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# Wild zebra finches choose neighbours for synchronized breeding

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Organisms should aim to time their reproduction to match the optimal ecological conditions and thus maximise their fitness. However, social cues have been identified as determinants of reproductive decisions and might also be involved in coordinating the timing of reproduction. Breeding synchronously with other individuals can bring several advantages, including a reduced individual predation risk and an increased opportunity for social foraging. The behavioural mechanisms underlying reproductive synchrony are versatile and not extremely well understood, particularly in species inhabiting unpredictable environments. In contrast to highly seasonal environments, more variable and unpredictable environments can support periods of extended breeding with lower levels of synchronous breeding overall, but opportunities for individuals to breed synchronously at a finer temporal and spatial scale. Zebra finches (*Taeniopygia guttata*) are a highly social species, naturally inhabiting the ecologically unpredictable arid zone of Australia. In the wild, the reproduction at a broad population level is not highly synchronised and at any time, during a period of breeding activity, reproductive attempts can be found at all different stages. However, previous work has suggested that at a finer spatial scale neighbours tend to breed at approximately the same time. Through the experimentally placement of nest boxes, we tested whether wild zebra finches preferentially seek to settle and initiate a breeding attempt adjacent to conspecifics at an early stage of breeding (nest building), as opposed to others at later stages of breeding and with whom the opportunity to breed synchronously was reduced, or absent. Pairs were more likely to initiate egg laying in nest boxes close to conspecifics at an early stage of breeding, suggesting that they do try to maximise the level of synchronicity with neighbours. Our results indicate the importance of social effects on both the phenology and spatial distribution of breeding.

**Keywords**

colonial breeding; nest prospecting; nest synchronization; reproductive timing; social information; *Taeniopygia guttata;* unpredictable conditions

Individuals will optimize their reproductive output by timing their reproduction to match the best ecological conditions, resulting in high levels of reproductive synchrony across many plant (e.g. Franklin, 2004; Satake & Iwasa, 2000) and animal populations (e.g. Hodge, Bell, & Cant, 2011; Koenig & Liebhold, 2005; Youngflesh et al., 2018). In temperate and highly seasonal climates, breeding seasons can be restricted to relatively short periods and are often driven by a variety of abiotic factors such as temperature, photoperiod, humidity (e.g. Ims, 1990a) as well as food availability (e.g. Both, 2010; Seress et al., 2018). However, even in habitats with less pronounced seasonality, such as the tropics, reproduction is temporally much more clustered than would be expected by chance (e.g. Helm, Piersma, & van der Jeugd, 2006; Ims, 1990a). Following this observation, several other ecological (e.g. predation, pollination and seed dispersal) and sociobiological (e.g. mating system, density and communal breeding) factors have been identified, which might contribute to the timing of reproduction and promote synchrony across individuals within a population (or asynchrony; reviewed in Ims, 1990a). For example, an experimental playback of colony sounds was demonstrated to stimulate breeding activity and *to* positively affect clutch size in the zebra finch (*Taeniopygia guttata*; Waas, Colgan, & Boag, 2005). Thus, in colonially breeding species in particular, breeding synchronization might be strongly influenced by social information (Helm et al., 2006).

Many potential advantages of reproductive synchrony have been postulated, entailing fitness benefits (e.g. Di Maggio, Campobello, & Sarà, 2013). The ‘predator swamping hypothesis’ (Fraser Darling, 1938), for example, suggests that synchronized reproduction of colonial breeders can increase offspring survival rate by saturating predators with high numbers of potential prey emerging at the same time (e.g. Ims, 1990b; O'Donoghue & Boutin, 1995; Sweeney & Vannote, 1982). Similar to the predator swamping hypothesis, but a more general advantage of group living can be the ‘encounter’ and the ‘dilution’ effect, which describe the decreased likelihood of an individual being detected or attacked by predators with increasing group size (e.g. Bellinato & Bogliani, 1995; Inman & Krebs, 1987). Synchronous breeding will likely lead to fledglings emerging from different nests in a short time window, which proportionally lowers the individual predation risk. Another potential anti-predation benefit is that parents on a similar breeding schedule will also spend time around the nest at around the same time. In colonial species this means that pairs breeding in close proximity to one another may effectively act as sentinels for one another, potentially reducing the likelihood of predation on the nest by predators approaching undetected (e.g. Mainwaring & Griffith, 2013).

An alternative set of benefits are those derived by social interactions between either offspring or adults from nests in close proximity. Fledglings may have an increased opportunity to join social foraging groups and to collectively discover and visit food sources (e.g. Emlen & Demong, 1975). Parents are likely to have the same physiological requirements as their synchronously breeding neighbours and to be on a similar behavioural schedule (i.e. foraging for their offspring) and thus will share a similar feeding and offspring provisioning schedule to their neighbours, which can increase their foraging efficiency (e.g. Ims, 1990a). However, a counter argument is that highly synchronised breeding in a population might also lead to increased food competition amongst the parents foraging for their offspring (e.g. Hodge et al., 2011; Ims, 1990a). Another aspect of behavioural ecology that has been linked to reproductive synchrony, is the ability of individuals to assess potential partners and engage in extra-pair behaviour

(Spottiswoode & Møller, 2004), and again this could be viewed as either a positive or negative thing, from an individual perspective.

Zebra finches are small, granivorous passerines living in the arid zone of Australia. Adapted to an opportunistic breeding strategy, the reproductive physiology of the zebra finch is in a permanently activated state which allows breeding at any time of the year (Perfito, Zann, Bentley, & Hau, 2007), and they can have multiple successive broods within an extended period of reproduction (Zann, 1996). Previous observational work has provided support for the idea that a pair starting a new reproductive attempt will preferentially breed near conspecifics (i.e. conspecific attraction) (Mariette & Griffith, 2012a). Wild zebra finches live in social colonies and it is highly likely that the coordination of reproductive timing is underpinned by social information transfer across the population. In the wild, zebra finches frequently prospect at conspecific nests (Brandl, Griffith, & Schuett, 2018; Mariette & Griffith, 2012a), which would provide a good opportunity to gather cues for reproductive coordination. Though we can assume that this prospecting is driven by the potential to gather social information, the experimental evidence so far suggests that it does not play a role in determining either the nest site choice (i.e. the choice between areas with breeders of high or low reproductive output) or the level of investment in a reproductive attempt (Brandl et al., 2018). This habitat selection theory is described as the main benefit of nest prospecting in temperate breeding birds in the northern hemisphere (e.g. Doligez, Pärt, & Danchin, 2004; Pärt, Arlt, Doligez, Low, & Qvarnström, 2011). The unpredictable ecology of the arid zone (Morton et al., 2011), however, might make social information an unreliable predictor for habitat quality (e.g. Boulinier & Danchin, 1997; Erwin, Nichols, Eyler, Stotts, & Truitt, 1998). Furthermore, in the Australian arid zone, reproductive activity across many species typically lasts across a period of time that is more than twice as long as in species breeding in the temperate zone of the northern hemisphere (Duursma, Gallagher, & Griffith, 2017). As a result of these characteristics of reproductive ecology in the unpredictable arid zone, nest prospecting might be focused on gathering social information at a more immediate temporal scale, and perhaps is primarily used to coordinate reproductive timing between pairs in close proximity. If this is true, it opens up a new perspective on the benefits and determinants of nest prospecting in birds and will expand the scope of the work to date, that has largely been focused on studies of seasonal breeders in the northern hemisphere temperate zone (e.g. Aparicio, Bonal, & Muñoz, 2007; Boulinier, McCoy, Yoccoz, Gasparini, & Tveraa, 2008; Doligez, Danchin, & Clobert, 2002).

We conducted an experimental field study testing the hypothesis that wild zebra finches preferentially choose to settle and breed next to neighbours who provide the opportunity for a synchronized reproductive attempt. With an experimental approach, we offered zebra finches vacant nest boxes adjacent to conspecifics which were at either an early (nest building), mid (egg incubation), or late stage (chick rearing) of the reproductive cycle. If zebra finches try to synchronize breeding with close neighbours, we expect them to be more likely to choose to settle and initiate breeding attempts next to zebra finch nests at the nest building stage than those at later breeding stages (eggs and chicks). This strategy would entail prioritizing the value of being spatially and temporally connected with another simultaneous breeding attempt over the potential value of nesting near a successful conspecific (given that the presence of chicks in a nest provides a signal of success to that point). Thus, the aim of our study was to provide new insight into the importance of reproductive synchrony in an opportunistic breeder.

## METHODS

### *Study site and study species*

The experiment was conducted 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 December of 2016. The study site covers about 1.5 x 2 km and has an artificial dam in the centre, holding a relatively stable source of water for drinking. We provided 180 wooden nest boxes (12/18 cm front/back height, 9.3 cm width, 14 cm depth; entry hole 3 cm diameter), attached to metal stakes (further details: Griffith, Pryke, & Mariette, 2008), each located next to a small tree or large bush to provide shade and protection. Nest boxes were arranged in six clusters (mean distance to nearest neighbouring cluster = 413.6 ± SD 142.0 m) of 30 nest boxes each (mean distance to nearest neighbouring nest box within clusters = 10.4 ± SD 4.8 m; Fig. 1a) and are readily accepted for breeding (Griffith et al., 2008). Only five of the nest box clusters were used for this experiment, as one cluster had no active nests throughout the study period.

Zebra finches are socially (Zann, 1996) and genetically (Griffith, Holleley, Mariette, Pryke, & Svedin, 2010) monogamous and exhibit biparental brood care (Mariette & Griffith, 2012b). On a larger scale, the distribution of food and water in the landscape determines their nest site choice (max. observed nest distance from water 25 km; Zann, 1996), but the distribution of resources does not appear to have an effect on a small scale (in areas 1-2 km wide; Mariette & Griffith, 2012a). While zebra finches form aggregations whilst foraging and visiting water, they mostly move around in small groups of 3-10 individuals, mostly made up from mixed-sex pairs, with the pair being the most important social unit (McCowan, Mariette, & Griffith, 2015).

***Experimental procedure***

For each trial of the experiment, three existing, occupied nest boxes at three different stages were selected as stimulus boxes. The nests in the stimulus boxes were each at one of the following stages: nest building (i.e. 5-50% nest material, no eggs at start of trial), egg incubation (i.e. clutch completed and being incubated), and chick rearing (i.e. post-hatching). Each stimulus box had one empty nest box, the experimental box, erected in close proximity (2 – 4 m; Fig. 1a-c). The empty experimental boxes (which were identical in construction to the stimulus ones) were matched with the stimulus boxes in height and orientation, and were also attached to the same kind of metal post. The complete setup for each one trial (consisting of three stimulus boxes each in a different stage and each matched with one experimental box) was located within one of the five nest box clusters (7.0 + 3.2 SD trials per cluster; mean distance between stimulus boxes within trials = 80.8 ± SD 41.9 m). Our complete blocked design with stimulus nests of all stages co-occurring in the same area, at the same time, ensured that variation of environmental conditions (e.g. food availability, temperature, humidity) within trials was very low.

A total of 35 trials (i.e. 105 stimulus boxes and 105 experimental boxes in total; three each per trial) was conducted, each lasting for five days. During the five days of a trial, the experimental boxes were checked daily for the initiation of nest building (indicated by nest material in the box) or egg laying, which was each encoded as a binary variable (yes/no). The number of days it took for nest building and egg laying to begin was also recorded for each experimental nest box. After five days, the experimental nest boxes were removed. The time period of five days was chosen as it was just long enough to allow for nest building and egg laying to be initiated, but not longer than necessary, for ethical and logistical reasons.

The work was approved by the Macquarie University Animal Ethics Committee (Animal Research Authority 2015/017) and the Australian Bird and Bat Banding Scheme and followed ASAB/ABS Guidelines for the treatment of animals in research.

***Data analysis***

We fitted two generalized linear mixed effect models (GLMMs) with binomial error structure to assess the effect of the treatment (i.e. nest stage of stimulus box at the initiation of trial; three levels: nest building, egg incubation, chick rearing) on the probability of zebra finches initiating nest building and egg laying during a trial, respectively, in the corresponding experimental boxes. Whether nest building or egg laying was initiated was evaluated once per trial, i.e. as the final outcome of a five-day trial. We used two additional GLMMs with Poisson error structure to test the effect of the treatment on the latency to initiate nest building and egg laying, this time only using the subset of the data where nest building and egg laying, respectively, had been initiated in the experimental nest boxes during the trials. All four models included treatment (nest building, egg incubation, chick rearing) and nest continuation of the stimulus nest as fixed terms. The variable nest continuation was introduced to account for the fact that the nests used as stimuli appeared to vary in the success of their progression (see below). All models included nest box (ID of stimulus box), cluster and trial as random terms.

In order to control for variation in the progression of stimulus nests, the binomial variable 'nest continuation' (yes/no; 'no' meaning that nests were presumably abandoned) was included into the models. In 20 of the 35 stimulus boxes at the nest building stage, egg laying commenced within the five-day duration of the trials. The other 15 nests remained at the nest building stage for five days without any apparent progress, in which case we suspected that the nesting attempt was aborted at some point. Further, in four stimulus nests of the egg incubation stage eggs appeared cold at the end of the trial and were presumably abandoned during the trial. Stimulus nests of the chick rearing treatment group were always coded as 'yes' for nest progress. In five stimulus nests of the chick rearing treatment the chicks died or were predated before the end of a trial, upon which this treatment was aborted and the data completely removed from the data set (N = 5 stimulus nests), leaving a total of 100 stimulus nests (35 trials with 3 stimulus nest boxes each, minus 5 failed nests at chick stage). The reason for not including the failed nests of the chick rearing treatment was that dead or missing chicks clearly present either no cue or a negative cue. In the case of stimulus nests being abandoned at the nest building or egg incubation stage it is not clear when exactly they were not active anymore and the content of the box might still serve as a cue. Thus, these nests were included in the analysis, but the fact that their stimulus function might have been altered was acknowledged by including the nest continuation variable.

Throughout the experiment, 73 unique nest boxes were used to serve as the 100 stimulus nests, i.e. 21 nest boxes were used as stimulus boxes twice, and 3 nest boxes were used thrice (in consecutive trials). The boxes which were used as stimulus more than once were used for different treatments (i.e. at different reproductive stages) in 15 cases. Eight of the reused boxes were used again for the same treatment – in half of these cases they were reused within the same breeding attempt (e.g. during the 14 days of egg incubation), in the other half they were reused for the same treatment but with a new nest (i.e. at least three weeks later). We controlled for the repeated measures by including the nest box ID as a random term. All statistical tests were repeated after excluding the eight nest boxes which were used twice for the same stimulus (i.e. the second trial of each box was removed from the data), and the obtained results were qualitatively the same (i.e. regarding statistical significance).

We obtained minimal adequate models by stepwise reducing full models, i.e. the least significant term, as determined by likelihood ratio test between models, was removed, one after another (Crawley 2007). Only terms that did not significantly increase the explanatory power of a model, when compared to the more complex model, were removed (Crawley 2007). We conservatively did not reduce random effects. For significant terms with more than two levels Tukey's pairwise comparison was performed with fdr-adjustment for the reported p-values (Benjamini & Hochberg, 1995). All statistical analyses were conducted in the R environment (R Core Team 2014). For GLMMs we used the package lme4 (Bates, Maechler, Bolker, & Walker, 2014). Multiple pairwise comparison was performed with the package multcomp (Hothorn, Bretz, & Westfall, 2008). The boxplots were created using estimated model predictions based on 1,000 simulations for each observation using the R package merTools (Knowles & Frederick, 2016). Ggplot2 (Wickham, 2010), ggsignif (Ahlmann-Eltze, 2017) and cowplot (Wilke, 2017) were used for visualization. Statistics are presented as mean ± standard deviation throughout.

## RESULTS

Nest building was initiated in 47 out of 100 experimental nest boxes (19 in the nest building, 14 in the egg incubation and 14 in the chick rearing treatment). Egg laying commenced in 26 of the experimental boxes (13 in nest building, 6 in egg incubation and 7 in the chick rearing treatment). Neither treatment (i.e. stage of the stimulus box) nor nest continuation in the stimulus box had a significant effect on the likelihood of nest building being initiated in an experimental nest box (Table 1, Fig. 2a).

The probability of egg laying in an experimental box, however, was significantly affected by both the treatment and by whether a stimulus nest was continued throughout the trial (Table 1, Fig. 2b). The probability of egg laying was highest in boxes adjacent to the nest building stimulus and lowest close to boxes with the egg incubation stimulus. Post-hoc testing revealed that the probability of egg laying was significantly different between nest building and both egg incubation ($z = -2.493$; $p = 0.038$; $N_{trials} = 35$) and chick rearing treatment ($z = -2.164$; $p = 0.046$; $N_{trials} = 30$). Further, if the nest in the stimulus nest box continued successfully, there was a higher likelihood of egg laying in the corresponding experimental boxes (Table 1, Fig. 2b). In the experimental boxes where nest building was initiated, the mean latency to nest initiation was 2.89 ± 0.99 days; in the boxes where eggs were laid, this commenced on average after 3.85 ± 0.99 days. The number of days until the initiation of nest building and egg laying was not significantly different between treatments or affected by whether the nest in the stimulus box was continued (Table 2).

## DISCUSSION

In a field experiment on wild zebra finches, we found that breeding pairs were significantly more likely to lay eggs in a nest box adjacent to a box that was at a very early stage (i.e. nest building), compared to those neighbouring boxes at later stages (i.e. egg incubation or chick rearing). This finding represents strong evidence that zebra finches try to synchronize their nesting schedule with that of conspecifics. The fact that individuals were not more likely to nest near individuals that had already achieved a level of reproductive success (by the ongoing presence of incubated eggs, or nestlings), suggests that in this species and context, the zebra finches were more motivated by the presence of simultaneously active conspecifics, than by the information on successful breeding by temporally slightly more advanced breeders. The association with synchronized neighbours can have far-reaching consequences, as the traits of interacting (conspecific) neighbours can also contribute to individual fitness (e.g. Campobello, Hare, & Sarà, 2015; Formica et al., 2011; McDonald, Farine, Foster, & Biernaskie, 2017).

We found no significant difference in the likelihood of initiating nest building in response to treatments. This could mean that nest building activity alone is not a good indicator for actual settlement, as not all of these nests were continued. Nest building itself is not very costly, thus it might pay off for animals to reconsider their nest site choice before the investment in egg laying is made. Another explanation would be that nest building and egg laying was initiated earlier close to nest building stimulus boxes and we thus did not find eggs within the first five days close to the other stimulus boxes. However, we did not find a difference in the latency of nest building and egg laying between the three treatment groups. Further, the finding that successful nest continuation in the stimulus boxes increased the probability of settling next to early-stage neighbours provides additional support for our hypothesis that the activity of the neighbours is the determining factor.

Considerable benefits arising from synchronized reproduction can be expected, particularly in the context of predation avoidance and social foraging (Evans, Votier, & Dall, 2016; Møller, 1987). Regarding the predation risk, we presume that the risk of attacks from the air by raptors on adults and fledglings outside of the nest could be strongly reduced through breeding synchrony (e.g. Westneat, 1992). In this population, previous work has found that members of a breeding pair act as sentinels for one another during incubation, with the bird inside the enclosed nest departing earlier when its partner is present outside as an investigator moves towards the nest (Mainwaring & Griffith, 2013). This sentinel behaviour, presumably achieved through the presence or absence of an acoustic signal, may perhaps be equally likely amongst close neighbours, and could potentially significantly reduce the rate of adult mortality through predation of an adult caught inside the enclosed nest by predators such as snakes, cats, and birds that might otherwise approach a nest undetected. Having neighbours at a similar nest stage, i.e. with similar nest attendance rates, might increase the chances of early predator detection. A model developed for black-headed gulls (*Larus ridibundus*), another species with partial reproductive synchrony, suggests that this behaviour might represent a form of cooperation for predator avoidance (Wissel & Brandl, 1988). Individuals at different stages might contribute to predator avoidance in different ways, for example, pairs which are currently incubating could benefit from stronger vigilance of colony members currently feeding their offspring (Wissel & Brandl, 1988). The latter hypothesis does not explain the close spatial proximity of synchronized breeders but could be a reason why partial synchrony is favoured over fully synchronized reproduction across the colony.

The other main advantage that may explain our result is the increased potential for social foraging (e.g. Brown, 1988). Neighbours in close proximity will have the same physiological requirements and a parental care schedule as they move through the reproductive cycle. Foraging together means that social information on the location of food sources can be exploited and, even in times of scarcity of resources, the probability that patches of yet unexploited seed may be discovered is increased in the flock (Zann, 1996). Further, the individual predation risk will also be reduced during the foraging activity through the dilution and encounter effect (e.g. Bellinato & Bogliani, 1995; Inman & Krebs, 1987).

The advantage of temporal synchronization with a pair that is also just initiating its reproductive attempt means, on one hand, that the association between the neighbouring nests will last for a longer period (till fledging of both nests). Finally, if the chicks fledge from the nests simultaneously, they can also benefit from the same advantages which increase the fitness of both parents and offspring. For example, we have observed aggregations of fledglings in a single bush, at a similar age, in higher numbers than one nest could have produced, which strongly suggests that the species forms creches, with multiple parents sequestering their offspring in a single group. Again, this would be facilitated if multiple broods fledged in the same location at a similar time.

An alternative explanation for the higher breeding initiation close to early stage nests could be that birds are actually deterred by breeders at late stages. However, the causation for such a phenomenon is not very obvious, at least in zebra finches. They are neither territorial nor aggressive, have extremely low rates of extra pair fertilizations and use easily sharable resources, thus, competition from advanced conspecifics is expected to be very low.

Within a population of wild zebra finches, the pattern of reproduction overall appears to be rather staggered than highly synchronized and nest initiation in a population will regularly extend over periods of six to eight weeks, but the duration of breeding bouts can strongly vary within and between years (Griffith et al., 2008; Mariette & Griffith, 2012a). From this general pattern of reproductive timing in zebra finches, it appears that breeding synchrony within a population is low when compared to some other, particularly temperate species, with a much more fixed breeding schedule, e.g. in sand martins (*Riparia riparia*; Emlen & Demong, 1975) or lesser snow geese (*Anser caerulescens caerulescens*; Findlay & Cooke, 1982). However, theory suggests, that breeding synchrony in unpredictable habitats should be high, because of potentially short time windows for rearing offspring before conditions change again (Findlay & Cooke, 1982). While several studies reported a tendency for breeding asynchrony in tropical species (e.g. Moore, Bonier, & Wingfield, 2005; Stutchbury & Morton, 1995), no field studies from arid zones exist, to our knowledge.

A previous observational study had already suggested that zebra finches are more likely to initiate breeding in close proximity to already ongoing conspecific nests than would be expected by chance (Mariette & Griffith, 2012a), but the exact mechanism through which this was achieved was unclear. Building on the findings of our experiment, we can now conclude that stage of neighbouring nests is an essential aspect in the synchronization. It could be argued, that nest synchronization might have occurred if nesting sites are scarce and hence, the new boxes we put up during the experiment were simply attractive nesting locations. However, the maximum number of occupied nest boxes at our study site was 115 out of 180 at any one point during the experiment; hence, there were always other, unoccupied nest boxes available. Additionally, this could not explain the significant difference that we found between treatments. The nest box locations of the egg incubation and chick rearing stimulus boxes were unlikely to have been inherently worse than the nest building ones, as all of the stimulus boxes had equally been chosen by zebra finches to breed in. Further, the stimulus boxes of one trial were always located within the same nest box cluster, thus, even if environmental factors changed over time the spatial proximity would have presumably affected all nests within one trial equally.

As breeding synchrony requires social coordination, we believe that it is highly likely that social cues are involved in the behavioural process. Wild zebra finches often make prospecting visits to the nests of conspecifics (Mariette & Griffith, 2012a). So far, both the unpredictable conditions of the habitat (Boulinier & Danchin, 1997; Erwin et al., 1998) and the experimental evidence suggest that social information is not used for nest site choice in zebra finches (Brandl et al., 2018), which is a common strategy of breeders in temperate habitats (e.g. Boulinier & Danchin, 1997; Brown, Brown, & Danchin, 2000; Doligez et al., 2002). Alternative explanations for prospecting behaviour in seasonal habitats have often focused on aspects of sexual selection, e.g. in the case of nest decorations (García-Navas, Valera, & Griggio, 2015) or the role of territoriality and extrapair matings (Firth, Verhelst, Crates, Garroway, & Sheldon, 2018). In the case of the zebra finch, as a model of a monogamous, opportunistic breeder, we propose that it is possible that prospecting visits could be used to gather information on the reproductive timing of conspecifics. While further experimental work is needed to investigate this link, it could be an important step in the understanding of information use in fluctuating habitats.

Our study demonstrates that nest synchronization is actively initiated in an opportunistic breeder of the arid zone. This study thus contributes to the limited understanding of the breeding ecology of unpredictable habitats. We propose that the reproductive coordination might be linked to a different strategy of information use in fluctuating environments, in contrast to the more seasonal and predictable environments in which most previous work has been conducted. The value of social information in unpredictable habitats is worthy of further exploration, and will in addition provide useful context to work on the zebra finch, which is the focus of important work in this area in the laboratory (e.g. Farine, Spencer, & Boogert, 2015). Further, we hope to fill some gaps in the understanding of the breeding ecology of a bird that is one of the most frequently studied species in the laboratory but has received so little attention in the wild.

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**Table 1.** Probability of initiating nest building or egg laying**.**

| Response variable | Fixed effects | *N* | Coefficients | $X^2$ | DF | $R^2$ | p |
|---|---|---|---|---|---|---|---|
| nest building | treatment | 100 | | 1.68 | 2 | 0.136 | 0.431 |
| (yes/no) | *[nest building]* (intercept) | | (0.160) | | | | |
| | *[eggs]* | | (-0.694) | | | | |
| | *[chicks]* | | (-0.420) | | | | |
| | nest continuation [yes] | | (0.092) | 0.02 | 1 | | 0.883 |
| egg laying | treatment | 100 | | 8.24 | 2 | 0.308 | **0.016** |
| (yes/no) | *[nest building]* (intercept) | | -1.469 | | | | |
| | *[eggs]* | | -1.838 | | | | |
| | *[chicks]* | | -1.596 | | | | |
| | nest continuation [yes] | | 1.773 | 5.25 | 1 | | **0.022** |

GLMMs with binomial error structure were used to assess the effect of treatment (nest building, egg laying or chick rearing in neighbouring stimulus box) on initiation of nest building (yes/no) or egg laying (yes/no), respectively. Nest continuation (yes/no) refers to the stimulus nest box, i.e. whether nest building or egg laying was continued in the stimulus nest throughout the whole trial. N represents the total number of valid observations during 35 trials (consisting of three treatments; exception *N* = 5 trials where chick rearing treatment had to be removed because the chicks disappeared). Coefficients for a factor level (specified in square brackets) give the difference to the reference level (intercept). Significant p-values are highlighted in bold. Coefficients are not back-transformed from model outputs. Values in brackets represent coefficients in full models. Trial, cluster, and nest box ID (of the stimulus boxes) were included as random terms.

**Table 2.** Latency to initiate nest building or egg laying.

| **Response variable** | **Fixed effects** | ***N*** | **Coefficients** | **$X^2$** | **DF** | **$R^2$** | **p** |
|---|---|---|---|---|---|---|---|
| days until nest building | treatment | 47 | | 0.84 | 2 | 0.022 | 0.656 |
| | *[nest building]* (intercept) | | 1.223 | | | | |
| | *[eggs]* | | 0.080 | | | | |
| | *[chicks]* | | 0.216 | | | | |
| | nest continuation [*yes*] | | -0.194 | 0.18 | 1 | | 0.668 |
| days until egg laying | treatment | 26 | | 0.52 | 2 | 0.018 | 0.773 |
| | *[nest building]* (intercept) | | 0.916 | | | | |
| | *[eggs]* | | -0.182 | | | | |
| | *[chicks]* | | 0.047 | | | | |
| | nest continuation [*yes*] | | 0.182 | 0.21 | 1 | | 0.650 |

Summaries of GLMMs with Poisson error structure assessing the effect of treatment (nest building, egg laying or chick rearing in neighbouring stimulus box), and nest continuation (yes/no) in the stimulus box on latency to initiate nest building or egg laying, respectively. Coefficients for a factor level give the difference to the reference level (intercept). The values of the coefficients are taken from the full models and were not back-transformed from model outputs. Trial, cluster, and nest box ID (of the stimulus boxes) were included as random terms.

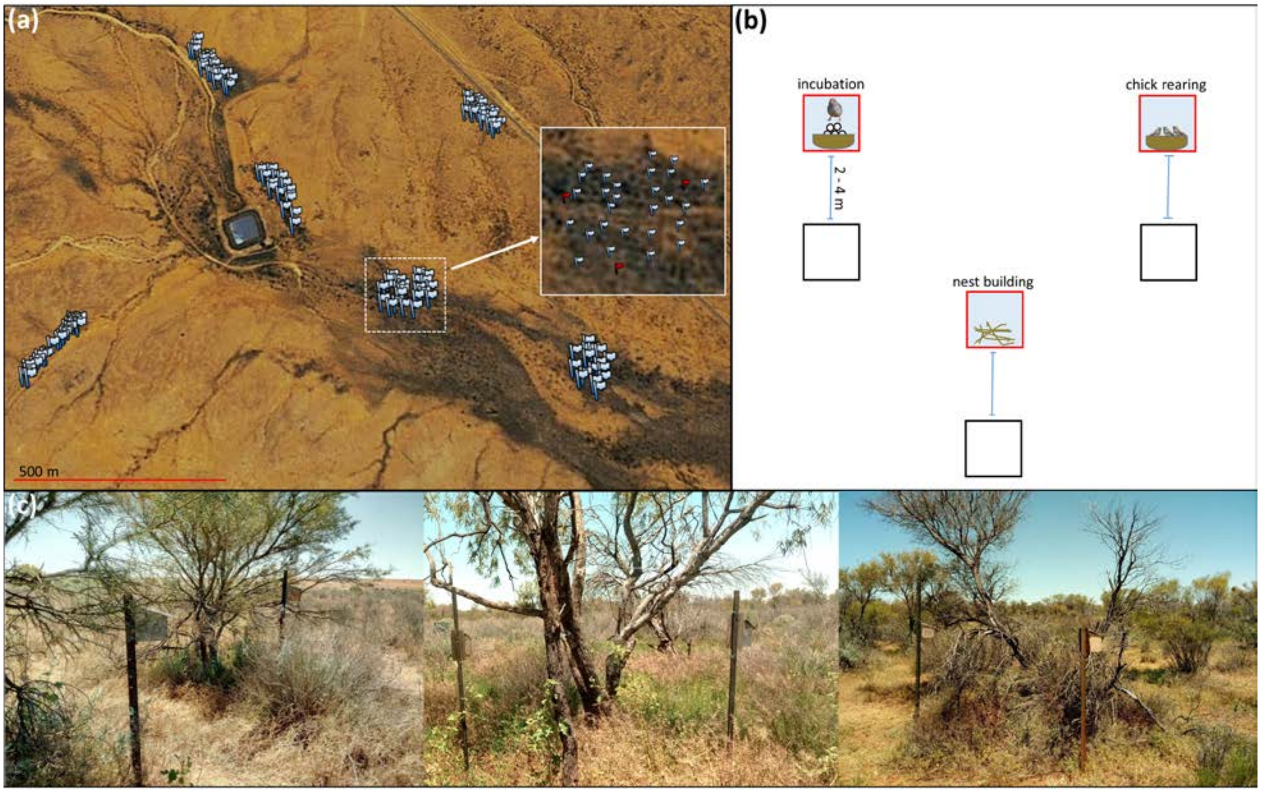


**Figure 1.** Map of the study site (a) showing the six cluster of nest boxes (light blue flags). The white square highlights a zoomed-in view of one of the nest box cluster (dashed white line). In this magnified view, the red flags exemplarily indicate the three nest boxes which served as stimulus boxes in one trial. The stimulus boxes (red squares) (b) were each at one of the following nest stages: nest building, egg laying, or chick rearing, respectively. Each stimulus box was paired with one newly added experimental nest box (black squares). The experimental nest boxes were set up to match the stimulus nest boxes regarding height, orientation and vegetation cover (c). The area depicted in the map is 1.87 x 1.36 km. Copyright of Google Earth image: Google, CNES/Spot Image 2016. Fowlers Gap, NSW 2880, Australia. 30°57'11.65"S, 141°46'7.77"E, Eye alt 2.44 km.

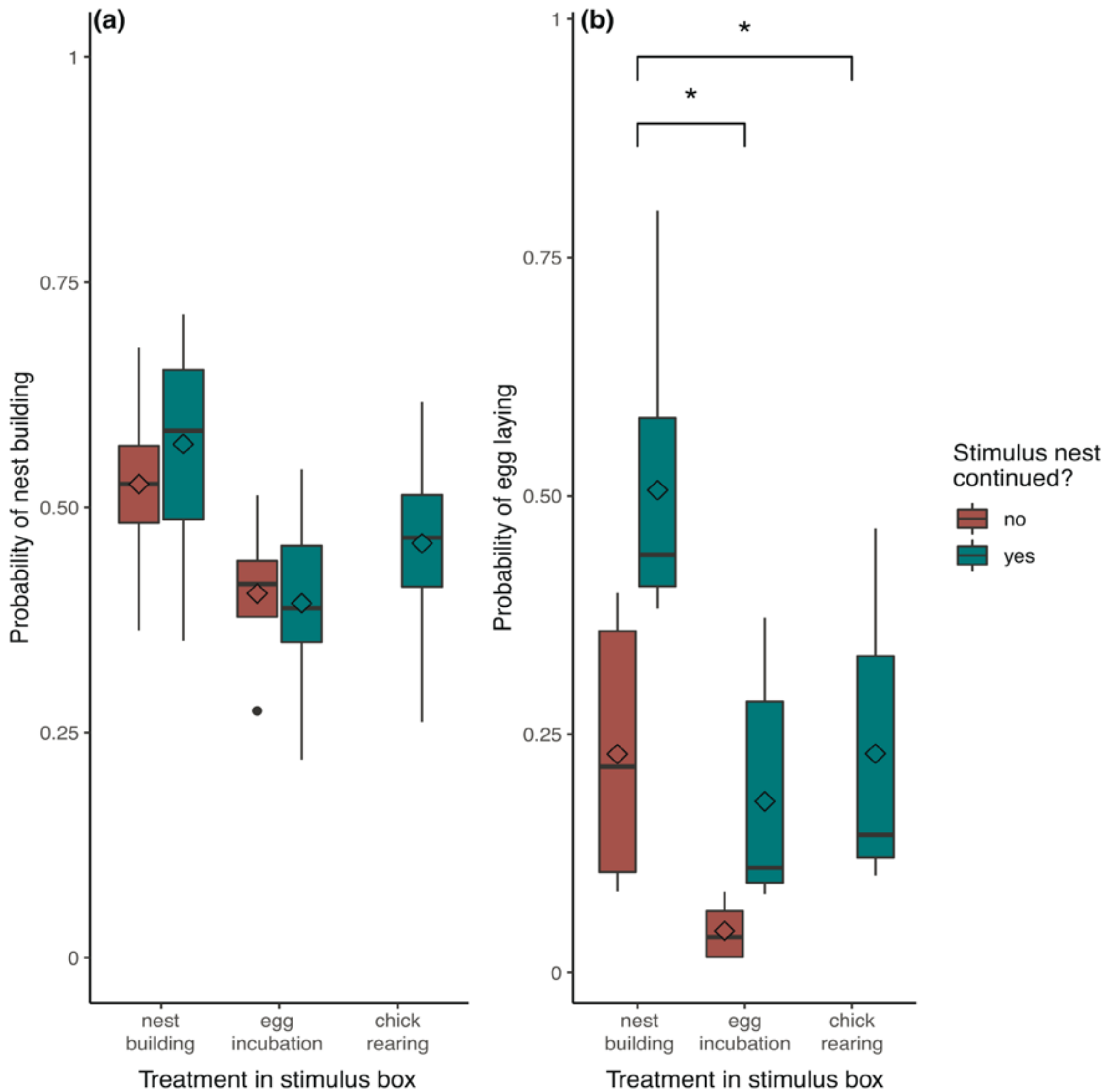


**Figure 2.** Probabilities of nest building (a) or egg laying (b) being initiated in an experimental nest box adjacent to a stimulus nest box of one of three treatments: nest building (left), egg incubation (middle) or chick rearing (right), respectively. Teal coloured box plots represent quartiles of trials where the stimulus nest continued to progress during trials; dark red box plots show quartiles for trials where nests in the stimulus boxes were not continued (i.e. they were abandoned), in the treatments nest building and egg incubation. Horizontal lines in box plots indicate medians, diamonds (◊) indicate means and the edges of the boxes represent the first and the third

quartiles. Whiskers indicate the 1.5 × interquartile range; data outside of the whiskers is represented as a black dot. The boxplots were created using estimated model predictions based on 1,000 simulations for each observation. Significant differences between treatments are marked with asterisks; one asterisk (*) indicating a significance level of $p \leq 0.05$.