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5 **Wild zebra finches do not use social information from conspecific reproductive success for**
6 **nest site choice and clutch size decisions**

7

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24

25

26 **Abstract**

27 Information about the quality of local habitat can greatly help to improve an individual's decision
28 making and, ultimately, its fitness. Nevertheless, little is known about the mechanisms and significance
29 of information use in reproductive decisions, especially in unpredictable environments. We tested the
30 hypothesis that perceived breeding success of conspecifics serves as a cue for habitat quality and hence
31 influences breeding decisions (nest site choice and clutch size), using the zebra finch (*Taeniopygia*
32 *guttata*) as a model species. Zebra finches breed opportunistically in the unpredictable, arid zone of
33 Australia. They often inspect the nests of conspecifics, potentially to prospect on conspecific
34 reproductive success, i.e. to collect social information. We conducted a clutch and brood size
35 manipulation to experimentally create the perception of high and low quality areas. In six areas, clutch
36 sizes of almost 300 zebra finch nests were either all increased (N = 3 areas) or reduced (N = 3 areas)
37 throughout one breeding season. The number of breeding pairs and sizes of newly laid clutches were
38 not significantly affected by the manipulated reproductive success of the areas. Thus, zebra finches did
39 not use social cues for their reproductive decisions, which contrasts with findings of species in
40 temperate zones, and could be an adaptation to the high unpredictability of their habitat. Even the
41 personal experience of rebreeding birds did not directly affect their clutch size. Our study suggests that
42 zebra finches employ a high level of opportunism as a key strategy for reproduction. Further, this is
43 the first study to our knowledge using an experimental approach in the wild to demonstrate that
44 decision-making in unpredictable natural environments might differ from decision-making in
45 temperate environments with seasonal breeding.

46

47 **Significance statement**

48 Social information can help to optimize the behavior of animals. Birds in temperate climates with
49 seasonality use breeding success of others to predict where they should breed. However, very little is
50 known about information use in less predictable environments. In a field experiment we created a
51 patchy environment by increasing and decreasing brood sizes of wild zebra finches to test if social
52 information is also used in unpredictable conditions. We found no evidence that zebra finches in the
53 Australian outback use social information from their conspecifics when deciding on nest site and clutch
54 size. They probably gather personal information on environmental parameters and the current
55 availability of resources, which might be more reliable than social information.

56

57 **Keywords**

58 brood size manipulation; decision-making; fluctuating conditions; information use; prospecting;
59 unstable environment

60

61 INTRODUCTION

62 Having reliable information about the environment can be key to survival and high reproductive
63 success in animals, due to the way it can affect adaptive decision making. Gathering information is a
64 continuous process and being informed about possible alternatives is a prerequisite for making optimal
65 decisions in variable conditions (Dall et al. 2005). Often a variety of information sources is available to
66 animals and different strategies can be used to exploit them. Individuals can acquire personal
67 information through a trial-and-error approach and investment of their time and energy. Alternatively,
68 social information can be obtained by observing the actions, decisions, and performance of other
69 individuals (Danchin et al. 2004). Social information use is often thought to be less costly than gathering
70 personally acquired information (Boyd and Richerson 1988; Webster and Hart 2006; Webster and
71 Laland 2008) and can lead to an increase in the fitness of the receiver (Boyd and Richerson 1988;
72 Danchin et al. 2004; Valone 2007). However, as a trade-off, relying on social information can involve a
73 loss of accuracy and reliability or give less up-to-date information (reviewed by Kendal et al. 2005).
74 This was demonstrated, for example, in yellow warblers, (*Setophaga petechia*) which are hosts for the
75 brood parasitic brown-headed cowbirds (*Molothrus ater*). The frequency of nest parasitism by
76 cowbirds underlie strong annual fluctuation and the hosts therefore rely on more current individually
77 learned defense rather than social cues (Campobello and Sealy 2011a). Reed warblers (*Acrocephalus*
78 *scirpaceus*), on the other hand, which are very frequent victims of parasitism by the common cuckoo
79 (*Cuculus canorus*) can enhance their nest defense by using social information (Campobello and Sealy
80 2011b).

81 While the number of existing empirical studies on information use in general is high, the
82 minority of them have addressed the use of social information with respect to breeding-site and
83 habitat selection (Brown et al. 2000; Parejo et al. 2006; Jaakkonen et al. 2013) or reproductive
84 investment decisions (Forsman et al. 2011; Schuett et al. 2015). It has been suggested that the current
85 reproductive success of conspecifics might give a more accurate prediction for the quality of a breeding
86 habitat than other environmental parameters (Boulinier and Danchin 1997). Depending on the

87 context, some species can even switch between con- and heterospecific information use (e.g. pied and
88 collared flycatcher, *Ficedula hypoleuca* and *F. albicollis*, switch depending on which have the higher
89 density; Jaakkonen et al. 2014; Samplonius et al. 2017). Indeed, individuals of many species ‘prospect’,
90 i.e. visit breeding sites of other individuals (e.g. reviewed in Reed et al. 1999), likely to assess the quality
91 of potential breeding sites in advance (e.g. Cadiou et al. 1994; Pärt and Doligez 2003; Doligez et al.
92 2004). A good example of this behavior and its functional value was shown in an experimental study
93 on collared flycatchers (Doligez et al. 2002). This European passerine reacted to patches of habitat with
94 experimentally increased brood sizes with higher settlement of breeders in the following year,
95 demonstrating the use of social information from conspecifics as a predictor for habitat quality (Doligez
96 et al. 2002).

97 One important aspect that the collared flycatcher (Doligez et al. 2002) shares with most other
98 avian species studied in this context (e.g. *Rissa tridactyla*: Boulinier et al. 1996; *Corvus monedula*:
99 Schuett et al. 2012; *F. hypoleuca*: Schuett et al. 2017) is that their breeding grounds are in temperate
100 climates with an underlying annual periodicity, making the resources relatively predictable and the
101 breeding schedules quite fixed. This means that the knowledge we have about information use and
102 decision-making in a breeding context almost exclusively comes from studies conducted in rather
103 stable and foreseeable environmental conditions. Other climatic regions, however, offer very different
104 ecological conditions and challenges for animals. Arid zones, for example, are characterized by high
105 spatial and temporal variability and are subject to drastic fluctuations of climatic elements (Morton et
106 al. 2011), which is a stark contrast to the much more stable and certain conditions in the temperate
107 zones. The difference in the predictability of environments is likely to affect how information is
108 collected and used (Feldman et al. 1996; Doligez et al. 2003; Rafacz and Templeton 2003), providing a
109 basis for adaptive animal behavior (Dall et al. 2005). Therefore empirical studies on information use in
110 highly unpredictable habitats will provide important insights into the more general importance of
111 social information and its role in driving adaptive decisions (Schmidt et al. 2010).

112 The zebra finch (*Taeniopygia guttata*) is a commonly studied passerine in the laboratory that
113 is known to use social information in the context of foraging behavior (Farine et al. 2015). In the wild,
114 however, little is known about the importance of social information in this colonial species that is
115 endemic to the arid zone of Australia. Confronted with a patchy habitat of varying quality it is
116 conceivable that zebra finches would apply the same strategy of prospecting on the local reproductive
117 success of conspecifics that has been seen in European passerines (e.g. Doligez et al. 2002, 2004;
118 Boulinier et al. 2008) to adjust their own choice of nesting site and investment in reproduction
119 accordingly. Several models predict that social information could be perceived as an unreliable
120 predictor for future reproductive success in an unpredictable environment, because of the lack of
121 temporal autocorrelation in patch quality (Boulinier and Danchin 1997; Erwin et al. 1998; Doligez et al.
122 2003). Attraction to breeding conspecifics, however, still seems to be a beneficial strategy in unstable
123 environments (Parejo et al. 2006; Mariette and Griffith 2012a). Additionally, data from a laboratory
124 experiment on foraging starlings (*Sturnus vulgaris*), shows that social information can be perceived as
125 more valuable in unpredictable conditions (Rafacz and Templeton 2003).

126 Therefore, and in the light of the low number of empirical studies, it is currently not clear
127 whether a social bird, such as the zebra finch living in an unpredictable environment, will disregard
128 social information as predicted (Boulinier and Danchin 1997; Doligez et al. 2003) and make decisions
129 on the basis of personal information (Kendal et al. 2004, 2005; Dall et al. 2005). The personal
130 information can either be obtained directly through prior breeding experience or from more recent
131 indirect cues (Dall et al. 2005), such as rainfall, temperature or food availability (Zann et al. 1995).

132 In this study, we used an experimental approach to test whether zebra finch reproductive
133 decisions could be influenced by social information. We differentially manipulated perceived
134 reproductive investment by creating three areas in which all laid clutches were artificially enlarged and
135 three areas in which all clutches were reduced. Subsequent reproductive decisions were recorded to
136 deduce what type of information was used. Zebra finches frequently prospect on the nests of

137 conspecifics (Mariette and Griffith 2012a) and we hence infer that individuals had the possibility to
138 collect social information about the reproductive performance of conspecifics.

139 If zebra finches use social information for their reproductive decisions we expect them to settle
140 primarily in perceived high quality patches and to lay larger clutches when breeding in those areas, as
141 compared to the low quality patches. In the case that personal information on recent breeding success
142 is preferred or outweighs the social cues we should observe a direct effect of the prior experience on
143 the next brood. While breeding site choice and breeding investment should be random in the first
144 brood, the subsequent brood would be affected by the respective personal breeding experience. Pairs
145 that were only allowed to raise a small brood should be more likely to leave the area or lay a smaller
146 clutch in the next breeding attempt, while their latency to rebreed might also be shorter. If neither
147 social information nor personal breeding experience is exploited we may conclude that the birds relied
148 on other environmental cues (Zann et al. 1995) or other social cues not measured in this study (e.g.
149 acoustic cues: Waas et al. 2005).

150

151 **METHODS**

152 ***Study site and study species***

153 Zebra finches are small passerines that live on a diet of grass seeds and employ a strategy of
154 opportunistic breeding adapted to the harsh and fluctuating desert environment (Zann 1996) Zebra
155 finches show a high degree of mobility and presumably move over large distances to find patches of
156 good condition in which to settle and breed (Zann 1996). The often extended breeding periods are
157 aseasonal and nest initiation is not strongly synchronized between pairs (Zann 1996; Mariette and
158 Griffith 2012a). Zebra finches can have multiple successive broods if conditions are favourable and
159 they are socially (Zann 1996) and genetically monogamous (Griffith et al. 2010), with bi-parental brood
160 care (Mariette and Griffith 2012b). They live in loose colonies (Zann 1996), which are held together by
161 conspecific attraction (Mariette and Griffith 2012a). Despite these aggregations in social groups, which

162 also occur when drinking or foraging, zebra finches mostly move around in mixed-sex pairs, which thus
163 seems to be the most important social unit (McCowan et al. 2015).

164 The study was performed at Gap Hills, located at Fowlers Gap, UNSW Arid Zone Research
165 Station (31°05'13.1"S 141°42'17.4"E), New South Wales, Australia, between August and November
166 2015. The study site is a roughly rectangular area of 1.5 x 2 km with a dam in the centre that contains
167 the only relatively permanent water body in the area. At this study site, 180 nest boxes were provided
168 attached to metal stakes, which are readily accepted and even preferred as nesting locations over
169 natural nesting sites (Griffith et al. 2008). Previous studies at the same site have shown that zebra
170 finches move across the whole study area multiple times a day (Mariette et al. 2011; Mariette and
171 Griffith 2012a), thus they should have access to information about the whole study site. Nests were
172 monitored between August 1st and December 7th 2015. The first pairs had already commenced
173 breeding by the beginning of August and birds continued breeding until March of 2016.

174

175 ***Clutch and brood manipulation***

176 The manipulation of clutch and brood size was conducted for 80 days between August 28st and
177 November 15th of 2015. Nest boxes were grouped in six clusters (mean distance to nearest
178 neighbouring cluster = $413.6 \pm \text{SD } 142$ m) of 30 nest boxes each (mean distance to nearest
179 neighbouring nest box within clusters = $10.4 \pm \text{SD } 4.8$ m). Three of these areas were randomly assigned
180 to the 'high quality' (HQ) and three areas to the 'low quality' (LQ) treatment in pairs that were roughly
181 equidistant from the central dam. Almost all clutches laid throughout the experiment were reduced or
182 enlarged to a final clutch size of 3 eggs in the LQ areas and 7 eggs in HQ areas (mean clutch size in
183 zebra finches = $4.9 \pm \text{SD } 1.05$ eggs; Griffith et al. 2008). Manipulations were conducted 6 days after
184 clutch completion (± 2 days, as necessary for matching eggs, see below), in the middle of the incubation
185 period (incubation period ranging from 11-16 days; Zann 1996). Zebra finches lay one egg per day (Zann
186 1996) and clutches were considered complete when no new egg was added within a 24 hour period.

187 All pairs that initiated breeding within the duration of the experiment started as focal individuals (and
188 potential prospectors), before they became demonstrators (with manipulated clutch sizes) for later
189 breeders. When an individual arrived at the study area it could collect information from individuals
190 already breeding. At the time a breeding pair had decided where to build a nest and how many eggs
191 to lay, the investment of these focal individuals, i.e. their natural clutch sizes, was recorded. Thereafter,
192 the manipulations occurred and all previous focal individuals served as demonstrators for birds
193 initiating nests at any later time point.

194 Eggs from clutches that were reduced were transferred to nests that were enlarged, matching
195 the developmental stages of eggs in the respective nests. When not enough eggs at a certain stage
196 were available, infertile eggs or eggs with hatching failure that had been collected from abandoned
197 nests were used to increase clutch sizes (out of a total of 278 manipulated clutches: one non-viable
198 egg was added to 23 clutches, two were added to 14 clutches, and three to 3 clutches). All nest box
199 areas were regularly scanned for the occurrence of natural nests, which were removed immediately
200 to prevent birds from gathering information from uncontrolled sources.

201

202 ***Nest box and bird monitoring***

203 Nest boxes were routinely inspected every four days to monitor nest building and egg laying and then
204 daily around the calculated approximate hatch date. Nesting attempts were only counted if the
205 number of eggs was within range of natural clutch sizes (2-8 eggs; Griffith et al. 2008); any nests that
206 did not meet the criteria, mostly cases of egg dumping and a few nests with one single egg, were
207 excluded from the data. Besides the number of eggs laid (natural clutch size before manipulation), also
208 the actual hatch date was recorded. Post manipulation, we counted the number of chicks on day 3 and
209 day 11 (day 0 as hatch date). Between day 6 and 11 adults were caught in the nest boxes using nest
210 box traps. We successfully trapped at least one adult at 236 out of 288 nests. All trapped adults and
211 11-day-old chicks were banded with a uniquely numbered metal band (Australian Bird and Bat Banding

212 Scheme). We did not check nest boxes after day 11 to avoid the risk of premature fledging and assumed
213 that they had fledged if the box was empty on day 19. Throughout the experiment we provided
214 supplementary food by placing a permanent feeder in the centre of each area (for details on feeders
215 see Mariette and Griffith 2012a). Since it was not possible to quantify the availability of natural food,
216 these feeders were used to ensure that the provision of artificial food was constant across the
217 experimental areas and reduce the likelihood that food was a limiting factor when raising increased
218 size broods. All feeders were checked daily and refilled with commercial finch seed mix when empty.
219 Previous studies have shown that the distribution of food and water in the landscape determines the
220 nest site choice of zebra finches on a larger scale (max. observed nest distance from water 25 km; Zann
221 1996), but not on a small scale (in areas 1-2 km wide; Mariette and Griffith 2012a).

222

223 ***Data analysis***

224 To test for any potential bias before the start of the experiment, we ran a linear mixed effect model
225 (LMM) with the clutch size of all nests that were laid in the monitoring period before the start of the
226 experiment as response variable, and the prospective treatment (HQ, LQ) of the areas as fixed effect
227 (Table 1, Model 1). The model included area as a random term (i.e. random intercept). To assess
228 whether the effects of our manipulation were sufficient to carry-over until chicks were close to
229 fledging, we fitted an LMM with treatment as fixed effect and the number of chicks on day 11 after
230 hatching as a response variable. Here, we only included nests that had hatched at least one chick. Area
231 and nest box were included as random terms. The latter was included in the model, because up to four
232 nests had been initiated in some nest boxes during the experiment.

233 We tested whether the total number of initiated broods in the HQ and LQ areas differed from
234 one another with a χ^2 -goodness-of-fit test, only including the first brood of each pair to exclude
235 personal information effects. χ^2 -tests of independence were conducted to compare the number of

236 successful nests (i.e. nests that did/did not hatch at least one chick) and survival rates (i.e. number of
237 chicks that survived/died between day 3 and day 11) between treatments.

238 We fitted another LMM to analyse the effect of our manipulation on breeding investment
239 (Table 1, Model 2). We assessed the effects of treatment using the natural clutch size as response
240 variable and day of experiment (days since beginning of experiment) and the two-way interaction
241 between treatment and day of experiment as fixed effects. The interaction between treatment and
242 day was included to control for the fact that the amount of manipulation increased over time (also see
243 below). To further investigate whether an effect of the treatment was potentially only significant at a
244 certain stage in the experiment we also fitted LMMs with the natural clutch size as response variable
245 and treatment as fixed effect using data from three different stages of the experiment: 'early', i.e. day
246 1 - 27; 'mid', i.e. day 28 - 54; and 'late', i.e. day 55 - 80 of the experiment. We included nest box and
247 area as random effects. Only the first breeding attempt of each pair within the experiment was
248 included in these models to exclude the effect of personal experience.

249 The number of already manipulated nest boxes and thus, also the amount of social information
250 that was currently available for breeding pairs increased throughout the experiment. Even though this
251 factor is important, we did not include the total number of manipulated nest boxes at each day in any
252 models to avoid multicollinearity: the number of manipulated boxes and day of experiment were
253 strongly positively correlated (Spearman rank correlation: $r_s = 0.976$, $N = 288$, $P < 0.001$). Thus, we were
254 not able to disentangle the effects of the number of manipulated boxes from other time dependent
255 effects such as seasonal variation. Hence, we only used 'days of experiment' in models to represent all
256 time-dependent variation. The 'number of manipulated nest boxes' for each nest was calculated as
257 the total number of boxes in the study site that were manipulated at the date the female
258 approximately instigated egg laying (i.e. 22 days before hatch date; 5 days to make an egg, an average
259 of 5 days for egg laying, plus around 12 days of incubation; Zann 1996; Blount et al. 2006).

260 In two additional LMMs we tested the effects of personal experience through repeated
261 breeding on breeding investment and in another LMM the effect on latency to rebreed (Table 2). Here
262 we included only data of pairs that bred twice during the experimental phase (at least the first brood

263 during manipulations, some bred again after). We tested whether birds that had experienced the
264 treatment of their respective breeding area first-hand would use this information to make adjustments
265 for their next brood. In a first model we analysed whether natural clutch size (response variable)
266 changed with the brood order, i.e. first or second brood (also including treatment and days of
267 experiment as fixed effects) to test for a general effect of repeated breeding (Table 2, Model 3). To
268 analyse the impact of prior experience in more detail, we fitted another LMM focusing on the influence
269 that the specific investment in the first brood has on the second brood (Table 2, Model 4). In this model
270 we used natural clutch sizes of the second broods as a response variable and included the natural
271 clutch size and the treatment of the corresponding first broods as fixed terms. Another LMM was used
272 to assess whether personal experience affected the latency to rebreed between the start of the first
273 brood and the start of the next brood (Table 2, Model 5). Number of days between start of egg laying
274 in consecutive broods was used as response variable in a model including clutch size, treatment and
275 fledging success (yes/no, at least one chick fledged) of the first brood as fixed terms. In the first LMM
276 we used pair ID, nest box and area as random terms, in the second model we included the area of the
277 second brood and in the last model area of the first brood was used as random term.

278 Full models were always reduced by stepwise removing the least significant terms, as
279 determined by likelihood ratio test between models (Crawley 2007). Terms were only removed if the
280 explanatory power of the simpler model was not significantly reduced, when compared to the more
281 complex model with likelihood ratio tests (Crawley 2007). Random effects were conservatively not
282 reduced. We checked that model assumptions of LMMs were not violated using diagnostic plots and
283 based on this selected normal error structure as the best fit. Profile likelihood ratio confidence intervals
284 were calculated for all fixed effects (Colegrave and Ruxton 2003). All statistical analysis were conducted
285 with R (R Core Team 2014). For LMMs we used the package 'lme4' (Bates et al. 2014). Statistics are
286 presented as mean \pm standard deviation (SD) throughout.

287 A total of 38 clutches were removed from the data because the eggs were found already
288 abandoned before, or at the time the manipulation should have taken place, or the eggs disappeared

289 from the nest (e.g. due to predation). These nests were then removed from the nest boxes and hence
290 should not have strongly affected potential prospectors. It was not possible to record data blind
291 because our study involved focal animals in the field.

292

293

294 **RESULTS**

295 ***Effect of manipulation on clutch size and brood success***

296 The clutch sizes of the nests that were recorded in August, before manipulations started, did not differ
297 between prospective treatment areas (Table 1, Model 1). We manipulated the size of 278 (of 288)
298 clutches laid in 170 nest boxes by 273 zebra finch breeding pairs. Eighty of the nest boxes were used
299 twice, seventeen nest boxes were used three times, and one nest box was used for a total of four
300 consecutive breeding attempts during the duration of the experiment. While 17 zebra finch pairs had
301 multiple broods (see below), the remaining nesting attempts were always initiated by new pairs. After
302 the manipulations mean clutch size was 6.88 ± 0.50 eggs in the HQ nests and 3.07 ± 0.36 eggs in the
303 LQ nests. The effect of the manipulation was also carried over to the number of surviving chicks: on
304 day 11 after hatching broods in the HQ areas were still larger (mean number chicks day 11: 4.13 ± 2.10
305 chicks) compared to broods in the LQ areas (mean number chicks day 11: 2.38 ± 1.06 chicks; $\chi^2_1 =$
306 14.345 , $N = 246$, $P < 0.001$).

307

308 ***Effects of treatment on natural clutch sizes***

309 There was no significant difference in the total number of broods initiated in HQ areas (140 broods;
310 mean no. broods per area = 46.67 ± 1.53) compared to LQ areas (133 broods; mean no. broods per LQ
311 area = 44.33 ± 5.51 ; $\chi^2_1 = 0.179$, $P = 0.672$) we recorded throughout the experiment (not including
312 second broods some individuals had). Overall, 94% of the experimental nests hatched at least one

313 chick with no significant difference between the treatment areas ($\chi^2_1 = 0.015$, $P = 0.903$). Likewise, the
314 mean rate of surviving chicks from day 3 to day 11 was not significantly different between HQ ($82 \pm$
315 34% of the nestlings on day 3 were still alive on day 11) and LQ areas ($85 \pm 33\%$ nestlings survived; χ^2_1
316 $= 2.207$, $P = 0.137$). In 70% of the HQ broods and 81% of the LQ broods all chicks survived between day
317 3 and day 11. In 18% of the HQ broods 1 or 2 chicks died and in 11% of broods 3 - 7 chicks died.

318 The natural number of eggs laid per nest was not affected by the treatment or an interaction
319 between treatment and day of experiment. However, clutch sizes decreased significantly over the
320 duration of the experiment (Fig. 1; Table 1, Model 2). Also when the effect of treatment was analyzed
321 separately for each of three different stages of the experiment it was non-significant ('early': $\chi^2_1 =$
322 0.001 , $N = 73$, $P = 0.984$, 'mid': $\chi^2_1 = 0.175$, $N = 98$, $P = 0.676$; 'late': $\chi^2_1 = 1.398$, $N = 102$, $P = 0.237$).

323

324

325 ***Effects of personal information through repeated breeding***

326 During the monitoring period 24 breeding pairs bred multiple times (one pair three times, the others
327 twice). However, eight of them laid their first clutch before the start of the experimental period, leaving
328 34 broods from 17 pairs for analyses of the effect of personal information. Most of these pairs with
329 multiple broods did not move to another area after the first brood. They continued breeding in the
330 same experimental area, but did not continue to use the same nest box. Only three pairs switched
331 areas; two pairs raised their second brood in a HQ area after breeding in LQ area before and one pair
332 moved from one LQ area to another LQ area. Including only pairs that had the experience of a first
333 brood in the experiment (8 pairs in HQ, 9 in LQ), second clutches were significantly smaller than their
334 first clutches reflecting the overall pattern in the broader dataset with declining clutch size as the
335 season progressed. Treatment and lay date in relation to the duration of the experiment, however, did
336 not predict clutch size (Table 2, Model 3). When analyzing the specific effect of prior experience on

337 number of eggs in the second brood, neither clutch size nor treatment of the first brood had a
338 significant effect on number of eggs laid in the second brood (Table 2, Model 4).

339 The time between the start of two consecutive breeding attempts of the same pair was not
340 significantly affected by clutch size or treatment of the first brood (Table 2, Model 5). Only fledging
341 success explained some of the variation, i.e. the interval between broods was significantly longer when
342 at least one chick of the first brood fledged successfully. The mean time interval between the start
343 dates of two consecutive breeding attempts of the same pair, as estimated in the model, was $53.7 \pm$
344 10.9 days in broods that fledged successfully and 31.3 ± 5.56 days in nests where all chicks died before
345 fledging.

346

347

348 **DISCUSSION**

349 In this study we used an experimental approach to test the hypothesis that wild zebra finches exploit
350 social information in making reproductive decisions. We manipulated clutch size in a relatively high
351 number of zebra finch nests, creating the perception of a patchy environment, with respect to
352 conspecific reproductive investment. The zebra finches in our experiment did not strongly rely on
353 socially acquired information as shown by the results that clutch sizes were equal between treatments
354 and areas of higher reproductive success were not preferred areas for new nesting activity.

355 The lack of evidence for social information use in our study is compelling, because it is in stark
356 contrast to the findings of a series of other studies showing that social cues are successfully used as a
357 predictor for reproductive success in birds (e.g. Danchin et al. 1998; Doligez et al. 2002; Ward 2005;
358 Parejo et al. 2007). These studies all offer substantive evidence for birds relying on social cues from
359 conspecifics when breeding in a temperate climate where they can rely on relatively stable
360 environmental conditions and seasonal predictability.

361 Social information in fluctuating and unpredictable conditions has mainly been dealt with in
362 theoretical models, which have predicted a less frequent use with an increasing probability of
363 environmental change (Boyd and Richerson 1988; Feldman et al. 1996; Boulinier and Danchin 1997;
364 Doligez et al. 2003). This prediction is justified for certain scenarios and information needs to be up-
365 to-date to be reliable. However, empirical studies in the field (e.g. Boulinier and Danchin 1997; Doligez
366 et al. 2002; Ward 2005; Parejo et al. 2007) have all been based on the premise that information on
367 patch quality is firstly always collected in the preceding season and secondly, that in this preceding
368 season a trade-off between information gathering and reproduction exists. The first assumption is
369 unlikely to be valid for zebra finches and the latter also needs to be put in question. Birds living in arid
370 environments have greatly extended potential breeding seasons, compared with those in the more
371 seasonally predictable northern hemisphere temperate zone (Duursma et al. 2017) and in any one
372 year, can also breed multiple times. Shorter intervals between breeding attempts increase the chance
373 that information is still valid for the subsequent brood. Also nest initiation in zebra finches is not
374 strongly synchronized (Mariette and Griffith 2012a). Hence zebra finches have conspecific cues
375 available not only at the end of a breeding cycle and could potentially both collect information and
376 initiate a brood shortly thereafter. Therefore, the trade-off between information gathering and
377 breeding (if still existing) should be less pronounced.

378 While it is important to point out these ecological differences, the results of our study are still
379 in line with theoretical predictions (Feldman et al. 1996; Boulinier and Danchin 1997; Doligez et al.
380 2003). It is still plausible that the absence of social information use in our study might be due to the
381 low predictability of the environment zebra finches live in. It is perhaps disadvantageous to take cues
382 from others when conditions and hence the outcome is inconsistent even on a relatively short intra-
383 annual timescale. Additionally, it is also possible that a mix of different sources of information is used
384 and social information was over-ridden by personal information. Another study has demonstrated the
385 opposite effect, with an experiment in which social cues outweighed personal habitat preferences of
386 a migrant passerine usually breeding in very stable hardwood forests (Betts et al. 2008). In the context

387 of defense against brood parasites combining personal and social information has been identified as a
388 successful strategy (Thorogood and Davies 2016). In our study, it appears that the social information
389 was, if maybe not completely ignored, at least outweighed by other factors. The mechanisms are
390 diverse and it becomes increasingly obvious that the specific ecological circumstances need to be
391 regarded as a significant factor in the study of information use.

392 Two of the key variables defining what type of information will be used are the cost of
393 obtaining information and its reliability (Dall et al. 2005). The cost of obtaining social information in
394 the context of our study is mainly the time and energy invested in prospecting. The cost for personal
395 experience, on the other hand, is a breeding attempt with potentially sub-optimal parameters. The
396 acquisition of social information should therefore be the less costly strategy (Giraldeau et al. 1994;
397 Doligez et al. 2003; Laland 2004). In our experiment, social information indicating either high or low
398 reproductive success of conspecifics was readily available for individuals prospecting on neighboring
399 nest boxes, which was frequently observed (see also Mariette and Griffith 2012a). This behavior has
400 also been described in many other bird species (e.g. Reed et al. 1999). Zebra finches are not territorial,
401 and we have not observed any overt conspecific aggression around nest boxes. Furthermore, there are
402 usually many nests within 100 m of a focal nest. Thus, there is unlikely to be a significant cost in finding
403 and inspecting neighboring nests. We can assume that this investment of time and energy (probably
404 also involving increased predation risk) also brings along benefits. Hence, it seems likely that
405 prospecting is used to gather social information, but in different ways than tested by our hypothesis.
406 For instance, social cues could be used for predation avoidance or to help with optimal timing. Such
407 hypotheses will need to be tested in further experiments.

408 Our experiment did not include a treatment with average brood sizes as a control and thus did
409 not test the response to the average brood size. Our manipulation, however, was within the range of
410 natural clutch and brood sizes in this species and therefore was unlikely to have been perceived as
411 unnatural. Even if zebra finches had a preference for an average brood size, it is reasonable to expect
412 that offered a binary choice (smaller or larger brood), they would have been able to make a decision,

413 given the likely fitness consequences of producing either too many, or too few offspring in the
414 prevailing conditions (as signaled by conspecifics, if this did serve as a source of information).

415 Our results showed quite clearly that social information was not the main cue used for
416 reproductive investment decisions (at least for the parameters we measured), leaving personal
417 information as an alternative source of information. Our experimental brood manipulation also
418 affected the personal experience of breeding individuals. In the succession of multiple broods, it was
419 possible for zebra finches to collect personal information on their own (manipulated) breeding success
420 and make decisions accordingly in subsequent broods. When birds first entered the experiment, they
421 had no personal experience with the treatment of the different nest box areas (breeding activity was
422 very low in the area in the months before our experiment started, so most of the pairs in our
423 experiment would have been breeding for the first time in this area). Decisions made at this point were
424 either based on social cues from conspecifics (which we have largely excluded) or based on other
425 sources of personal information (e.g. food availability or other environmental parameters). In any
426 following brood, however, personal information on an individuals' own breeding success in a
427 respective treatment area was existing. We found no indication that individuals altered their behavior
428 or investment in relation to the component of personal information manipulated in our experiment.
429 Pairs breeding multiple times did not alter their clutch size in response to the previously experienced
430 treatment and movements between areas from one brood to the next were very rare, and not
431 predicted by the experimental treatments. In a rapidly changing ecological situation, even the personal
432 information from a previous brood might be more outdated than the contemporary available personal
433 information on the intrinsic quality of the habitat, such as food availability. Personal information
434 obtained by monitoring other environmental parameters might give the most reliable representation
435 of a quickly changing environment and hence allow for the best response. Once favorable conditions
436 arise, zebra finches are able to time the hatching of the first chicks accordingly (Zann et al. 1995).

437 Our prediction for this experiment was that birds from LQ areas would move to HQ areas.
438 However, birds rarely changed the area between breeding attempts at all. Our results confirmed a

439 previous finding that zebra finches move to another box for a subsequent brood, but stay closer to the
440 old one than expected by chance (Mariette and Griffith 2012a). It is remarkable that this strategy is
441 still valid for the birds even after we had manipulated their own brood and that of the conspecifics
442 breeding nearby. Even in the LQ areas, where individuals suffered low reproductive success during the
443 experiment, zebra finches mostly remained in that area. There may have been benefits of becoming
444 familiar with the area, as shown in birds and lizards (Stamps 1987; Bruinzeel and van de Pol 2004; Piper
445 2011). Another explanation could be that birds simply perceived all areas as equally high quality
446 habitats due to the food supplementation. This would mean that they ranked the personal information
447 on available resources higher than personal breeding success (or social information). Another study on
448 the same population, however, has shown that zebra finches did not cluster their nests around either
449 food or water (Mariette and Griffith 2012a).

450 Our prediction that parents raising larger broods would have a longer interval between
451 consecutive breeding attempts, as demonstrated in great tits (*Parus major*; Slagsvold 1984), was not
452 supported. Lemon (1993) showed that zebra finches with experimentally extended time required for
453 foraging increased the time interval between successive broods. In our experiment, food availability
454 was equal in both treatments, thus perhaps levelling some of these associated effects. Only the
455 successful fledging of chicks led to a longer time interval between broods in our study. This is not
456 surprising, since fledglings require a period of 15-20 days further care until full nutritional
457 independence from parents (Zann 1996). During this period where fledglings are still provisioned by
458 parents the next breeding attempt cannot be initiated. The relative high survival rate throughout may
459 also be explained by birds having sufficient food available. This could have enabled them to partially
460 or fully compensate for the challenge of raising additional chicks. Studies have shown negative impact
461 of increases in reproductive effort on future competitiveness, at least for species in temperate climates
462 (Fokkema et al. 2016, 2017). Unfortunately no such data are available for wild zebra finches and the
463 extremely low return rate of individuals to the same site between years makes it hard to impossible to
464 study this effect.

465 Zebra finches generally employ a high level of opportunism in their breeding strategy. They
466 breed whenever conditions are favorable in terms of food availability, which can be at any time of the
467 year (e.g. Zann 1996). As adaption to the unpredictability of breeding periods and in contrast to
468 seasonally breeding vertebrates their reproductive system is constantly activated (Wingfield et al.
469 1992; Perfito et al. 2007). We were not able to change the breeding decisions of the birds in any
470 obvious way with our manipulations. Thus, perhaps there is also a certain degree of opportunism
471 involved in other reproductive aspects (e.g. nest site choice and clutch size), besides the timing. The
472 factors involved in determining the clutch size of zebra finches are not fully understood, but nutritional
473 aspects appear to be involved (Zann 1996). While the energetic costs of foraging were not found to
474 directly affect clutch sizes of immediate broods (Lemon 1993), other studies showed that optimized
475 female nutrition early in life (Haywood and Perrins 1992) and in the pre-breeding period (Selman and
476 Houston 1996) increase clutch sizes. It is possible that zebra finches opportunistically maximize their
477 reproductive output given their state and quality as soon as environmental conditions become
478 favorable. Therefore, they might primarily rely on abiotic environmental cues (e.g. density and
479 abundance of grass seed) rather than social cues or information obtained from previous breeding.
480 Especially in quickly changing environments information on own or conspecific breeding success might
481 be outdated quickly.

482 Our results suggest that species (or populations) reproducing in unpredictable environments
483 might substantially differ in their information use from those living in more predictable environments,
484 such as temperate environments with fixed and constrained schedules for reproduction. More studies
485 outside temperate environments are now needed to shore up our findings and to advance our
486 understanding of information use under a range of environmental conditions.

487

488

489 **Ethical approval**

490 All applicable international, national, and/or institutional guidelines for the care and use of animals
491 were followed. All procedures performed in studies involving animals were in accordance with the
492 ethical standards of the institution or practice at which the studies were conducted. The work was
493 approved by the Macquarie University Animal Ethics Committee (Animal Research Authority
494 2015/017) and the Australian Bird and Bat Banding Scheme.

495

496 **Conflict of Interest**

497 The authors declare that they have no conflict of interest.

498

499 **Data Availability statement**

500 The datasets analysed during the current study are available from the corresponding author on
501 reasonable request.

502

503

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641

642 **Table 1** Summaries of LMMs to assess the differences in reproductive measures between treatment areas before the start of the experiment (Model 1) and to assess
 643 the effect of treatment (HQ, LQ) and day (days since start of the experiment) on the number of eggs laid by zebra finches in their first broods within the experiment
 644 (Model 2). Significant p-value is highlighted in bold. Estimates of coefficients and 95% confidence intervals (CI) are estimates for the variables in minimal adequate
 645 model; values in brackets represent coefficients and confidence intervals in full model. (exp. = experiment, manip. = manipulation, treatm. = treatment)

Model number	Response variable	Predictor variables	Estimates	CI	N	X ²	df	P
1 (before manip.)	<i>Natural clutch size</i>	(intercept)	4.145	3.78 – 4.55	34	1.19	1	0.275
		treatment [LQ]	(0.263)	(-0.41 – 0.90)				
2 (after start of manip.)	<i>Natural clutch size</i>	(intercept)	5.108	4.81 – 5.40	273	0.17	1	0.679
		treatment [LQ] * day	(-0.002)	(-0.01 – 0.01)				
		treatment [LQ]	(-0.092)	(-0.66 – 0.48)				
		day	-0.007	-0.01 – <-0.01				

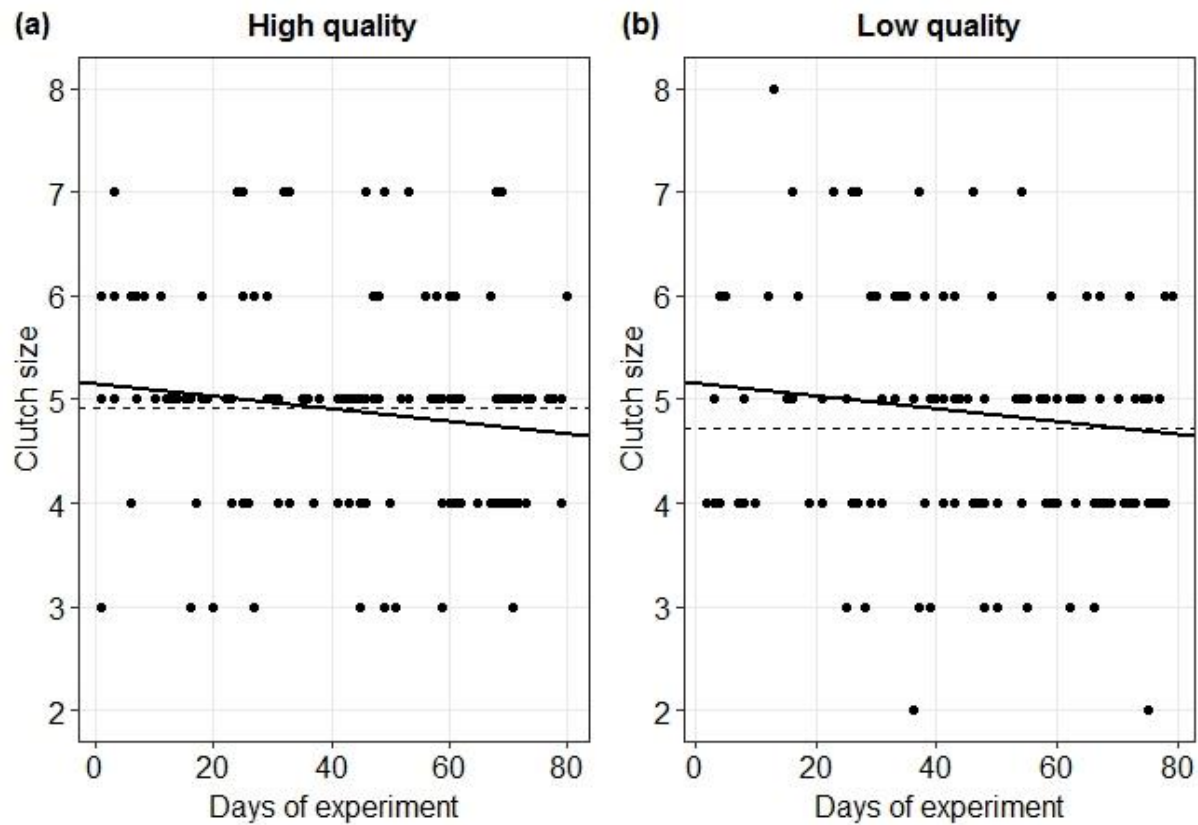
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647

648 **Table 2** Summaries of LMMs assessing the effect of personal experience for subsequent breeding attempts (Model 3 and 4) and the time interval till the next breeding
649 event of the same pair (Model 5). The first model (Model 3) uses a general approach exploring effects of brood order, treatment (HQ, LQ) and day of experiment on
650 clutch sizes, whereas the second model (Model 4) uses a more direct approach exploring effects of variables linked to the experience of the first brood on the clutch
651 size of the second brood. Fledging success (fledge succ.) was coded as yes (at least one chick presumably fledged) or no (all chicks died before fledging). Significant p-
652 values are highlighted in bold. Estimates of coefficients and 95% confidence intervals (CI) are estimates for the variables in minimal adequate model; values in brackets
653 represent coefficients and confidence intervals in full model. (exp. = experiment, nat. = natural, treatm. = treatment)

Model number	Response variable	Predictor variables	Estimates	CI	N	χ^2	df	P
3	<i>Nat. clutch size</i>	(intercept)	5.353	4.82 – 5.89	34			
		brood order [second]	-0.824	-1.48 – -0.17		5.78	1	0.016
		treatment [LQ]	(-0.130)	(-0.99 – 0.82)		0.12	1	0.725
		day	(0.015)	(-0.01 – 0.04)		1.14	1	0.285
4	<i>Nat. clutch size in 2nd brood</i>	(intercept)	4.529	4.01 – 5.05	17			
		nat. clutch size of 1 st brood	(0.293)	(-0.12 – 0.71)		2.05	1	0.153
		treatment of 1 st brood [LQ]	(-0.710)	(-1.65 – 0.23)		1.77	1	0.183
5	<i>Time between broods</i>	(intercept)	31.333	19.54 – 43.13	17			
		nat. clutch size of 1 st brood	(3.751)	(0.56 – 6.43)		0.03	1	0.869
		treatment of 1 st brood [LQ]	(0.450)	(-11.60 – 9.58)		2.60	1	0.107
		fledge succ. 1 st brood [yes]	22.381	9.39 – 35.38		9.48	1	0.002

654



655

656 **Fig. 1** Number of eggs per clutch in (a) HQ and (b) LQ treatment areas laid at each day of the experiment, respectively. The dashed lines represent mean clutch sizes

657 (calculated from raw data), the solid line predicts clutch sizes at each day of the experiment (based on the output of the minimal model, see Table 1, Model 2)