a perceived increase in material-collection effort by their
606 mate (Soler et al. 1996; Soler et al. 2001), and the timing of clutch initiation can have
607 knock-on effects on recruitment in wild bird populations (Verhulst & Tinbergen, 1991;
608 Weggler, 2006). There is much scope for future research.

609

610 **Conclusions**

611 The current study confirms that the early-life socio-ecological environment *can* drive
612 variation in animal material technology. Phenotypic variation is essential to evolution
613 by natural selection. Understanding advancements in animal material technology,
614 then, demands focus on the early-life environment. Indeed, our finding that both
615 juvenile early-life adult and raw-material access affect novice builders' material
616 preference and construction speed has important implications for the profitability of
617 construction endeavors—individuals may avoid selecting 'bad' (e.g., too conspicuous
618 Bailey et al. 2015; too long Muth and Healy 2014; or too flexible Bailey et al. 2014)

619 material and losing valuable time (Mainwaring and Hartley 2013)—and, thus, for
620 individual survivorship and reproductive success, which likely affects the evolution of
621 animal construction. We suggest that the zebra finch, then, is not only a useful model
622 system for understanding how experience shapes construction behavior (Breen et al.
623 2016), but also how differences in animal material technology arise and persist.

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Figure 1

Schematic of the experimental protocol. Males hatched into a (i) *natal environment* of either a nest built with pink or orange material ($n = 16$ males per material type), which we removed at ~23 days post-hatch. At 60 days post-hatch, males were placed in same-aged non-sibling pairs from natal nests of the same color and assigned to one of four (ii) *juvenile environment* treatments ($n = 8$ males per treatment): A-/M-: no juvenile access to an adult or material; A+/M-: provided only an adult group-mate for the four-week period; A-/M+: provided access to two piles of either pink or orange material for one hour, three times per week (12 times in total); A+/M+: experimental conditions were identical to treatment A-/M+ except that males were also always provided access to an experienced nest-constructing, unrelated adult conspecific. At sexual maturity (90 days post-hatch), the 32 males were paired with females (from the same natal environment), given a nestbox, and provided with three different types of colored material ($n = 20$ pieces per material type) for (iii) *first-time nest construction*: (I) material that matched their natal environment, (II) material that matched their juvenile environment (where applicable i.e., M+ treatments), and (III) material that was novel (an opt out option; two of these options were novel for males in M- treatments—this allowed for meaningful between-treatment comparisons).

Figure 2

Early-life socio-ecological effects on avian nest construction. (a) Top panel: proportion of males (y -axis) in each treatment (all $n = 7$ except for the A+/M+ treatment where $n = 8$; x -axis) that preferred to construct their first nest with material that (left) matched their natal environment, (middle) matched their juvenile

environment (if provided material as a juvenile; males in M+ treatments), or (right) was novel. Material preference (that is, depositing >10 pieces of one type of material out of the first 20 deposits) was determined from Monte Carlo simulation—see Materials and methods. (b) Middle panel: cumulative proportion of males (y -axis) to initiate (measured from when material was provided; x -axis) and complete (measured from nest-construction initiation; x -axis) nest construction in each of the four treatments (A-/M-, $n = 6$; A+/M-, $n = 7$; A-/M+, $n = 7$; A+/M+, $n = 8$). The steepness of each slope in the middle panel indicates the speed at which males in each treatment initiated and completed their first nest; a steeper slope indicates quicker speed. (c) Bottom panel: total amount of time (left) juveniles in the M+ treatments ($n = 167$ observations from 16 birds) and (right) adults in the A+/M+ treatment ($n = 41$ observations from 4 birds) spent handling material with their bill in each of the 12 one-hour material experience sessions (assayed from 190 and 48 hours of juvenile and adult video recordings, respectively), ruling out that adults (I) increase juvenile group-mates' material handling and (II) handle material more than juvenile group-mates. Each symbol in the bottom panel represents a single observation (A-/M+, open circle; A+/M+, filled circle; adults in A+/M+, filled diamond); linear least squares regression 'trend' lines and 95% confidence intervals are plotted for each treatment.

Figure 1

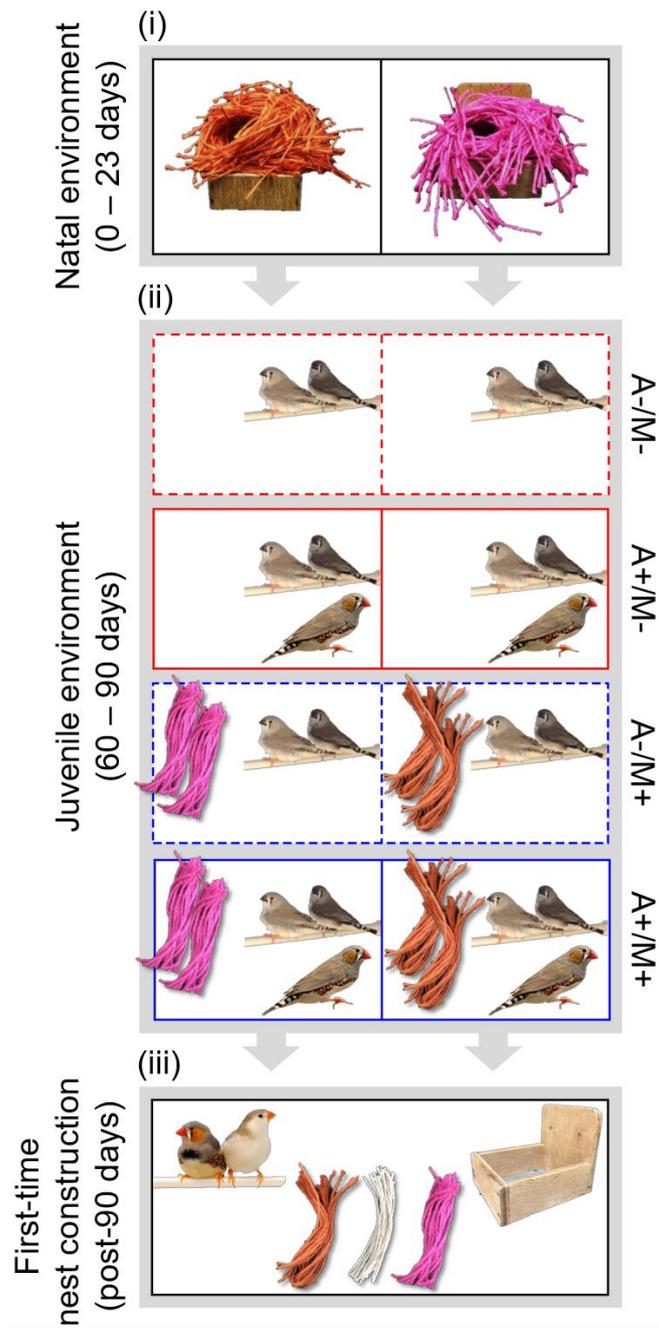


Figure 2

