Constant companions: Wild zebra finch pairs display extreme spatial cohesion

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Abstract

Many animals maintain long-term monogamous partnerships, but the extent to which partners interact varies substantially and has implications for the scope of cooperation between pair members. Zebra finches are monogamously paired for life, raising questions as to if and how they maintain pair cohesion in the absence of having territories and in the absence of long-range signals. While zebra finches are the best studied songbird in captivity, their social and spatial behaviour in the wild is poorly understood. Determining pair cohesion in songbirds to date has almost exclusively been studied only at specific locations, such as nesting or feeding sites where bird presence can be logged incidentally, without quantifying broader movements. Here, we used automated tracking to continuously monitor the movements of radio-tagged zebra finch pairs during a period with breeding activity. We reveal extremely high pair cohesion with pairs using nearly identical home ranges and maintaining close spatial proximity throughout the day. This characterisation of extremely high spatio-temporal coordination of zebra finch pairs provides novel and important insights into the operation and benefits of monogamous relationships in highly mobile taxa, such as birds.

Keywords: monogamy, coordination, pair bond, automated radio tracking

I. Introduction

Monogamous relationships in animals have been characterised by surprisingly long associations between males and females that can last over decades in birds (e.g., [1,2]) or as long as 27 years in the Australian sleepy lizard (*rugosa*) [3]. It has been well established that the longevity of a partnership [4,5] and/or coordination, or compatibility of partners [6] will positively affect measures of reproductive success at the pair level. Whilst such findings have demonstrated remarkable levels of social cohesion over often quite long periods of time, they have not been able to investigate the operation of partnerships at a fine scale, either temporally, or spatially. Some progress, however, has been made in this area by using automated loggers to track arrival time of partners incidentally at landmarks such as nests or feeding stations [7–9].

The zebra finch is a widely studied bird in captivity, with several studies focusing on the importance of the strength of the pair bond [5,6,10]. Yet while the zebra finch is the best-studied songbird in captivity, the avian supermodel, little is known about their natural spatial and social organization [11]. Moreover, many characteristics of zebra finches (*Taeniopygia guttata*) living in the wild contrast starkly with how birds are kept in the laboratory. In the wild, zebra finches are nomadic, moving throughout semi-arid regions in search of grass seed and water [12]. Zebra finches are non-territorial, breed in loose colonies and synchronize their timing of breeding with their neighbours [13]. They forage in small flocks and use communal, social areas where they gather temporarily in larger groups [12,14,15]. Though both males and females display individually recognizable contact calls [16], these are short range signals (i.e., the loudest call type, the distance call, is only detectable within about 14 m) and so would not effectively serve to reunite partners once separated in an open landscape [17]. As such, given that natural conditions differ importantly from those experienced by individuals in the lab, it is unclear whether the same behavioural mechanisms for maintaining partnerships are observed in the wild.

Here, we use a novel solar-powered automated radio tracking system to monitor continuously the movement patterns of wild zebra finch pairs. In doing so, our objective was to assess whether spatial cohesion functions as an important mechanism in maintaining continuous partnerships. We examined space use and movement patterns between zebra finch pairs and neighbouring birds. We predicted that pairs would display higher home range overlap compared to neighbours. Additionally, we predicted that pairs would remain in close proximity throughout the home range.

II. Methods

Research was approved by the Macquarie University Animal Ethics Committee and covered by a New South Wales DPIE Scientific License SL100378, Ethics ARA 2018/027, and ABBBS Banding Permit.

a) Data collection

We caught adult zebra finches in September 2022 by mist net at Gap Hills, Fowlers Gap Research Station, New South Wales, (30°56'58"S, 141°46'02"E). During this period, zebra finches were actively breeding in nest boxes as well as in natural nests. Mist netting was conducted at three sites each with 30 nest boxes within the larger Gap Hills breeding colony. A female and a male caught simultaneously were considered a pair based on previous observations that breeding partners are commonly seen flying together [12]. All birds were weighed with a 20 g Pesola and, if above 10 g, were tagged with a 0.48 g solar-powered radio tag with nitinol antennas (Cellular Tracking Technologies LifeTag, New Jersey, USA) that was programmed to signal every 5 seconds. Tags were attached with a nylon leg-loop harness [18]. While 13 pairs were tagged, the antenna of one tag broke after 1 day, which was indicated by a substantial decrease in signal strength and the number of nodes detecting the tag, and so we excluded this individual and the partner from our analyses. The remaining tags operated normally for between 5 to 29 days before a similar change in signal transmission strength was observed indicating the antenna likely broke off.

b) Automated radio tracking

To monitor tagged individuals, an automated radio tracking system was installed within the study site, covering ~1.5 km^2. 70 radio receivers (Cellular Tracking Technologies Node v2, New Jersey, USA) were mounted every 150 m in a triangular grid with 23 additional receivers placed in areas expected to have increased zebra finch activity, such as near nest boxes, water sources, and areas of grass used for foraging. Receivers recorded the tag ID, the received signal strength (RSS), and the time of the detection. Receiver data was then sent to a central base station.

Tag locations were estimated using RSS-based multilateration. RSS values were first averaged within a 15 second window with a -5 second lag to remove large fluctuations in signal strength due to interference or multipathing. Within each 15 second interval, the averaged RSS value from receivers within 200 m of the receiver with the strongest averaged signal strength were retained following Paxton

et al. [19]. To calibrate the RSS-distance relationship, six tags were held at set distances (1 –150 m) from four receivers for 2 minutes at each distance interval. The common logarithm of RSS was then modelled as a function of distance, yielding the relationship:

$$\text{distance (m)} \approx 10^{-1.27009 - (0.03302 \times \text{RSS})}$$

which was used to estimate the Euclidean distance from each receiver. If at least three receivers detected a tag within the interval, then a non-linear least squares model was fit to estimate the location of the tag [19]. For each interval, this process was repeated 100 times by sampling from ± 1 SE around the mean distance for a given RSS-value. Since we calibrated the RSS-distance relationship up to 150 m, distance estimates beyond 150 m were truncated to this value. From the 100 replicated localizations, an error ellipse corresponding to the $\sqrt{2}$-sigma ellipse of a bivariate normal distribution was calculated to estimate the uncertainty around each localization. Localization accuracy was assessed through field calibrations which indicated a median difference of 35 m between the estimated and predicted coordinates of tags at known locations.

c) Data analysis

We removed outlying points that were greater than 2.5 km from the median coordinates of the localizations for each tracked individual. Continuous-time movement models (ctmm) were then fit to these filtered location estimates with their associated error ellipses to identify the autocorrelation structure of the data. The best fitting model was selected based on AIC and used in autocorrelated kernel density estimation (AKDE) to derive home range estimates for each individual. This procedure was done using the R package 'ctmm' [20,21]. To assess the home range similarity between within and between pairs, we calculated the overlap between home ranges using the Bhattacharyya coefficient, which measures the similarity between two probability distributions [22]. Estimated home range overlap was compared between pairs and neighbouring birds (i.e., individuals caught in the same area) using a mixed-effect beta regression model with individual and partner ID as crossed random effects using the R package 'glmmTMB' [23]. This model was then compared to a model excluding pair type as a predictor using a likelihood-ratio test (LRT).

Next, we examined the extent to which pairs moved together throughout their home range in order to assess spatiotemporal associations between partners. To do so, we calculated a proximity ratio for each dyad (84 possible dyads in total) using the 'ctmm' function *proximity*. The proximity ratio

compares the observed separation distances between simultaneous fixes for dyads to the simulated separation distances assuming random movement. Proximity ratios less than 1 indicate that two individuals are closer together on average than expected given independent movement whereas values greater than 1 indicate avoidance and ratios overlapping 1 indicate independent movement. We fit a linear mixed effect model to examine whether proximity ratios differed between pairs and neighbours with site as an additional fixed effect and individual and partner ID as crossed random effects using the R package 'lme4' [24]. Models without pair type and without site were then compared to the full model using a likelihood ratio test. We also examined whether time of day (minutes post-sunrise, log-transformed) influenced the proximity between pairs using a hierarchical generalized additive model [25] with a gaussian distribution, which we fit with the 'mgcv' R package [26]. We specified a global smoother for time as well as factor smoothers where the effects may vary by each pair. This structure is analogous to random slopes in mixed models [25].

III. Results

The 12 pairs were tracked for between 5 to 29 days (mean 18 days). During this period, individuals were localized on average every 80 seconds with longer intervals between detections occurring occasionally when a tag was not detected, likely due to insufficient solar power. Overall, across all simultaneous localizations, the median distance between pair members was 101 m compared to 393 m between neighbouring individuals. There was substantial variation between pairs, however, with median separation distances ranging from 60 m in most pairs to upwards of 600 m in one case (Figure 1). Four ostensible pairs were more separated compared to neighbouring individuals suggesting that these dyads were likely not actually pairs. To avoid circularly defining pairs based on high spatial proximity, however, all male-female dyads caught simultaneously in the field were included in the 'pair' group in all analyses.

The average home range area of tracked individuals was 0.47 km^2 (95% CI: 0.36 – 0.61 km^2) but varied from 0.39 km^2 for individuals in sites B and E to 0.63 km^2 for individuals in site D (Figure 2A-C). Home range overlap for pairs ranged from 0.99 to 0.17 (Bhattacharyya coefficient, median 0.95), which was significantly higher than the overlap between neighbouring individuals, i.e., those caught at the same site but not together (Bhattacharyya coefficient, median 0.68; LRT $p < 0.001$; Figure 2D).

The majority of dyads (82 out of the 84 possible) had estimated proximity ratios less than 1, indicating that birds were closer on average than expected given independent movement (Figure 3A).

Pairs, however, had significantly lower proximity ratios compared to neighbouring birds (LRT, $p < 0.001$). While proximity ratios were slightly higher for dyads in site D, this trend was not significant (LRT, $p = 0.15$). A hierarchical generalized additive model indicated that separation distance was not significantly affected by time of day ($p = 0.96$, Figure 3B).

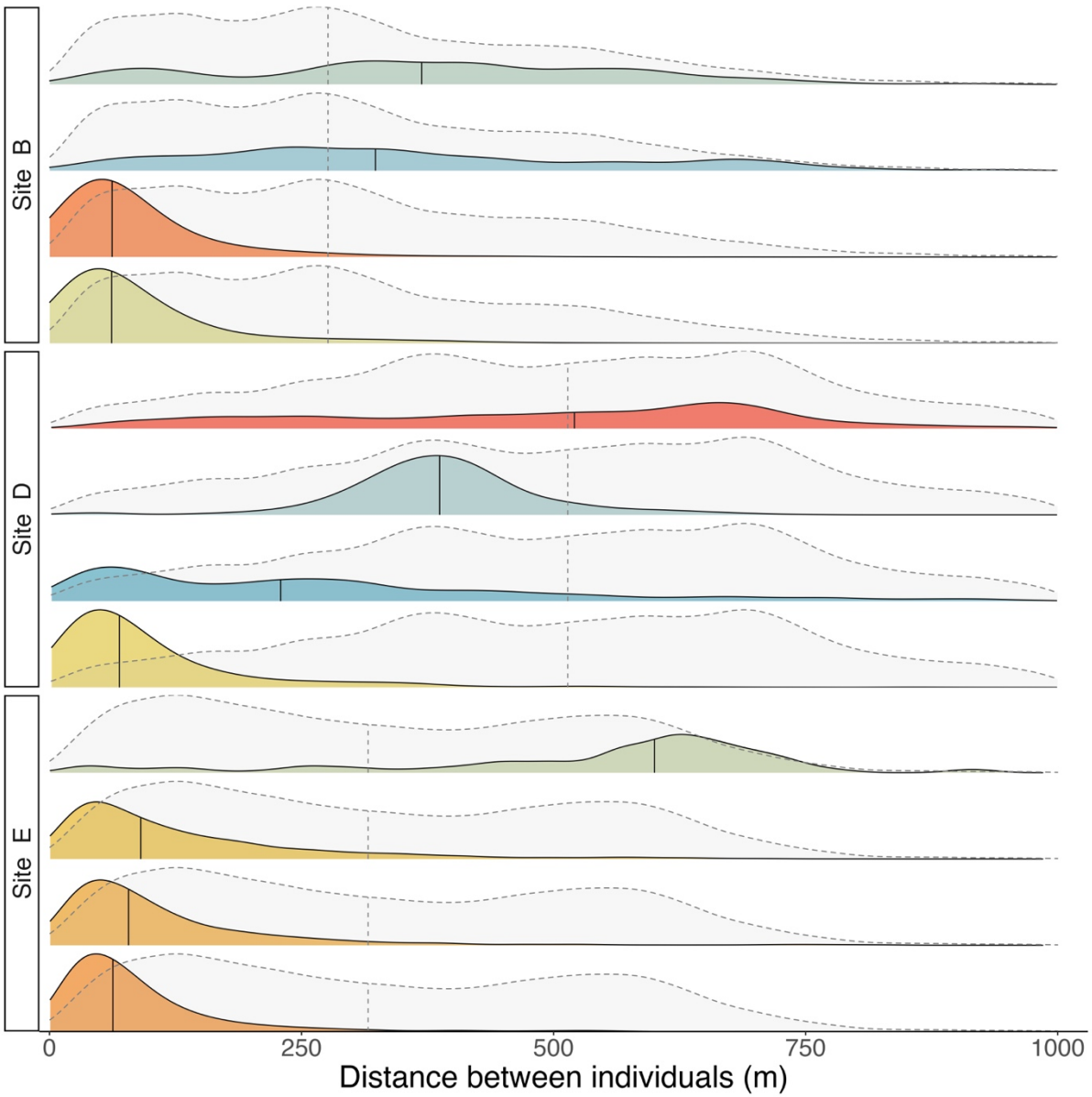

Figure 1. Density plots of the distance (m) between simultaneous localizations of pair members compared to the distance between neighbors (light grey) at each site. Black vertical lines indicate the median value for each pair. Dashed vertical lines indicate the median distance between neighboring

individuals. Each density plot is colored according to the pair ID, which corresponds to the color used for each pair in Figures 2 and 3.

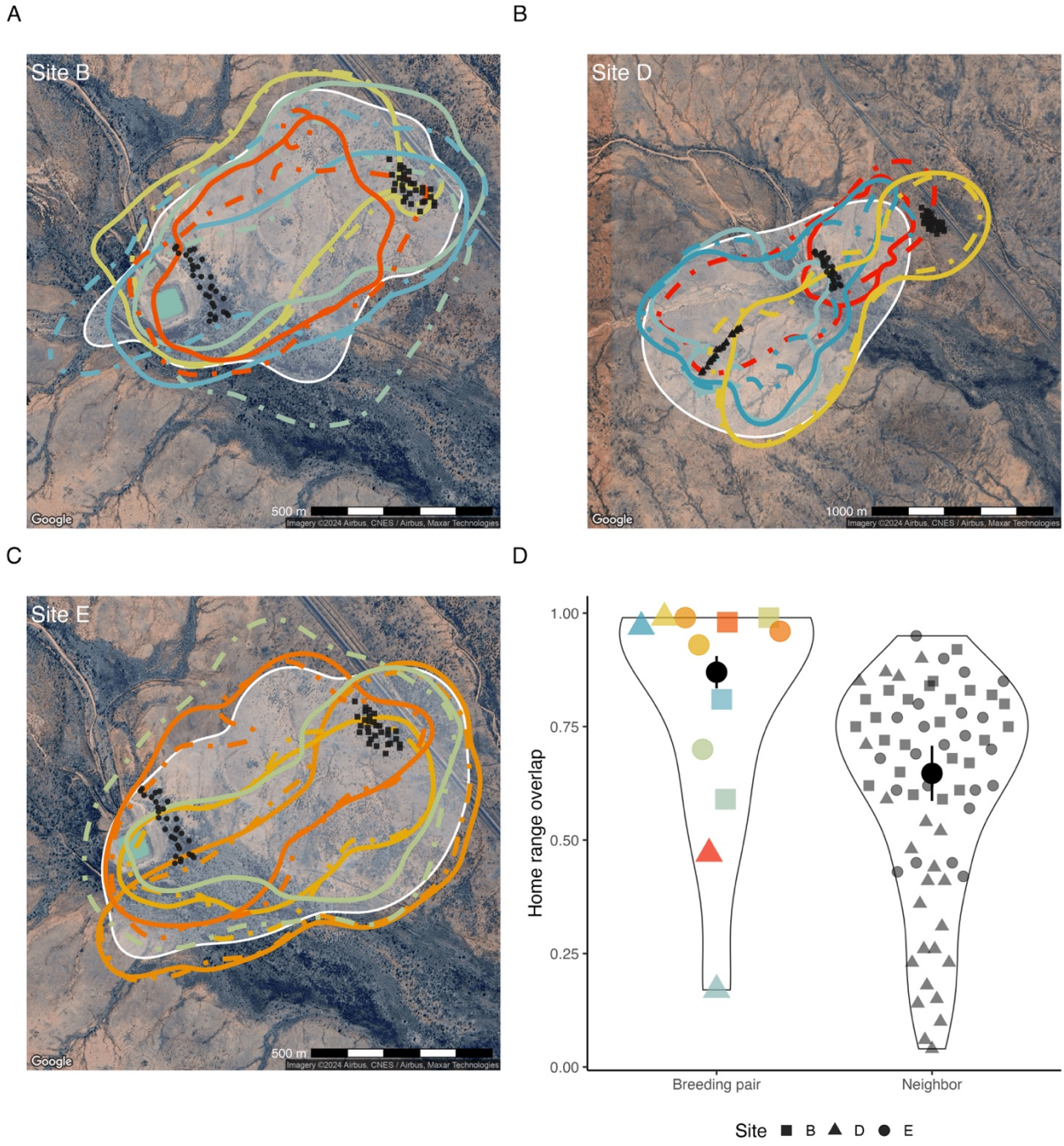

Figure 2. Panels A-C: Home range areas (95% utilization distribution contour) for pairs in each of the three sites (E, B, D). Lines (males, solid; females, dashed) are uniquely coloured for each pair. Shaded white regions show the mean population home range for all individuals ('neighbours') in each sub-colony site. Black points show the nest boxes within each site with shapes corresponding to the site

(legend shown in panel D). Satellite imagery was obtained using the R package 'ggmaps' [27]. Panel D: Violin plots of the home range overlap (of pairs and neighbouring pairs. Black points show the mean (± SE) from a mixed-effect beta regression model of home range overlap as a function of each pair group. Coloured points (pairs) and grey points (neighbours) show the raw estimated home range overlap for each pair. For pairs, the shape corresponds to the pair's site.

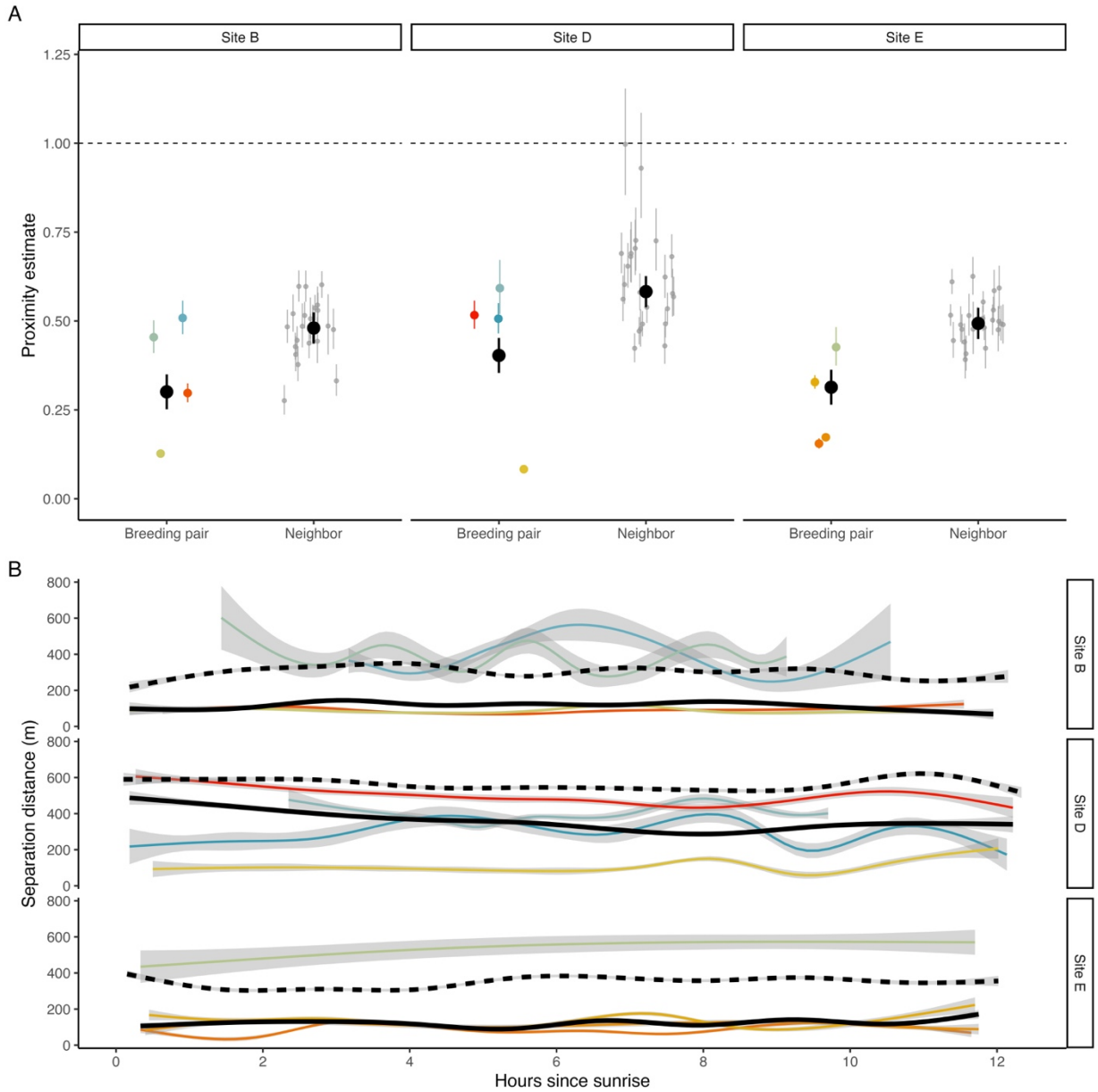

Figure 3. Panel A: Proximity estimates for pairs and neighbours in the three sub-colony sites. Black points show the modelled mean (± SE) proximity estimate for each group. Pairwise proximity estimates (with confidence intervals) for pairs (coloured points, corresponding to pair ID) and neighbours (grey

points) are also shown. Proximity estimates less than 1 correspond to individuals being closer on average than expected given independent movement whereas values greater than 1 indicate that individuals are farther apart than expected. Panel B: Observed separation distances for pairs as a function of hours since sunrise. Coloured lines show pairs (with 95% confidence intervals) and black lines (pairs, solid; neighbours, dashed) show the modelled group mean values (generalized additive models).

IV. Discussion

Using automated radio tracking to characterize the movement patterns of zebra finch pairs in the wild, we observed that multiple measures of space-use were substantially more similar for pairs than between neighbouring individuals. Home range overlap was significantly greater for pairs compared to neighbouring individuals, though pairs were clearly not territorial and home range overlap with neighbouring birds was high. Beyond sharing similar home ranges, pairs also remained within close proximity throughout the home range, significantly more so than compared with neighbouring birds. This proximity was maintained throughout the day for paired birds. As such, despite conservatively classifying pairs based on a single instance where a male and a female were simultaneously captured, which may have misclassified some pairs, we nevertheless observed that pairs displayed significantly stronger spatial cohesion compared to neighbouring individuals. Taken together, these findings indicate that in the wild, zebra finch pairs maintain high levels of spatial cohesion across large areas.

Unlike many passerine species, zebra finches are not territorial during the breeding period [12,28]. This is consistent with our finding that overall, home range overlap was high for neighbouring birds (mean overlap of 75%). This lack of territoriality is likely related to the distribution of water and grass seeds within the arid and semi-arid regions inhabited by zebra finches, which does not permit pairs to exclude competitors [12]. Water points are patchily distributed at isolated sources, such as naturally occurring ephemeral ponds, and also at anthropogenic sources, such as livestock troughs, tanks, and dams; none of which could be defended as part of a territory. Additionally, as obligate granivores, zebra finches forage in open grasslands where seed is relatively homogeneously distributed over large areas. Such ecological factors presumably account for the relatively large mean home range zebra finches (0.47 km^2), compared to home ranges for generalist species breeding in temperate regions, such as great tits (*Parus major*, 0.02 km^2) where resources can be locally defended [29]. Furthermore, though pair proximity was greater compared to neighbours, proximity estimates between neighbouring birds

201 indicates that neighbours were closer together than would be expected given independent movement,
202 which suggests that neighbouring birds concurrently visited similar areas, such as foraging and drinking
203 locations. Instead of competing for these locally abundant resources, it is likely that birds benefit from
204 exploiting them in the safety of a group, which is reflected in the home range overlap and movements of
205 both pairs and neighbouring individuals.

206 Continually maintaining close proximity to a partner may serve multiple functions in zebra
207 finches. As there is expected to be strong selection for individuals to rapidly initiate breeding in
208 response to unpredictable favourable conditions in order to maximize reproductive output during this
209 period, pairs would benefit from constantly maintaining breeding readiness [10]. In captivity,
210 experimentally isolating zebra finch partners increases plasma corticosterone levels, which only returns
211 to pre-separation baseline levels after partners have been reunited for 48 hours [30]. Given that
212 corticosterone tends to inhibit breeding and parental care behaviours, maintaining pair cohesion is likely
213 critical to facilitating rapid reproduction. Additionally, as wild zebra finch pairs are nomadic and might
214 undertake extensive movements (>100 kms) to locate water sources [12], continual contact with a
215 partner would facilitate pairs jointly relocating. During breeding, spatial cohesion may have multiple
216 benefits as well, such as augmenting nest visit synchrony, which has been linked with higher
217 reproductive success in zebra finches [7], or potentially by increasing predator awareness while foraging
218 with a pair member [31]. Taken together, these possible multiple benefits suggest that maintaining
219 constant proximity is a critical behaviour of wild zebra finch pairs.

220 Although sexual conflict received significant attention in the behavioural ecological research on
221 socially monogamous mating systems during the previous decades, there is growing appreciation of the
222 importance of cooperation between breeding partners in many species [32]. In socially monogamous
223 species with long-term partnerships and low rates of extra-pair paternity [33], such as the zebra finch,
224 partners will share a greater proportion of each other's reproductive output. In this situation, the
225 evolutionary interests of pairs are more aligned, which will favour cooperation and coordination
226 between pair members [32]. Spatial cohesion is a behavioural interaction where both partners must
227 coordinate to remain in contact. To date, only one other study (to our knowledge) has simultaneously
228 tracked the fine-scale spatial movements of songbird pairs, where it was shown that great tit pairs
229 coordinate provisioning by utilizing the same core area around the nest during foraging [34]. In great
230 tits, however, spatial cohesion is suggested to enable partners to monitor one another's provisioning
231 levels and thereby to reduce sexual conflict, rather than for the reasons suggested here. Additionally,

great tits are more likely to alternate provisioning bouts, in a tit-for-tat fashion, rather than synchronously provisioning as zebra finches do [7,35]. Nonetheless, given that in both of the two studies tracking fine-scale movements of songbird pairs it was found that pairs show high spatio-temporal synchrony, this suggests that such behaviours may be widespread. These findings demonstrate that spatial cohesion may play an important role in many socially monogamous partnerships.

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