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

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## Abstract

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

## Significance statement

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

**Keywords** Brood size manipulation · Decision-making · Fluctuating conditions · Information use · Prospecting · Unstable environment

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## Introduction

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

While the number of existing empirical studies on information use in general is high, the minority of them have addressed the use of social information with respect to breeding site and habitat selection (Brown et al. 2000; Parejo et al. 2006; Jaakkonen et al. 2013) or reproductive investment decisions (Forsman et al. 2011; Schuett et al. 2015). It has been suggested that the current reproductive success of conspecifics might give a more accurate prediction for the quality of a breeding habitat than other environmental parameters (Boulinier and Danchin 1997). Depending on the context, some species can even switch between con- and heterospecific information use (e.g., pied and collared flycatcher, *Ficedula hypoleuca* and *F. albicollis*, switch depending on which have the higher density; Jaakkonen et al. 2014; Samplonius et al. 2017). Indeed, individuals of many species “prospect,” i.e., visit breeding sites of other individuals (e.g., reviewed in Reed et al. 1999), likely to assess the quality of potential breeding sites in advance (e.g., Cadiou et al. 1994; Pärt and Doligez 2003; Doligez et al. 2004). A good example of this behavior and its functional value was shown in an experimental study on collared flycatchers (Doligez et al. 2002). This European passerine reacted to patches of habitat with experimentally increased brood sizes with higher settlement of breeders in the following year, demonstrating the use of social information from conspecifics as a predictor for habitat quality (Doligez et al. 2002).

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

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

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

In this study, we used an experimental approach to test whether zebra finch reproductive decisions could be influenced by social information. We differentially manipulated perceived reproductive investment by creating three areas in which all laid clutches were artificially enlarged and three areas in which all clutches were reduced. Subsequent reproductive decisions were recorded to deduce what type of information was used. Zebra finches frequently prospect on the nests of conspecifics (Mariette and Griffith 2012a) and we hence infer that individuals had the possibility to collect social information about the reproductive performance of conspecifics.

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

## Methods

### Study site and study species

Zebra finches are small passerines that live on a diet of grass seeds and employ a strategy of opportunistic breeding adapted to the harsh and fluctuating desert environment (Zann 1996). Zebra finches show a high degree of mobility and presumably move over large distances to find patches of good condition in which to settle and breed (Zann 1996). The often extended breeding periods are aseasonal and nest initiation is not strongly synchronized between pairs (Zann 1996; Mariette and Griffith 2012a). Zebra finches can have multiple successive broods if conditions are favorable and they are socially (Zann 1996) and genetically monogamous (Griffith et al. 2010), with bi-parental brood care (Mariette and Griffith 2012b). They live in loose colonies (Zann 1996), which are held together by conspecific attraction (Mariette and Griffith 2012a). Despite these aggregations in social groups, which also occur when drinking or foraging, zebra finches mostly move around in mixed-sex pairs, which thus seems to be the most important social unit (McCowan et al. 2015).

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

### Clutch and brood manipulation

The manipulation of clutch and brood size was conducted for 80 days between August 28 and November 15, 2015. Nest boxes were grouped in six clusters (mean distance to nearest neighboring cluster = 413.6 ± SD 142 m) of 30 nest boxes each (mean distance to nearest neighboring nest box within clusters = 10.4 ± SD 4.8 m). Three of these areas were randomly assigned to the “high quality” (HQ) and three areas to the “low quality” (LQ) treatment in pairs that were roughly equidistant from the central dam. Almost all clutches laid throughout the experiment were reduced or enlarged to a final clutch size of three eggs in the LQ areas and seven eggs in HQ areas (mean clutch size in zebra finches = 4.9 ± SD 1.05 eggs; Griffith et al. 2008). Manipulations were conducted 6 days after clutch completion (± 2 days, as necessary for matching eggs, see below), in the middle of the incubation period (incubation period ranging from 11 to 16 days; Zann 1996). Zebra finches lay one egg per day (Zann 1996) and clutches were considered complete when no new egg was added within a 24-h period. All pairs that initiated breeding within the duration of the experiment started as focal individuals (and potential prospectors), before they became demonstrators (with manipulated clutch sizes) for later breeders. When an individual arrived at the study area, it could collect information from individuals already breeding. At the time a breeding pair had decided where to build a nest and how many eggs to lay, the investment of these focal individuals, i.e., their natural clutch sizes, was recorded. Thereafter, the manipulations occurred and all previous focal individuals served as demonstrators for birds initiating nests at any later time point.

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

## Nest box and bird monitoring

Nest boxes were routinely inspected every 4 days to monitor nest building and egg laying and then daily around the calculated approximate hatch date. Nesting attempts were only counted if the number of eggs was within range of natural clutch sizes (two to eight eggs; Griffith et al. 2008); any nests that did not meet the criteria, mostly cases of egg dumping and a few nests with one single egg, were excluded from the data. Besides the number of eggs laid (natural clutch size before manipulation), also the actual hatch date was recorded. Post manipulation, we counted the number of chicks on day 3 and day 11 (day 0 as hatch date). Between days 6 and 11, adults were caught in the nest boxes using nest box traps. We successfully trapped at least one adult at 236 out of 288 nests. All trapped adults and 11-day-old chicks were banded with a uniquely numbered metal band (Australian Bird and Bat Banding Scheme). We did not check nest boxes after day 11 to avoid the risk of premature fledging and assumed that they had fledged if the box was empty on day 19. Throughout the experiment, we provided supplementary food by placing a permanent feeder in the center of each area (for details on feeders, see Mariette and Griffith 2012a). Since it was not possible to quantify the availability of natural food, these feeders were used to ensure that the provision of artificial food was constant across the experimental areas and reduce the likelihood that food was a limiting factor when raising increased size broods. All feeders were checked daily and refilled with commercial finch seed mix when empty. Previous studies have shown that the distribution of food and water in the landscape determines the nest site choice of zebra finches on a larger scale (maximum observed nest distance from water 25 km; Zann 1996), but not on a small scale (in areas 1–2 km wide; Mariette and Griffith 2012a).

## Data analysis

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

We tested whether the total number of initiated broods in the HQ and LQ areas differed from one another with a $\chi^2$ goodness-of-fit test, only including the first brood of each pair to exclude personal information effects. $\chi^2$ tests of independence were conducted to compare the number of successful nests (i.e., nests that did/did not hatch at least one chick) and survival rates (i.e., number of chicks that survived/died between day 3 and day 11) between treatments.

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

The number of already manipulated nest boxes and thus, also the amount of social information that was currently available for breeding pairs increased throughout the experiment. Even though this factor is important, we did not include the total number of manipulated nest boxes at each day in any

**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 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 (model 2)

| Model number | Response variable | Predictor variables | Estimates | CI | *N* | $\chi^2$ | *df* | *P* value |
|---|---|---|---|---|---|---|---|---|
| 1 (before manipulation) | Natural clutch size | (intercept) | 4.145 | 3.78 to 4.55 | 34 | | | |
| | | Treatment (LQ) | (0.263) | (− 0.41 to 0.90) | | 1.19 | 1 | 0.275 |
| 2 (after start of manipulation) | Natural clutch size | (intercept) | 5.108 | 4.81 to 5.40 | 273 | | | |
| | | Treatment (LQ) × day | (− 0.002) | (− 0.01 to 0.01) | | 0.17 | 1 | 0.679 |
| | | Treatment (LQ) | (− 0.092) | (− 0.66 to 0.48) | | 1.23 | 1 | 0.268 |
| | | Day | − 0.007 | − 0.01 to <− 0.01 | | 5.87 | 1 | **0.015** |

Significant *P* value is highlighted in bold. Estimates of coefficients and 95% confidence intervals (CI) are estimates for the variables in minimal adequate model; values in brackets represent coefficients and confidence intervals in full model

models to avoid multicollinearity: the number of manipulated boxes and day of experiment were strongly positively correlated (Spearman rank correlation—$r_s = 0.976$, $N = 288$, $P < 0.001$). Thus, we were not able to disentangle the effects of the number of manipulated boxes from other time-dependent effects such as seasonal variation. Hence, we only used "days of experiment" in models to represent all time-dependent variation. The "number of manipulated nest boxes" for each nest was calculated as the total number of boxes in the study site that were manipulated at the date the female approximately instigated egg laying (i.e., 22 days before hatch date; 5 days to make an egg, an average of 5 days for egg laying, plus around 12 days of incubation; Zann 1996; Blount et al. 2006).

In two additional LMMs, we tested the effects of personal experience through repeated breeding on breeding investment and in another LMM the effect on latency to rebreed (Table 2). Here, we included only data of pairs that bred twice during the experimental phase (at least the first brood during manipulations, some bred again after). We tested whether birds that had experienced the treatment of their respective breeding area first-hand would use this information to make adjustments for their next brood. In a first model, we analyzed whether natural clutch size (response variable) changed with the brood order, i.e., first or second brood (also including treatment and days of experiment as fixed effects) to test for a general effect of repeated breeding (Table 2, model 3). To analyze the impact of prior experience in more detail, we fitted another LMM focusing on the influence that the specific investment in the first brood has on the second brood (Table 2, model 4). In this model, we used natural clutch sizes of the second broods as a response variable and included the natural clutch size and the treatment of the corresponding first broods as fixed terms. Another LMM was used to assess whether personal experience affected the latency to rebreed between the start of the first brood and the start of the next brood (Table 2, model 5). Number of days between start of egg

**Table 2** Summaries of LMMs assessing the effect of personal experience for subsequent breeding attempts (models 3 and 4) and the time interval till the next breeding event of the same pair (model 5)

| Model number | Response variable | Predictor variables | Estimates | CI | *N* | $\chi^2$ | *df* | *P* value |
|---|---|---|---|---|---|---|---|---|
| 3 | Natural clutch size | (intercept) | 5.353 | 4.82 to –5.89 | 34 | | | |
| | | Brood order (second) | − 0.824 | − 1.48 to − 0.17 | | 5.78 | 1 | **0.016** |
| | | Treatment (LQ) | (− 0.130) | (− 0.99 to 0.82) | | 0.12 | 1 | 0.725 |
| | | Day | (0.015) | (− 0.01 to 0.04) | | 1.14 | 1 | 0.285 |
| 4 | Natural clutch size in 2nd brood | (intercept) | 4.529 | 4.01 to 5.05 | 17 | | | |
| | | Natural clutch size of 1st brood | (0.293) | (− 0.12 to 0.71) | | 2.05 | 1 | 0.153 |
| | | Treatment of 1st brood (LQ) | (− 0.710) | (− 1.65 to 0.23) | | 1.77 | 1 | 0.183 |
| 5 | Time between broods | (intercept) | 31.333 | 19.54 to 43.13 | 17 | | | |
| | | Natural clutch size of 1st brood | (3.751) | (0.56 to 6.43) | | 0.03 | 1 | 0.869 |
| | | Treatment of 1st brood (LQ) | (0.450) | (− 11.60 to 9.58) | | 2.60 | 1 | 0.107 |
| | | Fledging success 1st brood (yes) | 22.381 | 9.39 to 35.38 | | 9.48 | 1 | **0.002** |

The first model (model 3) uses a general approach exploring effects of brood order, treatment (HQ, LQ) and day of experiment on 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 size of the second brood. Fledging success was coded as yes (at least one chick presumably fledged) or no (all chicks died before fledging). Significant *P* 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 represent coefficients and CIs in full model laying in consecutive broods was used as response variable in a model including clutch size, treatment, and fledging success (yes/no, at least one chick fledged) of the first brood as fixed terms. In the first LMM, we used pair ID, nest box, and area as random terms; in the second model, we included the area of the second brood; and in the last model, area of the first brood was used as random term.

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

A total of 38 clutches were removed from the data because the eggs were found already abandoned before, or at the time the manipulation should have taken place, or the eggs disappeared from the nest (e.g., due to predation). These nests were then removed from the nest boxes and hence should not have strongly affected potential prospectors. It was not possible to record data blind because our study involved focal animals in the field.

**Data availability statement** The datasets analyzed during the current study are available from the corresponding author on reasonable request.

## Results

### Effect of manipulation on clutch size and brood success

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

### Effects of treatment on natural clutch sizes

There was no significant difference in the total number of broods initiated in HQ areas (140 broods; mean number of broods per area = 46.67 ± 1.53) compared to LQ areas (133 broods; mean number of broods per LQ area = 44.33 ± 5.51; $\chi^2_1 = 0.179$, $P = 0.672$) we recorded throughout the experiment (not including second broods some individuals had). Overall, 94% of the experimental nests hatched at least one chick with no significant difference between the treatment areas ($\chi^2_1 = 0.015$, $P = 0.903$). Likewise, the mean rate of surviving chicks from day 3 to day 11 was not significantly different between HQ (82 ± 34% of the nestlings on day 3 were still alive on day 11) and LQ areas (85 ± 33% nestlings survived; $\chi^2_1 = 2.207$, $P = 0.137$). In 70% of the HQ broods and 81% of the LQ broods, all chicks survived between day 3 and day 11. In 18% of the HQ broods, one or two chicks died, and in 11% of broods, three to seven chicks died.

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

### Effects of personal information through repeated breeding

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

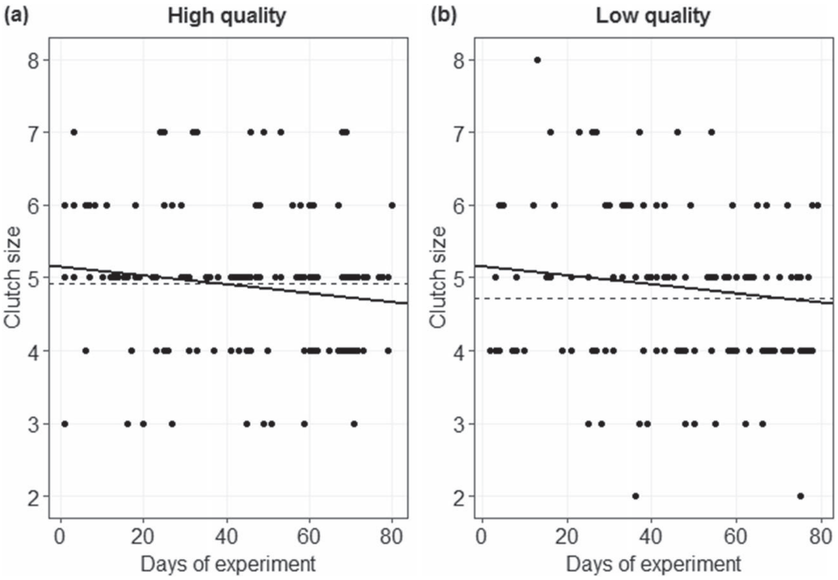

**Fig. 1** Number of eggs per clutch in **a** HQ and **b** LQ treatment areas laid at each day of the experiment, respectively. The dashed lines represent mean clutch sizes (calculated from raw data), the solid line predicts clutch sizes at each day of the experiment (based on the output of the minimal model, see Table 1, model 2)

(Table 2, model 3). When analyzing the specific effect of prior experience on number of eggs in the second brood, neither clutch size nor treatment of the first brood had a significant effect on number of eggs laid in the second brood (Table 2, model 4).

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

## Discussion

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

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

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

While it is important to point out these ecological differences, the results of our study are still in line with theoretical predictions (Feldman et al. 1996; Boulinier and Danchin

1997; Doligez et al. 2003). It is still plausible that the absence of social information use in our study might be due to the low predictability of the environment zebra finches live in. It is perhaps disadvantageous to take cues from others when conditions and hence the outcome is inconsistent even on a relatively short intra-annual timescale. Additionally, it is also possible that a mix of different sources of information is used and social information was over-ridden by personal information. Another study has demonstrated the opposite effect, with an experiment in which social cues outweighed personal habitat preferences of a migrant passerine usually breeding in very stable hardwood forests (Betts et al. 2008). In the context of defense against brood parasites, combining personal and social information has been identified as a successful strategy (Thorogood and Davies 2016). In our study, it appears that the social information was, if maybe not completely ignored, at least outweighed by other factors. The mechanisms are diverse and it becomes increasingly obvious that the specific ecological circumstances need to be regarded as a significant factor in the study of information use.

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

Our experiment did not include a treatment with average brood sizes as a control and thus did not test the response to the average brood size. Our manipulation, however, was within the range of natural clutch and brood sizes in this species and therefore was unlikely to have been perceived as unnatural. Even if zebra finches had a preference for an average brood size, it is reasonable to expect that offered a binary choice (smaller or larger brood), they would have been able to make a decision, given the likely fitness consequences of producing either too many or too few offspring in the prevailing conditions (as signaled by conspecifics, if this did serve as a source of information).

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

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

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

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

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

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## Compliance with ethical standards

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

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

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