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1 TITS (PARIDAE SP.) USE SOCIAL INFORMATION
2 WHEN LOCATING AND CHOOSING NEST LINING
3 MATERIAL

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21 Statements and Declarations

22 Conflict of Interest

23 The authors have no competing interests to declare that are relevant to the content
24 of this article.

25 Data availability

26 All data and R code for replicating analyses are available on
27 https://github.com/sonjawild/MS_lining_material

28 Author contributions

29 LMA and SW conceived the study. TJ and SV built equipment. SV and SW collected
30 data, ran analyses and drafted the manuscript. All authors contributed to writing.

31 Ethics Approval

32 The use of animals adheres to the guidelines set forth by the Association for the
33 Study of Animal Behaviour. Birds were ringed under ringing licenses held by LMA
34 and SW, granted by the Radolfzell Bird Observatory (55-8841.03; 8853.17).
35 Experimental procedures did not require ethical approval. Participation in the
36 experiments occurred on a voluntary basis.

37 Abstract

38 As an important determinant of reproductive success, avian nest building is under
39 strong selection and requires behavioral plasticity to optimize conditions in which
40 offspring develop. Learning is a one form of plasticity that allows adaptation to the
41 local environment. Birds may refine nest-building behavior with personal experience

42 or use social information to guide their choices. While there is mounting evidence
43 for an effect of experience-based learning on nest building and social information
44 use when selecting nesting material in the laboratory, experimental evidence for
45 social information use in wild birds is lacking. Here, we provided sources of two
46 differently colored wool as nest lining material in a wild mixed-species community of
47 tits (*Paridae* sp.) to investigate experimentally (i) whether females use social
48 information to locate lining materials, and (ii) whether preferences for specific
49 materials (here color) are socially influenced. We investigated pathways of social
50 transmission through a foraging association and a spatial breeding network using
51 the time of arrival at the wool in a network-based diffusion analysis. Our results
52 gave evidence that birds learned about the location of lining resources from
53 foraging associates. Furthermore, we found significant non-random clustering of
54 wool colors in nest boxes across the study area, suggestive of a social influence on
55 selecting lining materials. Taken together, we provide quantitative evidence for a
56 role of social information use in both finding and selecting lining material in wild tits
57 and demonstrate that social information use constitutes an important factor
58 towards behavioral plasticity in nest building in wild birds.

59 Keywords

60 Social information use, *Paridae*, nest construction, NBDA, social networks, social
61 learning

62 Significance statement

63 As vessels of reproduction, avian nests are under strong selection to provide
64 optimized conditions for developing offspring. Learning is one mechanism that
65 allows individuals to adapt to local environmental conditions. Previous work has
66 shown that nest-building birds use both social information and personal experience
67 to refine their nests. Yet, evidence for social information use for nest construction in
68 the wild has been purely anecdotal and experimental evidence lacking. Here, we
69 demonstrate for the first time experimentally that in wild tits (*Paridae* sp.), females
70 rely on social information from their foraging associates to locate and choose
71 material to line their nests. This research highlights the importance of social
72 information use as a potential mechanism of behavioral plasticity in wild nest-
73 building birds.

74 Introduction

75 Nest construction is a widespread behavior among many bird species (Hansell
76 2000). Nests serve to create a suitable microclimate during incubation of eggs and
77 for developing offspring and provide shelter to minimize predation risk (Mainwaring
78 et al. 2014). As ‘vessels of reproduction’ and determinants of reproductive success
79 (Järvinen and Brommer 2020), nest-building behavior – including nest site selection
80 and construction – are under strong selection (Mainwaring et al. 2014). Yet, contrary
81 to historical beliefs that nest construction was largely based on a fixed genetic
82 template (e.g. Nickell 1958), it is now well understood that nest building requires
83 behavioral plasticity to optimize conditions in which offspring develop (Britt and
84 Deeming 2011; Deeming et al. 2012; Mainwaring et al. 2012; Healy et al. 2015;
85 O’Neill et al. 2018).

86 Learning is a vital form of plasticity, allowing individuals to adapt to their local
87 environment (Snell-Rood 2013). Research from the past two decades has shown
88 that learning plays a significant role in a variety of behavior related to nest building
89 (reviewed in Breen et al. 2016). Thereby, individuals may refine their nests based
90 on personal breeding experiences. For example, birds of several species were found
91 to re-use or avoid breeding sites based on previous breeding success (e.g. Suryan
92 and Irons 2001; Fisher and Wiebe 2006). Furthermore, in captive zebra finches
93 (*Taeniopygia guttata*), males that successfully fledged chicks continued to prefer
94 one of two provided colors as nest material, while males that failed to fledge chicks
95 switched color preference when building a subsequent nest (Muth and Healy 2011).

96 Alternatively, individuals can use social cues to guide their decisions on nest-site
97 selection and building behavior, thereby incorporating the experience of others
98 (Laland 2004; Kendal et al. 2005). In the context of nest site selection, there is
99 strong evidence that several bird species use social information when choosing
100 breeding locations (Breen et al. 2016). For example, migratory flycatchers
101 (Muscicapidae) - when returning to breeding sites - were found to use the breeding
102 success of the resident tits (Paridae) to assess habitat quality and select nest sites
103 (Forsman and Thomson 2008; Forsman and Seppänen 2011; Jaakkonen et al. 2015).
104 Several studies have also suggested an influence of social information use in the
105 context of nest construction (reviewed in Breen et al. 2016; Breen 2021), through
106 observation and copying of material choice. The most comprehensive evidence for
107 social information use in material choice comes from experiments on captive zebra
108 finches (Guillette et al. 2016; Breen et al. 2019, 2020). Individuals with no prior
109 experience in nest building switched their initial color preference of nest material
110 after watching an experienced individual build a nest with their less preferred color
111 material, but only if the demonstrator was a familiar individual (Guillette et al.
112 2016). Even when presented with only a completed nest of their non-preferred color
113 without a demonstrator present, first-time builders lost their initial color preference
114 and picked material colors at random, indicative that a nest alone without a
115 demonstrator present may be sufficient to influence future preference for nest
116 material (Breen et al. 2019).

117 Meanwhile, evidence from the wild for social information use in material choice
118 remains both scarce and more mixed (Breen 2021). The first evidence comes from
119 as early as 1924, when Williams provided colored yarn to nest-building birds in his
120 backyard (Williams 1934). Over the years, orioles (Icteridae) seemed to follow the

121 'fashion of the season' when choosing yarn, with birds converging to choose only
122 white yarn after a conspecific had built its nest using only white yarn, indicative of a
123 social influence on color choice (Williams 1934). More recent, indirect evidence
124 comes from a study on blue tits (*Cyanistes caeruleus*) that reported local clustering
125 in preferences for particular plants used for nest lining. These preferences did not
126 appear to be predicted by local availability, suggesting the potential for social
127 transmission of plant preferences (Mennerat et al. 2009). Contrasting results were
128 found in a study providing colored wool to breeding tits, where females
129 opportunistically incorporated all materials close to the nest site (Surgey et al.
130 2012). Finally, a cross-fostering study between blue and great tits (*Parus major*) did
131 not find any evidence of cultural inheritance of nest lining material (Aasen and
132 Slagsvold 2020). Here, the authors compared the proportion of feathers (naturally
133 preferred by blue tits) and fur (naturally preferred by great tits) (Perrins 1979) in
134 the nests of cross-fostered and control young but found no effect of foster parents'
135 preference on the offspring's material choice (Aasen and Slagsvold 2020).

136 Here, we experimentally test the importance of social information use in finding and
137 choosing nest materials in a wild mixed-species community of tits (*Paridae* sp.)
138 marked with Passive Integrated Transponder (PIT) tags. In tits, females build a nest
139 consisting of a base layer made mostly of moss and a lining layer of various soft
140 materials such as hair, feathers, fur and wool for insulation of eggs and chicks
141 (Perrins 1979). These soft materials often represent ephemeral and potentially
142 limited resources. For example, fur may be obtained from a rabbit or badger
143 carcass, or even plucked from live mammals (Pollock et al. 2021). We provided PIT-
144 tag reading dispensers containing two different colors of wool across five replicate
145 areas and recorded both visits to dispensers and presence of wool in nests.

146 First, we investigated whether females used social information to *locate* lining
147 materials by using the time of arrival to dispensers in a ‘network-based diffusion
148 analysis’ (NBDA) (Hasenjager et al. 2020). We considered two different networks, a
149 foraging association and a spatial breeding network, which allowed to distinguish
150 between two possible pathways of information transmission. As tits are known to
151 rely on social information from both individuals of their own as well as other species
152 to locate food resources (Aplin et al. 2012; Farine et al. 2015), it is plausible that
153 breeding females may also obtain social information from foraging associates about
154 other types of resources, including the location of nest lining material. Alternatively,
155 birds may gather social information about the nest site and construction material by
156 inspecting other birds’ nest boxes (Forsman and Thomson 2008; Loukola et al.
157 2012; Schlicht et al. 2015; Szymkowiak et al. 2017). We therefore hypothesized that
158 tits may potentially develop a search image for the provided lining material through
159 inspection of other females’ nests breeding in close proximity or obtain indirect
160 social information about the location of the lining material through directional cues
161 when observing a female entering her neighbouring nest with the provided colored
162 wool. As we could not measure prospecting directly, we used spatial proximity as a
163 proxy network for this pathway.

164 Second, we investigated whether females socially acquired *preferences* for
165 particular lining material colors. In five replicate areas, we initially created local
166 preferences for one of the two provided colors by blocking access to the second
167 color before allowing access to both colors. We then monitored the specific wool
168 colors females first incorporated into their nests in each area, expecting to find
169 similarities between the seeded color and the color first incorporated into nests if
170 color preferences were socially influenced.

171 Material & Methods

172 a) Field methods

173 We conducted our experiment between 23 February and 11 May 2021 in a study
174 population around the Max Planck Institute of Animal Behavior in Radolfzell,
175 Germany, where 207 nest boxes (Schwegler type 1B, 2M, 3SV) have been provided
176 for the use of breeding tits. As part of a long-term project on this community, we
177 caught blue tits, great tits and marsh tits (*Poecile palustris*) in mist nests or trapped
178 them in nest boxes as nestlings or adults. All birds were equipped with a metal leg
179 ring (EURING 'Radolfzell Germania') and a plastic leg ring containing a PIT-tag (Eccel
180 Technology Ltd). Adults were aged and sexed based on plumage (Svensson 1992).

181 Over three periods of 48 hours (6 full days in total) between 23 February and 11
182 March 2021 - immediately prior to the breeding season - we recorded visits by PIT-
183 tagged birds to six bird feeders filled with a mix of kibbled peanuts and sunflower
184 seed. We spaced these feeders around the woodland in an approximate grid to
185 cover the entire study area (Fig. 1C). Access points to feeders were equipped with
186 radio-frequency identification (RFID) antennae (NatureCounters Ltd), with data
187 loggers (Priority1 Design, Australia) recording visits of PIT-tagged birds. We then
188 used the spatio-temporal patterning of these visits to build a foraging association
189 network (see below).

190 On 26 March 2021, we deployed five dispensers containing felting merino wool,
191 each offering two colors of similar hues *ad libitum* (Fig. 1A). We used a balanced
192 experimental design with three dispensers providing orange and pink wool, and two
193 containing blue and purple wool (Fig. 1C). These were spaced approximately 300 m
194 apart to avoid too much overlap between dispenser areas, based on Surgey et al.

195 (2012) that suggested that tits are unlikely to travel much further than 200 m to
196 collect wool. Each dispenser was equipped with RFID antennae and data loggers to
197 record visits to the wool by PIT-tagged birds. We initially created an artificial local
198 preference for one of two wool colors in each area by blocking access to the other
199 color with a transparent plastic sheet. Once provisioned material was observed by
200 experimenters in one or more nests in each dispenser area, we allowed access to
201 both colors (Table S1). To test for any potential innate color preferences, we
202 additionally deployed four dispensers in two separate control areas (not shown in
203 Fig. 1A), with unlimited access to the two-color pairs (orange/pink and blue/purple)
204 at all times.

205 Throughout the experiment, we monitored all nest boxes across the woodlands
206 every 2-4 days, recording nest stage and the presence (yes/no), color and amount
207 (categories 1-4, see Table S2) of any provisioned lining material. We identified PIT-
208 tagged breeding females by deploying 'faceplate loggers' (NatureCounters Ltd) with
209 an RFID antenna around the nest box entrance for 48 hours as nests reached
210 completion, i.e., as females started laying eggs (supplementary Information: SI).
211 This further allowed us to identify which females were not PIT-tagged and needed
212 trapping in nest boxes for ringing.

213 b) Statistical analysis

214 i) Constructing networks

215 To investigate whether tits relied on social information to locate lining resources
216 (irrespective of color choice), we used NBDA (Franz and Nunn 2009; Hoppitt et al.
217 2010; Hasenjager et al. 2020). NBDA tracks the spread of a behavior through a
218 network and infers that it is socially learned if the diffusion of the behavior follows

219 the network connections (Hasenjager et al. 2020). Here, we compared two
220 alternative pathways of information spread about locations of lining resources in a
221 multi-network NBDA (Farine et al. 2015; Wild et al. 2019) by including two different
222 networks: (i) the foraging association network and ii) the spatial breeding network.

223 To construct the foraging association network among females we recorded the
224 identity of all visiting birds with PIT-tags to the RFID feeders that we had deployed
225 around the woodland between 23 February and 11 March 2021 (see Field methods;
226 Fig. 1C). From these visits, we identified groups using a Gaussian mixture model to
227 detect clusters in the data stream (Psorakis et al. 2012). We then built social
228 networks using a gambit of the group approach and calculated edge weights using
229 the simple ratio index which ranges from 0 (never observed together in a group) to
230 1 (always observed in the same group) (Cairns and Schwager 1987; Farine 2013;
231 Farine and Whitehead 2015; Hoppitt and Farine 2018). Since the foraging network
232 was highly stable across the three weeks of data collection (week 1 to week 2:
233 Mantel $R=0.634$, $p=0.001$; week 2 to week 3: Mantel $R=0.650$, $p=0.001$), we used a
234 static network in NBDA based on all the association data (Hasenjager et al. 2020).

235 To construct the spatial breeding network, we calculated the Euclidean distances
236 between nest boxes using their GPS locations. We then used the inverted square
237 root of distances between nests to account for the fact that space use is non-linear
238 and that females breeding closer together had higher values. As tits occupy
239 relatively small home ranges during the breeding season (Naef-Daenzer 1994), we
240 the entries between females that were nesting more than 50 m apart to 0. This
241 network served as a proxy for prospecting opportunities, e.g. (Schlicht et al. 2015),
242 as well as a proxy for opportunities to observe other females carrying wool, which
243 are expected to occur at higher frequency among birds nesting in close proximity.

244 Recording of prospecting events on faceplate loggers were insufficient to create a
245 prospecting network directly (SI).

246 The maximum known distance travelled between a nest box and dispenser in our
247 study area was 184 m. We therefore subset both networks to only include birds that
248 were breeding in nest boxes within a 200 m radius of each dispenser and
249 considered dispenser areas as independent replicates (Fig. 1C). This meant that a
250 minority of birds was assigned to more than one dispenser area (Fig. 1C; Table S1).

251 ii) Locating lining resources

252 We used the ‘time of acquisition diffusion analysis’ (TADA) variant of NBDA v0.9.6
253 (Hasenjager et al. 2020) and used the time of first arrival of each female at the wool
254 dispensers as diffusion data. We restricted our analyses to visits by PIT-tagged
255 females. If no information on sex was available, we assigned sex either by a process
256 of exclusion if sex was known for the breeding partner, or as female if the bird
257 visited the wool dispensers at least three times, assuming that males would be
258 unlikely to re-visit a resource with lining material. Additionally, we included 10
259 females that had visited the dispenser but whose breeding location was unknown
260 and set their connections in the breeding network to 0.

261 We additionally included three individual-level variables (ILVs) that could potentially
262 influence social and asocial learning rates: First, we included species as an ILV as
263 ‘great tit’ or ‘other’. Great tits naturally prefer wool and fur-like material for lining
264 their nests, while blue tits show a preference for feathers if available (Perrins 1979),
265 which may lead to differences in the rates of social or asocial discovery of the
266 provisioned wool. Second, we included age of individuals as ‘adult’ or ‘first-year’ to
267 account for age-biased learning (e.g. Aplin et al. 2013), as first-time builders may

268 rely more strongly on social transmission of information compared to experienced
269 nest builders. Finally, we controlled for the distance of each female's nest to the
270 nearest wool dispenser, as females in close proximity to a dispenser are also
271 expected to be more likely to locate the resource. For females whose breeding
272 location was unknown, we assigned them the average distance between nest boxes
273 and dispenser within the respective area. We used the standardized square root of
274 distances for better model fitting (Hasenjager et al. 2020). We built unconstrained
275 models, which allow ILVs to influence the social and asocial learning rate
276 independently (Hoppitt and Laland 2013). We created models in all possible
277 combinations of the two networks and three ILVs (Hasenjager et al. 2020), resulting
278 in 200 different models, and used the Akaike Information Criterion corrected for
279 sample size (AICc) to infer model support (Burnham and Anderson 2002). For each
280 supported variable (with summed Akaike weights $\sum w_i > 0.5$), we extracted model
281 averaged estimates as weighted medians and extracted profile likelihood
282 confidence intervals based on the best performing model in which the respective
283 parameter occurred (Morgan 2008). All statistical analyses were conducted in R
284 v4.1.2 (R Core Team 2022).

285 ii) Selecting lining material

286 To investigate whether tits acquired the color preferences initially seeded in each
287 area, we compared the first color birds incorporated - i.e., the first color of provided
288 wool to appear in their nests - with the color seeded in each dispenser area using a
289 Fisher's Exact Test. We additionally accounted for any potential local environmental
290 influence of bucket placement (e.g. in case one bucket was more easily accessible).
291 We did this by extracting the number of reads of each visiting PIT-tagged female on

292 both antennae after access was granted to both colors, expecting females to use
293 both antennae for perching if equally accessible.

294 Results

295 Locating lining resources

296 A total of 46 PIT-tagged females - 31 great tits, 11 blue tits and 4 marsh tits - were
297 recorded in the foraging association network and subsequently observed breeding
298 in the study area. 36 of those were recorded in nest boxes, while 10 were recorded
299 only on the wool dispensers, and were presumably nesting in natural tree cavities
300 (Fig. 1B). Of those 46 females, 21 visited the dispensers - 13 great tits, 4 blue tits
301 and 4 marsh tits - between 1 and 64 times, with an average of 12 visits (Table S1;
302 Online Resource 2). With only one tagged learner, dispenser area 4 was excluded
303 from the NBDA analysis (Table S1). Overall, the foraging association and spatial
304 breeding network were not significantly correlated (Mantel test, $p=0.060$; $r=0.055$)
305 and were therefore both included in NBDA models.

306 NBDA strongly supported models that included social transmission of information
307 about the location of the lining dispensers through the foraging association network
308 (summed Akaike weights ($\sum w_i$) = 0.64). This was followed by purely asocial models
309 ($\sum w_i$ = 0.17), models that included transmission through both foraging association
310 and breeding network ($\sum w_i$ = 0.12), and models that included transmission
311 through the breeding network alone ($\sum w_i$ = 0.07). In the best performing model
312 (Table S3), 39.9% [95% CI 1.5-61.5%] of females were estimated to have used
313 social information to locate lining dispensers, with the rest learning asocially. This

314 asocial learning rate was highest in birds close to the dispenser and decreased by a
315 factor of 0.84 [0.60-0.99] per m increase in distance between a female's nest and
316 the dispenser ($\sum w_i = 0.60$; Table S4). Age and species had no influence on either
317 social or asocial learning rate (all $\sum w_i < 0.5$; Table S4).

318 **Selecting lining material**

319 We found provisioned wool in 26 out of 68 occupied nest boxes by 19 tagged and
320 seven untagged females (Fig. 1C). Of those 26, eight nests were built while access
321 was restricted to a single color. In the remaining 18 nests, 13 birds used only one
322 color in their nests. Of the 18 females, 1 first incorporated blue, 1 orange, 12 pink
323 and 4 purple wool. We found significant non-random spatial color clustering, with 10
324 out of the 18 females preferring the initially seeded color in their dispenser area as
325 their first choice (Fisher's Exact Test: $N=18$; $p=0.025$).

326 With only 18 nests (15 great tits, 1 blue tit, 2 of unknown species; 8 adults, 5 first-
327 years, 5 of unknown age), sample size was too small to investigate the effect of
328 species and age on color preference (Table S5). By contrast, we recorded eight
329 females in the control areas using provisioned wool. Data on the first incorporated
330 wool color was only available for two out of the eight nests (one pink, one yellow),
331 but females of all eight nests incorporated both colors.

332 Of the 23 tagged females that visited the dispensers after access was granted to
333 both colors, 16 were registered on both antennae, while seven were only registered
334 on one antenna (Fig. S1). This indicates that both antennae were used for perching
335 and that RFID data were not a reliable indicator of the color choice (see also Online
336 Resource 2).

337 Discussion

338 Our study provides experimental evidence that tits use social information when
339 locating sources of nest lining material, and that social information also influences
340 their choice of lining material color. Such quantitative evidence for social
341 information use in finding and using sources of nest lining material in wild birds has
342 been lacking thus far. Given that great and blue tits are well known to rely on social
343 information in a variety of behavioral contexts - including finding new food sources
344 (Aplin et al. 2012; Farine et al. 2015), selecting nest sites (Parejo et al. 2007;
345 Slagsvold et al. 2013) and acquiring foraging behavior (Slagsvold and Wiebe 2011;
346 Aplin et al. 2013, 2015) - our results are perhaps unsurprising. Yet, they add to our
347 understanding of the extensive influence of social information on the life history and
348 ecology of these species and highlight the importance of social information use as a
349 potential mechanism for behavioral plasticity in nest-building birds.

350 Our results from NBDA analyses suggest that social information on the location of
351 lining material was acquired from intra- and interspecific foraging associates, in line
352 with previous work showing that tits rely on social information for locating food
353 resources from both con- as well as heterospecifics (Farine et al. 2015). Meanwhile,
354 we found little evidence for transmission through the spatial breeding network. This
355 suggests that females did not obtain information about the location of the lining
356 material through prospecting, or through directional cues when observing
357 neighbouring females returning to their nest with color wool, but rather when in
358 foraging flocks. The lack of a correlation between foraging network and spatial
359 breeding suggests that even though foraging associations shape spatial breeding

360 decisions in great tits (Firth and Sheldon 2016), they may not necessarily predict
361 the identity of birds breeding in direct vicinity.

362 Females breeding closer to a lining dispenser were more likely to discover its
363 location asocially. Given the tits' territories are concentrated around the nest site
364 during breeding (Naef-Daenzer 1994), it appears plausible that they would be more
365 likely to discover resources that are in close proximity to the nest site. In fact, these
366 results are in line with a previous study providing colored wool to breeding tits,
367 finding that the proportion of birds that used the provided material declined with
368 increasing distance between the source of the material and the nest site (Surgey et
369 al. 2012).

370 We furthermore observed significant non-random spatial clustering of the
371 provisioned wool colors in each dispenser area, with females preferentially lining
372 their nests with the color that was first seeded in the respective area. In addition,
373 the majority of females in the experimental area (13/18) only incorporated one
374 color, while females in the control area all incorporated both provided colors. Taken
375 together, these results are suggestive of a potential social influence when initially
376 selecting wool color. Our findings are consistent with the early observations of
377 Williams who found that nest-building birds appeared to undergo 'fashions' across
378 the years when selecting colored nest material (Williams 1934), as well as the
379 previously documented local preferences for particular aromatic plants in wild blue
380 tits that appeared to be unrelated to the local abundance of those plants (Mennerat
381 et al. 2009). Yet, our results are in contrast to Surgey et al.'s (2012) study, in which
382 breeding tits did not appear to have any preference for a particular wool color. This
383 may, however, be explained by differences in experimental setup. Surgey et al.
384 (2012) initially provided wool in four different colors dispersed throughout the

385 woods during six breeding seasons, before placing four dispensers together in one
386 location to ascertain whether birds had preferences for a particular color. Therefore,
387 at the time of investigating color preferences, females may have already collected
388 extensive personal information, and could therefore have been less reliant on social
389 information when choosing colors.

390 Our study is also in contrast to Aasen and Slagsvold (2020) cross-fostering study
391 between great and blue tits that found no evidence for cultural inheritance of the
392 choice of nest lining material. However, their study investigated preferences at the
393 level of nest material (Aasen and Slagsvold 2020) rather than material color. It
394 seems quite likely that higher-level preferences for lining material, for example wool
395 or feathers, are a relatively fixed species-specific trait (Perrins 1979; Britt and
396 Deeming 2011), while behavioral flexibility acts within these preferences.

397 Alternatively, it is possible that transmission of social information about lining
398 material does not occur during early life from parent to offspring but is transmitted
399 later in life from peer to peer when birds build their own first nest (Aasen and
400 Slagsvold 2020).

401 It should be noted that our sample size for both NBDA analyses and investigating
402 color preferences were limited. That said, in NBDA, low sample size - e.g. through
403 missing observations due to untagged individuals - reduces power to detect social
404 transmission and increases uncertainty about the strength of a social transmission
405 effect (Wild and Hoppitt 2018). As such, our NBDA results provide a conservative
406 estimate for the plausibility of social transmission. However, the strength of the
407 effect size should be interpreted with caution, with confidence intervals providing a
408 plausible range (Hoppitt 2017). We were also unable to establish the pathways of
409 transmission of color preferences due to small sample size. Future studies including

410 larger sample size should therefore aim to investigate how females may socially
411 acquire preferences for certain colors, *i.e.*, whether this occurs through prospecting,
412 or whether they observe other females carrying wool while entering their nest
413 boxes or at dispensers or get cues from wool that may be scattered around the
414 dispensers. Studies including larger sample sizes could also investigate whether
415 females rely more strongly on social information for locating lining resources from
416 con- over heterospecifics, as has been demonstrated in a foraging context (Farine
417 et al. 2015). Furthermore, future studies should examine a possible effect of age or
418 species on whether females showed a preference for the initially seeded color. This
419 would give insights into potential learning strategies that nest-building females
420 employ, such as a transmission bias from more experienced to first-time builders
421 (e.g. Guillette et al. 2016; Breen et al. 2019, 2020), or a preference for con- over
422 heterospecific demonstrators (e.g. Farine et al. 2015; Jaakkonen et al. 2015).

423 Taken together, our study provides quantitative evidence for a role of social
424 information use in both finding and selecting nest-lining material in wild birds and
425 shows that this social transmission occurs horizontally through observation of other
426 breeding females. It demonstrates that while many aspects on material choices in
427 nest building may be based on an innate template (Perrins 1979; Britt and Deeming
428 2011), social information use can constitute an important factor towards plasticity
429 in nest building. Repeated social transmission of information or behavior can lead to
430 the establishment of local cultural traditions (Fragaszy and Perry 2003), as has
431 previously been demonstrated in wild birds in a foraging context (e.g. Aplin et al.
432 2015; Klump et al. 2021). We therefore concur with (Breen 2021) conclusions that
433 avian nest construction provides a promising avenue for studying animal cultural
434 phenomena and suggest that future studies should aim to investigate

435 experimentally whether such local preferences for nest lining material can persist
436 across generations.

437

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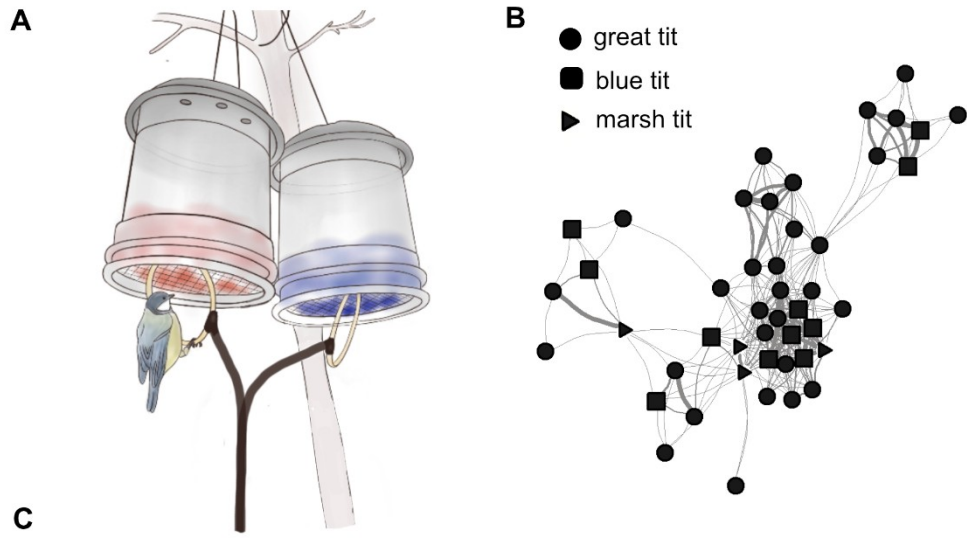
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594 **Fig. 1: A) Illustration of a wool dispenser.** Two transparent buckets presented felting wool that
595 could be pulled through mesh at the bottom. Wool colors were either paired as orange & pink, or blue
596 & purple, with RFID antennae registering visiting birds' PIT-tags. **B) Foraging association network**
597 **of females breeding in the study area.** Each node represents an individual bird with shapes
598 indicating the species it belongs to (circle = great tit; square = blue tit; triangle = marsh tit). Edge
599 thickness is proportional to the association strength among birds. **C) Map of the study area.** Dots:
600 nest boxes with colors indicating the color of incorporated wool (no fill = empty; grey = occupied, no
601 wool; pink = pink wool; purple = purple wool; orange = orange wool; blue = blue wool; if two colors in
602 nest: initial color at centre, second color as outline). Nests of demonstrator birds that started building
603 when only one color was accessible are additionally marked by a black bar across. Squares: locations
604 of wool dispensers - the first seeded color with a solid outline, the second color with a dashed line.
605 Dispenser areas are marked by a circle with 200m radius. Black stars: locations of RFID feeders for
606 collecting foraging association data



607