Title

High spatial pair cohesion during and after breeding in a socially monogamous territorial passerine

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Lay summary

Many birds form lasting partnerships, suggesting that spending time with one's partner is very beneficial. Still, we know surprisingly little about their close associations. We studied the movement of chirruping wedgebills and found breeding partners used almost the exact same areas, were consistently close to each other, and follow each other frequently during and after breeding. Overall, being with one's partner is important beyond reproducing together, and partnerships go beyond the requirements for current reproduction.

Abstract

Long-term social monogamy, a prevalent mating system in avian species, is often associated with increased cooperation and coordination as well as reduced sexual conflict. Although many studies have highlighted the benefits of long-term partnerships for individuals, there remains a lack of insight into how closely partners associate with one another behaviourally. To date, studies investigating pair cohesion in seasonal and long-term partnerships are typically restricted to arrivals at the nest or feeding sites during the breeding season. Using fine-scale automated tracking data on chirruping wedgebills (*Psopodes cristatus*), a territorial socially monogamous species, we characterised how partners coordinate their movement during and after the breeding season. We used 12 pair-bonded individuals with consistently high localisation rates that were tracked for a period between 32 and 69 days, with an average of 260,000 localisations per individual. We demonstrate that pairs (1) had extremely similar home ranges with a similarity index of 0.93 versus 0.18 for non-pairs, (2) maintained consistently closer proximity than expected from movement without paying attention to a partner, and (3) followed each other as they moved, with individuals following their moving partner in 42% of cases during and in 47% of cases after breeding. Our findings show that pair cohesion in socially monogamous territorial species can be very high in both a breeding and non-breeding context, illustrating that strong coordination among partners has important functions beyond reproduction and parental care.

Key words

coordination, partnerships, movement, non-breeding, territorial, automated radio tracking

Introduction

In socially monogamous species, pair bonds can persist over just one breeding attempt, multiple breeding attempts and even entire lifetimes, which can have fitness consequences such as increased survival (Culina *et al.* 2015; Jankowiak *et al.* 2018) and reproductive success (Adkins-Regan & Tomaszycki 2007; D'Amelio *et al.* 2024; Sánchez-Macouzet *et al.* 2014). Although findings on the fitness benefits of persistent partnerships in long-lived species are widespread, there is still a predominant focus on the sexual conflict between partners rather than cooperation among individuals reproducing together (Griffith 2019). When attempting to understand the evolution of social partnerships, the coordination within a partnership may be considerable and reduces sexual conflict since the evolutionary interest of both individuals are more aligned (Mariette & Griffith 2015; Patrick *et al.* 2020). Here, the degree and type of coordination as well as the strength of the association are crucial factors. Association strength is dependent on the decisions made by individual members of a dyad, and in turn, behavioural decisions depend on the association strength of a dyad (Cantor *et al.* 2021).

Decision-making processes within a dyad that influence social cohesion are closely linked to space use, as mobile animals must determine when and where to move. Thus, quantifying fine-scale individual movement across space and time in relation to their partner can reflect the strength of the pair association and even the level of cooperation. For example, work on nest-visitation rates of pairs in avian species has demonstrated reproductive benefits of arrival synchrony and provisioning coordination (Bebbington & Hatchwell 2016; Mariette & Griffith 2012; Tyson *et al.* 2017; Wojczulanis-Jakubas *et al.* 2023), but this only captures a small proportion of individual space-use. Pair coordination away from the nest has been scarcely investigated due to limitations in monitoring very fine-scale movement of multiple free-ranging and mobile animals across long periods of time in the wild. A recent exception is a study on zebra finches (*Taeniopygia castanosis*), a non-territorial species, where individuals were tracked continuously up to 29 days showing extremely high overlap in home ranges and consistently high spatial proximity of pairs (Tyson *et al.* 2024).

To date, we are aware of no studies on continuous pair movement coordination beyond offspring provisioning and on territorial species specifically. However, movement not directly related to parental care and whether a species is territorial are crucial aspects to consider when assessing social behaviour in highly mobile animals. As movement is more restricted and more organised between individuals in territorial species, territoriality has implications for spatial cohesion across individuals, pair-bonded or not, within a population. Previous studies showed the degree of territoriality and territory size is inherently linked to social and reproductive behaviours in many species (see Snijders & Naguib 2017), as it dictates which individuals encounter one another and at what rate. For example, in great tits (*Parus major*), larger home-ranges are associated with higher tolerance against intruders (Naguib *et al.* 2022), and higher population densities result in stronger territorial responses to simulated intruders (Araya-Ajoy & Dingemanse 2017). Additionally, territoriality may be more effective when a territory owner is more social. For example, male crested titmice (*Baeolophus atricristatus*) attack more threatening intruders more often when supported by juveniles (Borger *et al.* 2020).

Here, we quantify the movement patterns and level of spatial cohesion within and among pairs both in and after the breeding season in the chirruping wedgebill (*Psopodes cristatus*), a highly mobile and free-ranging animal that breeds opportunistically in pairs throughout the year in the Australian outback. Although little is known about the breeding ecology of these birds, field observations confirm chirruping wedgebill that pairs tend to stay together between and across breeding seasons (this study), similarly to their close relative the Eastern whipbird (*Psophodes olivaceus*; Rogers & Mulder 2004). Chirruping wedgebills are known to produce duets in pairs throughout the year, suggesting pairs may be closely associated and territorial (Austin *et al.* 2019), and indeed duetting species often form long term pair bonds and are territorial (Tobias *et al.* 2016). We used an automated radiotracking system including hybrid (solar- and battery-powered) radio tags to enable continuous long-term tracking of territorial pairs and their neighbours. First, we tested whether or not home range size changed across time (daily and weekly) regardless of pair-bondedness, characterising the territoriality of this species. To determine pair cohesion, we tested whether partners (1) had a larger home-range overlap than dyads that are not pair-bonded, (2) were in close proximity to one another, and (3) tended to follow each other as they move. We predicted that both pair members stay together most of the time, moving as pair through their home-range. For a species with long-term partnership and opportunistic we further predicted that social cohesion would persist beyond breeding.

Methods

a. Study species and data collection

Fieldwork was conducted at Gap Hills (30°56'58"S, 141°46'02"E), Fowlers Gap Research Station, New South Wales, Australia, from August to November 2023. Here, we monitored a local population of chirruping wedgebills, a passerine endemic to the Australian outback. We first monitored the population to establish where socially monogamous pairs reside in supposed territories based on locations where individuals forage and produce vocalisations together during the morning (up to 4 hours after sunrise), as well as based on territorial aggressive displays (chasing, attacking, and producing aggressive vocalisations in response to an intruder). Chirruping wedgebills produce sex-specific vocalisations and duet when pair-bonded (Austin *et al.* 2019), meaning we could identify breeding pairs through consistent duetting of male-female dyads every morning from their roost tree. All target breeding pairs were monitored at least once every two days for breeding behaviour (collecting nest material, incubating, provisioning chicks or fledglings) throughout the study period to ascertain the breeding status of individuals and the population.

Once target breeding pairs were established, we captured these pair-bonded chirruping wedgebills using mist-nets near their roost trees. All birds were banded using an ABBBS metal ring and three colour rings, blood-sampled (~10µl) via brachial venipuncture for molecular sexing (see below) and tagged with a solar-powered radio tag including a battery and a nylon-coated braided steel antenna (Cellular Tracking Technologies *HybridTag,* New Jersey, USA). Tags were attached using a nylon leg-loop harness, totalling to a maximum of 1.3g (≤3% of body mass). Banded individuals were monitored for a two-week period post-catching to ensure they were not hindered by the radio tag and to verify pair-bonds and territories previously established. When revisiting the field site in February and September 2024, all banded individuals that were resighted (*N*=16) remained with the same partner within their home ranges, suggesting they form long-term pair bonds.

Blood samples were used for individual sexing by extracting DNA and then using PCR to amplify the CHD locus which is polymorphic between the sex chromosomes and conserved across bird species (Lee *et al.* 2010). Molecularly verified sexing was consistent with sexing based on the vocalisation behaviour of individuals.

b. Radio-tracking

We tagged 23 pair-bonded adult chirruping wedgebills, that were tracked for between 34 and 69 days (mean = 60.2 days, sd = 12.5 days) in the period from 6th of September to 30th of November 2023 during daylight hours when birds were not roosting. We used an automated radiotracking system covering 1.27 km^2 already installed at the study site (Tyson *et al.* 2024), consisting of an array of 94 radio receivers (Cellular Tracking Technologies Node v2, New Jersey, USA) placed 100-150 m apart from one another. Tag identity, received signal strength (RSS, a negative value in decibels where values closer to 0 indicates a stronger signal) and time of detection were recorded when radio receivers detected a signal, and sent to the central station aggregating all detection data. We first calibrated the tags, by determining the RSS-distance relationship. We held six tags at 1.5m high at 18 set distance intervals between 1-200m from four receivers (1, 2, 3, 4, 5, 7.5, 10, 12.5, 15, 20, 25, 30, 40, 50, 75, 100, 150, 200) and determined the RSS for each distance. RSS values were modelled as a function of Euclidian distance from each receiver: distance (m) ≈ $10^{-1.27009 - 0.03302 \times \mathrm{RSS}}$ (Figure S1; see Tyson *et al.* 2024). We also verified how much the elevation of the bird above the ground affected detections by the receivers by mounting a total of 6 tags horizontally on 3 poles, one 10cm above ground and one 200cm above ground for each pole. Then, we held these poles at a total of 86 test points (26, 27, and 33 test points per pole) for 2 minutes at a time at uniformly distributed locations within the receiver array. At each test point, we determined the rate of detection, number of receivers picking up the tag, the mean and the maximum RSS for each tag. And tested whether there were significant differences using a Wilcoxon test.

Locations were determined within a 15-second window using two methods: (1) RSS-based multilateration and (2) based on the receiver with the strongest detection of the tag. For the first method using multilateration, we filtered windows in which at least three receivers detected the tag within an interval. We removed windows when the strongest detection had an RSS less than -80 dB (corresponding to a radius of 12.5m around a radio receiver) to prevent inclusion of inaccurate localisations. Then, we fit a non-linear least-squared model to estimate the location (see Paxton *et al.* 2022) 100 times sampling around ca. 1 SE around the mean distance for an RSS value (see Tyson *et al.* 2024). This yielded an error ellipse corresponding to the square root of two-sigma ellipse of a bivariate normal distribution, representing the level of uncertainty around each localisation. Previous field calibrations (Tyson *et al.* 2024) found a median difference of 35m between the estimated and true coordinates of a tag. For the second, simpler, method using the strongest detection of the tag, we estimated that the location of the tag corresponded to the location of the receiver with the strongest detection, and applying a signal cut-off (RSS ≥ -80 dB) meaning that all detections considered were within a 12.5m radius of the receiver.

To assess the effectiveness of both methods for continually tracking individuals, assuming that they stayed within the area of the grid, and that the tags were emitting a signal every 15 seconds, we determined the total number of 15-second signals during daylight hours for which the tagged bird could be localised and calculated the percentage of realised localisations during this time period. Then, we estimated the expected percentage of time intervals with detections that birds could be localised using the ‘strongest detection method’. This method will only detect an individual when it is found within ca. 12.5m of a receiver assuming a tag height of 1.5m. Therefore we compared the total area of the receiver array (1.27km^2) to the detectable area within the array (i.e. the summed area around each receiver with a 12.5m radius, 0.05km^2), as well as the total area used per individual (100% minimum convex polygon (MCP) per tagged individual) and the detectable area within this area (the summed area around each receiver with a 12.5m radius within the 100% MCP).

c. Data analyses

We performed all statistical analyses in R 4.4.0 (R Core Team 2024). First, we tested whether localisation rates for each method varied across days and time of day for all tags using hierarchical generalized additive models (HGAMs) with a beta distribution using *mgcv* 1.9.1 (Wood 2011), which allows for different nonlinear relationships across different groups (Pedersen *et al.* 2019). Here, localisation rates per method per tag was the predictor variable for separate. We fitted a global nonparametric smoothing parameter for date or hour of day, as well as factor smoothers for the parameter where the effect can vary by individual identity. All HGAMs that we fitted were checked the model for the appropriate number of basis functions (*k*), and whether the residuals were normally randomly distributed, and no assumptions were violated.

For all further analyses, we used pairs where both partners were radio-tagged and had high enough detection rates (i.e. comparable to expected detection rates) and home-ranges (see below) that did not include receivers on the edge of the receiver array, indicating that they spent most of their time inside the receiver array. We used continuous time movement models (CTMMs) using both the multilateration and strongest detection method to analyse space use and movement of each radio-tagged chirruping wedgebill. Localisations for each tag were fit using *ctmm* 1.2.0 (Calabrese *et al.* 2016) using maximum-likelihood approaches. These CTMMs account for serial autocorrelation inherent to movement data and estimate confidence intervals to space use and movement. For each tag, we visually inspected the autocorrelation structure with variograms. The best fitting model for each tag was selected based on AICc.

(i) Home range size across time

Space-use for each tagged individual was calculated with the best-fitting CTMM, from which we extracted the autocorrelated kernel density estimation (AKDE) describing the utilisation distribution of each individual (Fleming & Calabrese 2017). Time-dependent changes in space-use were determined by calculating the weekly AKDE of each individual, starting from September 7th, i.e. one day after the first individuals were radio-tagged. Weekly AKDEs were separated into 4 sections across time of day for each individual: (1) 0-3, (2) 3-6, (3) 6-9, and (4) 9-14 hours after sunrise, respectively. From each AKDE, we extracted the 95% CI home range area in km^2 and log-transformed this to ensure model assumptions were met. Then, we fitted HGAMs with a gaussian distribution with global nonparametric smoothing parameters for week and section of day and factor smoothers for each parameter with individual identity. Using the HGAM output, we inspected whether home range size changed after the breeding season, and all further analyses were separated between breeding season and post-breeding season.

(ii) Space-use overlap

To test space-use overlap, AKDEs (home ranges) of each tagged individual were calculated using the best-fitting global CTMMs including all detections between sunrise and sunset per individual, separated by breeding and post-breeding season. To assess space-use overlap, we calculated the overlap between these AKDEs for each possible dyad using the Bhattacharyya coefficient (BC), which describes the similarity between two probability distributions ranging from 0 (completely dissimilar) to 1 (identical). All possible dyads between the individuals that we tagged (*N*=66) were classified in a dyad type: (i) pair-bonded (ii) not pair-bonded. We fitted mixed-effects beta-regression models using *glmmTMB* 1.1.9 (Brooks *et al.* 2017) with, as a response variable, space-use overlap, as predictor variables dyad type, breeding season (yes/no), and an interaction between dyad type and breeding season to test if pairs specifically changed their space use sharing after breeding. We removed this interaction if it was not significant based on a likelihood-ratio test (LRT). As random effects we included identity of both dyad members. This model was compared to a model excluding dyad type using a LRT. Significance of pairwise comparisons within categorical variables was determined with estimated marginal means using *emmeans* 1.10.2 (Lenth 2016). We checked for any violations of the model assumptions (residual normality and homoscedasticity) using *DHARMa* 0.4.6 (Hartig 2022) and found none.

(iii) Pairwise distances

To test whether partners remain in close proximity to one another and move together throughout their territory, we quantified the separation distances between pair-bonded individuals for each 15-second point using the *distance* function of *ctmm* using the best-fitting global CTMMs per breeding/post-breeding season. As a control, we compared pairwise separation distances between the focal individual at day x and their partner at day x+1 at the same time of day, to assess whether pairs are closer to each other than expected if they were to move independently of their partner. We used this as a control rather than simulations, since we expect chirruping wedgebills to have certain movement patterns across the day that are not captured by simulations that assume random movement within their home range. We fitted gaussian HGAMs on separation distances (mean-centred and divided by 1 standard deviation to facilitate model convergence), with global nonparametric smoothing parameters for time of day (post-sunrise) and date, including factor smoothers for each parameter where the effect can vary by pair identity, and a factor smoother for time of day including whether it was the breeding or post-breeding season. Finally, we included the categorical parameters day (x or x+1) to test whether true separation distances differ (day x) from the control (day x+1) and breeding season (Yes/No).

(iv) Following behaviour

We quantified how much partners follow each other continuously by identifying following events. Following events were assessed using the strongest detection method as this allowed us to categorise shared locations as receiver identities. To do so we first identified to what extent either a male or female initiated movement away from a location where the pair were previously simultaneously present. Here, we first identified movement events of the partner to a location, i.e. when it was most strongly detected by a different receiver than the during the previous detection with high confidence (RSS>-80). To identify following events, we first quantified all movement events of the focal individual from location A to location B and following by the partner from location A to B. If the partner followed between the initiation of movement of the focal individual from location A to the last detection of the focal individual at location B, we identified this as a following event. Then, we set a threshold at the 90th percentile of time lag between the arrival time of the focal individual and the partner at location B, as some following events had extreme time-lags due to missing detections (up to 11 hours) that could not realistically be true following events. For further analysis, we captured all following events where the partner arrived within the threshold from the arrival of the partner. Following rates were determined by taking the fraction of movement events of the partner that included a following event of the focal individual, excluding all movement events where at least one bird was not detected within the time threshold (90th percentile). We fitted a binomial HGAM on whether the focal individual followed the partner after movement events (Yes/No), with a global nonparametric smoothing parameter for time of day (post-sunrise), including a factor smoother where the effect can vary by pair identity. Finally, we included the categorical parameters sex of follower, breeding season (Yes/No), and a two-way interaction between sex and breeding season to test whether the propensity to follow a partner differs per sex and whether it was the breeding season.

(d) Ethics statement

Fieldwork was conducted with permission of the Macquarie University Animal Ethics Committee (reference no. 2023/012) following the Australian Code of Practice for the Care and Use of Animals for Scientific Purposes NSW Animal Research Act 1985. Banding and handling permission was issued by the Australian Bird and Bat Banding Scheme (authority no. 3788). All data collection is in accordance with the ABS/ABAB guidelines for ethical treatment of animals.

Results

(a) Radio tag localisation

Localisation ratios (number of localisations relative to the total number possible) of the 23 radio-tagged Chirruping wedgebills varied considerably, using both the multilateration (range=1.5-33.7%) and strongest detection method (range=14.2-71.4%; Figure 1A, Table S1). Localisations also varied strongly by day (strongest detection: HGAM, χ^2=81.2, *p*<0.001; multilateration: χ^2=279.6, *p*<0.001; Figure 1B), and time of day (strongest detection: HGAM, χ^2=231.4, *p* <0.001; multilateration: χ^2=74.9, *p*<0.001; Figure 1C). Detection rates (Wilcoxon test: *W*=6, *p*<0.001), number of receivers detecting the tag (*W*=0, *p*<0.001), mean RSS (*W*=1299, *p*<0.001), and maximum RSS (*W*=415, *p*<0.001) were consistently higher for elevated tags than tags at ground level (Figure S2), indicating that the detection rate and accuracy (i.e. average RSS) are negatively affected by the height from the ground. Especially detection rate was much lower, with an 8.3-fold decrease in detection rate when tags are at 10cm versus 200cm from the ground, whereas average RSS values were not as different (max RSS: ground=-90., elevated=-73, mean RSS: ground=-103, elevated=-101).

Localisation rates for the strongest detection method were much higher (mean 40.7% of total possible detections per bird, sd=8.1%) than the multilateration method, which captured only a small proportion of the possible detections (mean=14.9%, sd=,16.6%) even though there was evidence that the bird was detected. This was largely driven by the fact that often the tag was not detected by at least three receivers with a high enough RSS (≥-80) to estimate its location. Since some radio-tagged chirruping wedgebills had consistently very low localisation rates even with the strongest detection method, we selected six pairs of chirruping wedgebills where both partners were radio-tagged and localisation rates of at least 30% during daytime. Although these rates were higher than 3.6%, which is percentage of the total array area (1.2km^2) that is detectable (12.5m radius around all receivers, 0.05km^2), these rates did correspond to or were higher than expected localisation rates within the area that the bird was detected (area of 12.5m radius around all receivers within 100% MCP of all localisations per individual; Table S1). The 12 pair-bonded individuals selected for further analyses were tracked for between 34 and 69 days (mean=60, sd=13), with pairs concurrently being tracked between 34 and 68 days (mean=56, sd=16).

Localisation rates did not vary strongly on average across the day (Figure 1C), and most gaps between localisations using the strongest detection method were not longer than 30 seconds (Table S2), meaning localisations were relatively evenly distributed across the day.

(b) Pair movement

We found 17 nests that were active between 11th Aug and 16th Oct 2023, with clutches between 1 and 2 eggs (Table S3). During the period when reproductive success was monitored, 5 out of 17 nests produced at least one fledgling. Pair-bonded tagged birds (N=12) used in the analyses were detected an average of 1,835 times per day (sd=510). Home range size varied nonlinearly by week, but became consistently larger after the last nest became inactive on Oct 16th (Figure 2). Given that there was a population-wide ending to breeding on this date, and the strong behavioural change related to this in space use, we divided the data into breeding and post-breeding periods (before and after Oct 16th) for all further analyses. Home ranges also decreased almost linearly across time of day, although this effect was relatively small (Figure S3).

Home-ranges of pair-bonded individuals covered on average 0.015km^2 (SE=0.002, range 0.011-0.028km^2) during and 0.139km^2 (SE=0.031, range 0.024-0.372km^2) after the breeding season (Figure 3). The home-range overlap (BC) of pair-bonded dyads (mean±SE = 0.93±0.03, N=6) was significantly higher than that of dyads that were not pair-bonded (mean±SE = 0.18±0.02, N=60; Figure 4, Table 1, LRT $p < 0.001$) for both the multilateration and strongest detection method. Although home ranges of non-pair bonded dyads overlapped (see also Figure S4), pairs still occupied distinct areas that were not or barely utilised by other pairs (Figure S5). Additionally, home-range overlap increased after the breeding season (Table 1).

Pairwise separation distances across all pairs averaged (±sd) on 70.5m±65.6m but varied substantively across pairs (mean per pair: 54.4-90.5m, SE=3.84) using the multilateration method. Since multilateration does not allow for highly precise localisations estimates, the localisations of both partner induced error (median of 35m error,) meaning this may inflate true pairwise separation distances. The strongest detections of partners was often at the same receiver during (55.7%±18.3% of all simultaneous detections across all pairs) and after breeding (70.3%±11.8%). The HGAMs indicated that control separation distances were significantly higher than true separation distances (strongest detection: $\beta=0.34$, SE=0.002, $p < 0.001$; multilateration: $\beta=0.28$, SE=0.003, $p < 0.001$; Figure 5), indicating that pairs moved closer to each other than expected if movement was independent from their partner. Separation distances were significantly higher during than after breeding using the strongest detection method ($\beta=0.37$, SE=0.023, $p<0.001$) but not the multilateration method ($\beta=-0.05$, SE=0.029, $p=0.086$). We also found that separation distances were affected by time of day (strongest detection: $F=59.9$, $p<0.001$, multilateration: $F=17.6$, $p<0.001$) and date (strongest detection: $F=515.1$, $p<0.001$, multilateration: $F=263.1$, $p<0.001$) when controlling for pair identity.

Although males were detected more often than the female (Table S4), both partners were detected in on average 40.5% of all detections within a pair-bond, of which an average of 23.6% detections was by the same receiver. Movement initiations away from a shared receiver location were equal between males and females (both on average 42.9%; Table S5), and in some cases both partners moved away from a shared location simultaneously (on average 14.2%). Of all following events, 90% happened within a span of 10 minutes, which was used as a threshold to remove extreme outliers (Figure S6). Following rates were dependent on time of day when controlling for pair identity (HGAM, $\chi^2=4891$, $p < 0.001$), and an interaction between sex of the follower and whether it was the breeding season (Figure 6). Specifically, males (47.9% of 68.3k movements, sd=19.5%, range = 26.2-83.4%) followed their partner more often than females (36.6% of 62.5k movements, sd=15.2%, range = 17.2-59.7%) during breeding. Both sexes increased their following rates after breeding, and whilst males (50.5% of 42.3k movements, sd=8.2%, range = 37.7-58.6%) still followed their partner more often than females

(44.2% of 34.6k movements, sd=13.7%, range = 20.9-59.5), this difference was smaller than during breeding (β=-0.20, SE=0.02, *p*<0.001).

Discussion

Here we show that chirruping wedgebills have high spatial pair cohesion both during and after the breeding season. Using automated radiotracking, we show that home ranges increased in size after the breeding season. This, however, did not affect home range overlap: the space use of partners was nearly identical both during and after the breeding season, and had a much greater overlap than non-pair bonded dyads. Not only did partners share the same area, but they also remained in consistent proximity to one another across time of day during and after the breeding season. Partners also followed each other consistently, with high occurrence of following behaviour of a partner when one individual moved to a new location. Following was more often displayed by males and occurred more often after the breeding season. Overall, socially monogamous pairs of territorial chirruping wedgebills display very high and consistent levels of spatial cohesion both during and outside of the reproductive period.

We found that localisations of individuals using the multilateration method were very limited, making this method - for birds often being on the ground with fewer detections by multiple receivers, as discussed below - less appropriate to assess consistent movement albeit localisations were relatively precise. The strongest detection method, where we identified locations of birds using the strongest detection of a receiver, yielded much higher localisation rates which coincided with expected localisation rates within the area that the bird was detectable. Additionally, we found that the height of the tag affected the likelihood of detection as well as detection strength, meaning that distance estimates may be strongly influenced by the elevation of the bird. This highlights the importance of identifying and using appropriate methods for animal telemetry, whilst optimizing precision of localisations as well as the number of localisations to fit the research question at hand.

We frequently observed chirruping wedgebills foraging on the ground for insects, and they often walked rather than flew when moving short distances between foraging locations. As we found that detection rates and strength were lower when tags were near the ground, we conclude that the foraging habits impaired the detections of this species, and we thus may have obtained lower coverage of their movement when foraging. However, our large dataset still yielded high enough detection rates and total numbers of detections per individual to make meaningful inferences about their movement and pair cohesion.

We defined breeding and post-breeding as a population-wide metric, since behaviour may be strongly influenced by breeding of conspecifics in the same area. Especially a fundamental behaviour like movement may be sensitive to this, especially given the territoriality of this species. Territoriality is often strongly influenced by the stage of the breeding cycle (Class & Moore 2011; Finck 1990; Odum & Kuenzler 1955; Reid *et al.* 2022), an in turn may be strongly related to movement (Finck 1990; Naguib *et al.* 2022). Indeed, territoriality, and thereby movement, should be strongly related to the social environment and structure (Snijders & Naguib 2017). Our results are in line with this notion, as we found a strong change in space use after the last nest became inactive.

The typical home range of chirruping wedgebills during breeding (0.015km^2) is similar to home ranges of other breeding territorial passerines such as great tits (*Parus major*, 0.022 km^2), even though the environments they inhabit vary drastically (arid zone versus temperate zone). A different resident to the Australian arid zone, the zebra finch, has considerably larger home ranges during breeding (0.45 km^2), likely due to their non-territoriality and strong reliance on water sources (Tyson *et al.* 2024). This suggests that the home range size per se does not necessarily depend on environmental harshness for territorial species, especially for insectivorous passerines who are less reliant to highly ephemeral sources like water in arid zones.

The home range areas within chirruping wedgebill pairs were nearly identical, supporting the notion of these birds being territorial, although some home range overlap with neighbours and nonneighbours exists. This suggests that, although both sexes of chirruping wedgebills are territorial, some overlap in space use with individuals outside of the pair-bond are tolerated. Besides sharing highly similar areas, partners tend to be in close proximity to each other consistently, both during and after the breeding season, indeed suggesting that pairs stay together beyond one breeding event. Although territoriality alone can explain the strong home range overlap, the continuously high levels of spatial proximity indicate that partners are likely coordinating their movement to each other. Additionally, partners follow each other at high rates, showing that the spatial proximity is driven by influence of one individual on another (Strandburg-Peshkin *et al.* 2018). This results in active decision-making (following your partner) rather than passive processes, such as a lack of movement by both partners that happen to be in the same area with a certain resource. Strikingly, partners tend to follow each other more after the breeding period, when there is no need for nest attendance and when home ranges are considerably larger. During breeding, nest attendance is a crucial part of nesting success, meaning partners may need to consistently alternate nest attendance (e.g. Bebbington & Hatchwell 2016). This, in turn, might result in lower rates of following behaviour.

Consistent proximity and coordination in movement may benefit socially monogamous pairs in multiple ways. Especially in species with biparental care, strong pair cohesion can improve cooperation to raise offspring. Continuous close contact enables partners to coordinate nest visiting and attendance during incubation and provisioning, resulting in higher reproductive success (Bebbington & Hatchwell 2016; Mariette & Griffith 2012; Tyson *et al.* 2017; Wojczulanis-Jakubas *et al.* 2023). It also prevents over-exertion of one partner during the reproductive event, which would be detrimental for potential future reproductive events for both partners if they would remain pair bonded (Mariette & Griffith 2015). This means that not only will coordination benefit the current reproductive attempt, but also potential future reproductive success of the pair. Maintaining consistent close context with a partner also may increase readiness to initiate breeding. For example, captive zebra finches that form more stable partnerships initiate breeding faster (Maldonado-chaparro *et al.* 2021). In great tits, individuals that meet earlier after the breeding season initiate breeding faster, and produce larger clutches (Culina *et al.* 2020). Especially in unpredictable and harsh environments like the habitat of the chirruping wedgebill, readiness to breed may be a crucial factor determining breeding success.

Benefits of strong pair cohesion in socially monogamous pairs extend outside the reproductive context. Partners that have strong spatial cohesion may increase their efficiency in locating and exploiting ephemeral resources. Here, individuals in strong partnerships attain the food sources faster as they are paying attention to (Dall & Griffith 2014) and helping (Mariette & Griffith 2015) one another. Indeed, socially monogamous partners can plastically adjust their foraging coordination to reproductive demands – such as clutch size – and pairs with high foraging coordination yield reproductive benefits (Mariette & Griffith 2015). Additionally, there may be a reduction in predation likelihood, as there is more predator awareness and potentially a lowered attraction of predators to non-solitary prey that are together with their partner (Beauchamp 2002). In the context of territorial species, a strong cohesion with a co-owner of the territory, in this case the partner, may result in more effective territory defence. Chirruping wedgebills produce antiphonal duets, whereby the male and female produce a joint song with alternating syllables (Austin *et al.* 2019). These types of duets have often been related to pair quality and territory defence (Dahlin & Benedict 2014; Hall 2004, 2009), where the rate and coordination of the male and female song exemplifies their quality (Hall 2000). Being in consistent close proximity enhances duetting rate and duet length, as partners are more likely to answer each other's call (Logue 2007). Thus, consistent proximity may allow more effective signalling against intruders through duetting. All this coincides with the persistently high home range overlap, continuous close proximity, and high following rates that we found in the chirruping wedgebills after breeding. In fact, chirruping wedgebills follow each other at higher rates during the non-reproductive period compared to the reproductive period. This is likely due to the absence of movements related to attendance and alternation at a nest, meaning partners can consistently stay together as they move.

Conclusion

This study continuously tracking partner movements, shows extremely high spatiotemporal synchrony within socially monogamous pairs of a territorial passerine both during and after the breeding season. This adds to existing findings of strong behavioural synchrony in movement in socially monogamous passerines (Baldan & van Loon 2022; Tyson *et al.* 2024), and shows that spatial cohesion persists outside the reproductive period. We suggest that cooperation within the partnership, rather than sexual conflict, largely drive these behaviours. Indeed, multiple studies have shown that there are fitness benefits associated with maintaining a partnership (e.g. D'Amelio *et al.* 2024; Ihle *et al.* 2015; van de Pol *et al.* 2006; Sánchez-Macouzet *et al.* 2014). We add to this by highlighting that paying attention to and moving with a partner is likely to be very important outside the breeding context, as cooperation and coordination are still highly valuable for functions other than parental care (Griffith 2019). Still, very few studies have explored association strength outside of the breeding context, and to our knowledge none using fine-scale movement in the wild. Overall, the strength of the association within the pair as a result of the decisions made by both partners is a crucial factor in these partnerships. We suggest that space-use is an important and appropriate metric to quantify association strength in the partnerships of mobile animals.

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Figure legends

Figure 1. Fraction of timestamps where a bird was localised using the multilateration method (black) and strongest detection method (grey) out of all possible detections, for (A) each tagged individual, (B) each calendar date, and (C) hour of the day (in hours past sunrise). Possible detections are all timestamps between the first and last detection of the bird during daylight hours. All bars are stacked.

Figure 2. Weekly home range sizes of chirruping wedgebills (*N*=12) between September and October 2023 calculated using the strongest detection method. Grey dots depict individual home ranges summarised by week and section of day (*N*=428), and the blue line depicts the global model predicted changes in home range size across time (in weeks). The dashed line indicates the end date of the breeding season (16/10).

Figure 3. Space-use (expressed as the 95% minimum convex polygon) of pair-bonded chirruping wedgebills during the breeding season (shaded area) with detection density per radio receiver (size of circles) of each individual. Each panel indicates a unique pair-bonded dyad. Colours depict the sex of the individual (orange = female, green = male). White dots depict the radio receivers. Satellite imagery was obtained using Esri World Imagery.

Figure 4. Violin plots of space use overlap (BC; Bhattacharyya coefficient) in dyads of chirruping wedgebills (*N*=66) during the breeding and post-breeding season calculated using the strongest detection method. Dyads are classified as non-pair bonded dyads (orange) and pair-bonded dyads (green). Black dots and lines depict the model prediction ± SE.

Figure 5. Pairwise separation distances of pair-bonded chirruping wedgebills across time after sunrise quantified using the strongest detection method. Lines depict the separation distances including the SE (shaded): true separation distances (blue; focal day x, partner day x) and (B) the control separation distances (black; focal day x, partner day x+1)

Figure 6. Rate of following of the focal bird after their partner initiated movement of pair-bonded chirruping wedgebills (*N*=12) per separated by sex (orange = female, green = male) across time of day (hours after sunrise) during and after the breeding season using the strongest detection method. Numbers at the bottom of the plot depict sample sizes of partner-initiated movement during the time of day.

Tables and table legends

Table 1. Beta regression of the effect of dyad-type, sex category, and breeding season on space use overlap (BC; Bhattacharyya coefficient) in dyads of chirruping wedgebills (*N*=132) for both localisation methods. Included are the model estimates (β), standard deviation (sd), and significance (z, *p*) of fixed effects. Random effect variances and number of levels are reported. Reference categories are dyad-type = not pair-bonded and breeding = yes.

Method		**Strongest detection**				**Multilateration**			
Fixed effects		**β**	**SE**	**z**	**p**	**β**	**SE**	**z**	**p**
Intercept		-2.077	0.168	-12.373	<0.001	-1.512	0.187	-8.107	<0.001
Dyad type	pair-bonded	3.868	0.315	12.283	<0.001	3.378	0.354	9.557	<0.001
Breeding	no	0.912	0.156	5.862	<0.001	1.020	0.164	6.238	<0.001
Random effects		**sd**	**N**			**sd**	**N**		
Focal individual ID		0.179	12			0.287	12		
Dyad partner ID		0.266	12			0.300	12		

Figures

Figure 1.

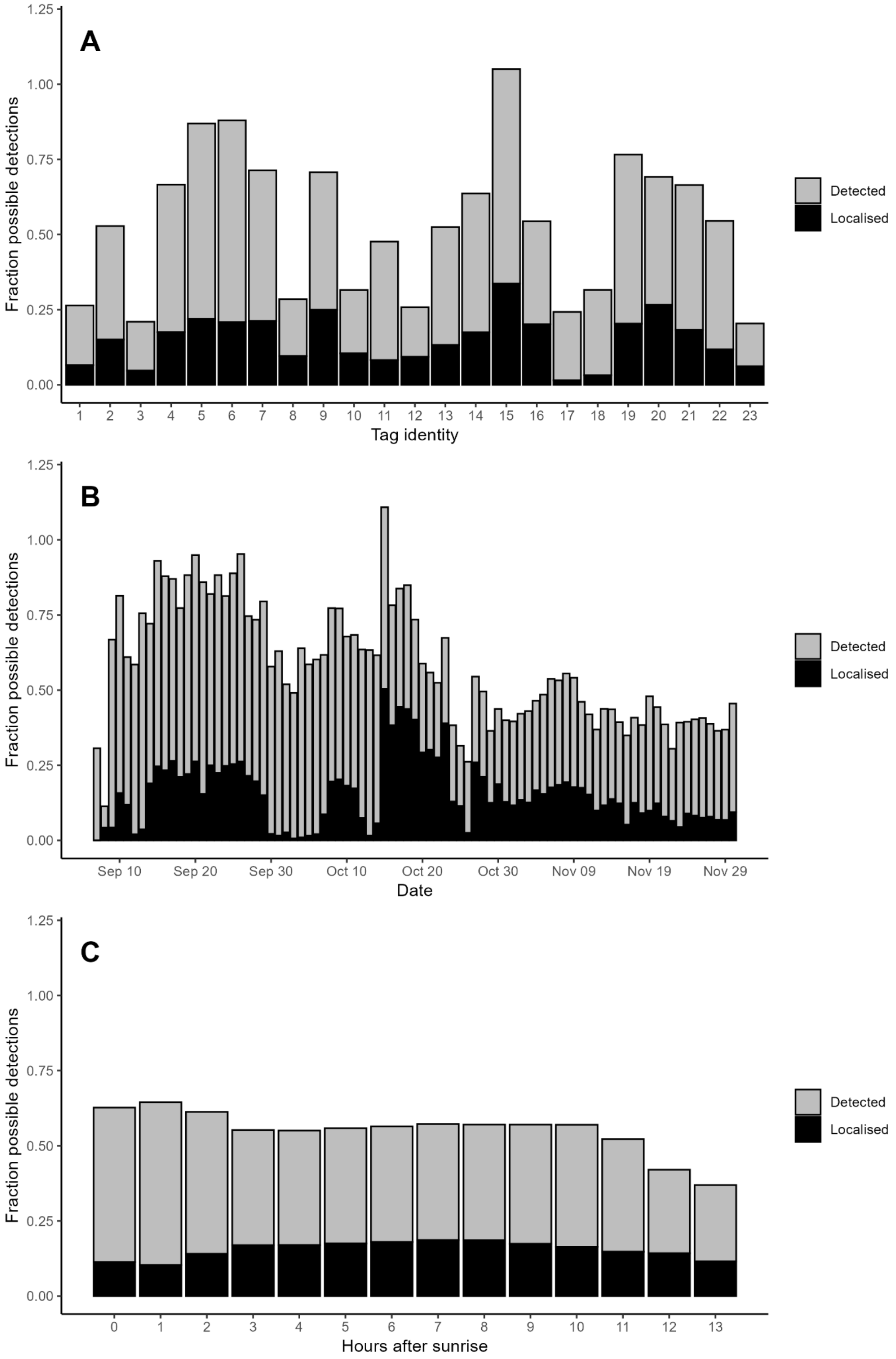
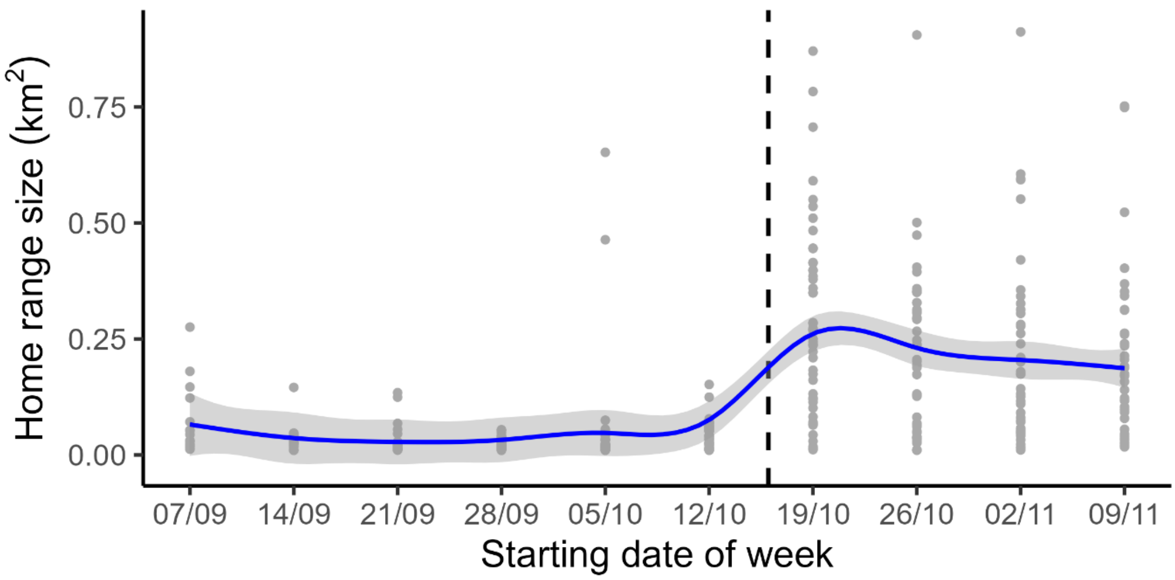


Figure 2.


Home range size (km^2)
0.75
0.50
0.25
0.00
07/09
14/09
21/09
28/09
05/10
12/10
19/10
26/10
02/11
09/11
Starting date of week

613 Figure 3.

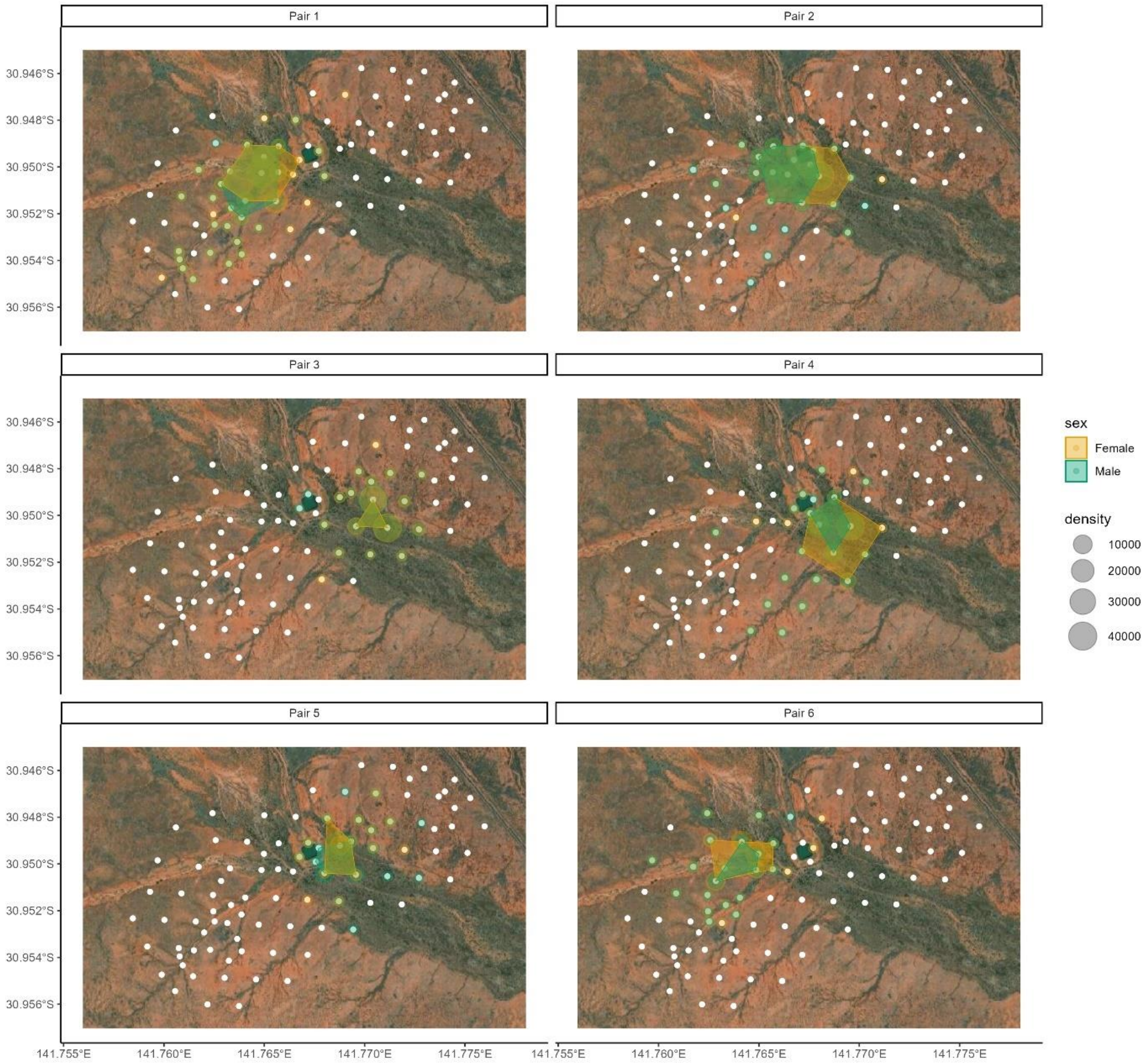


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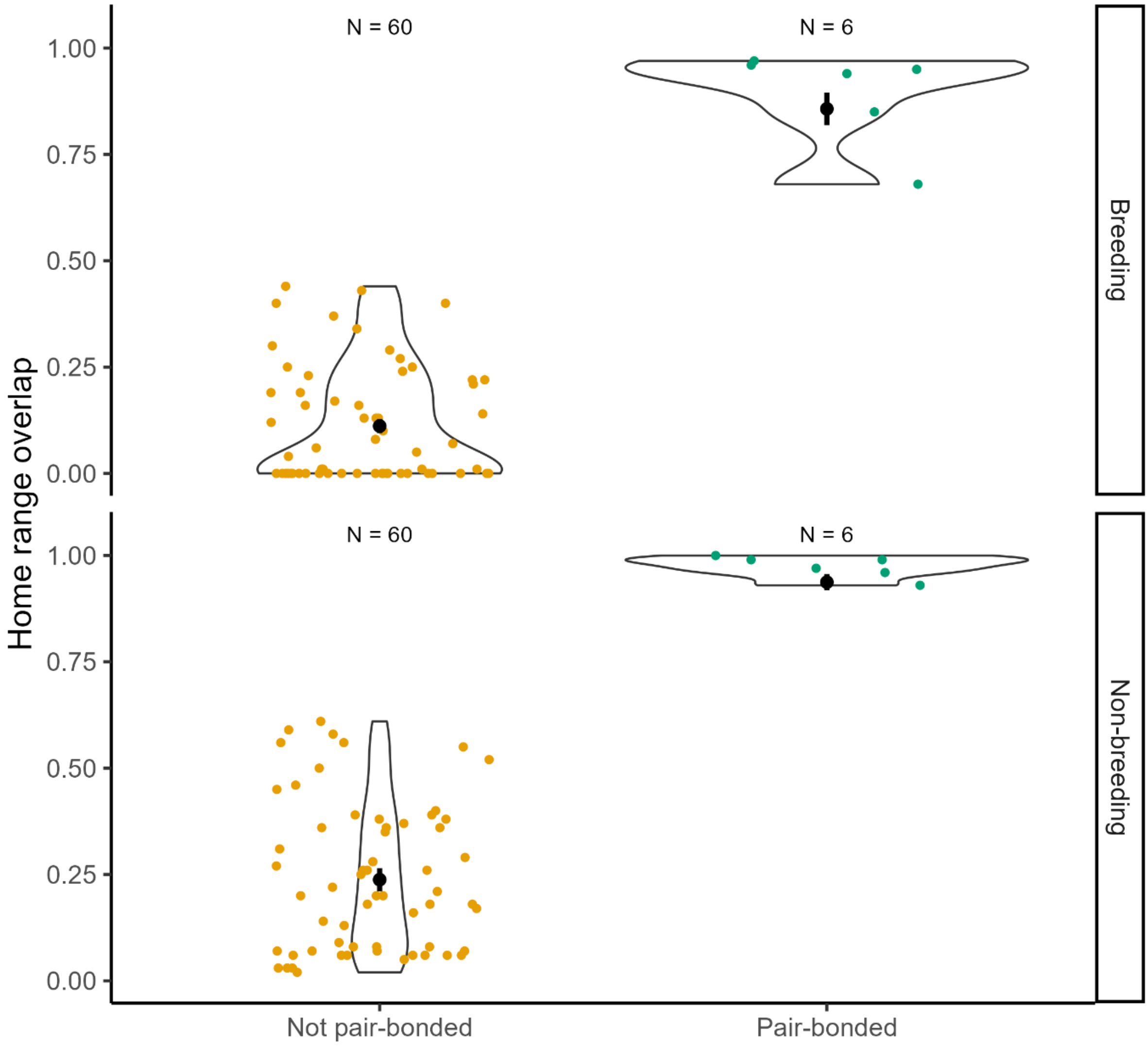
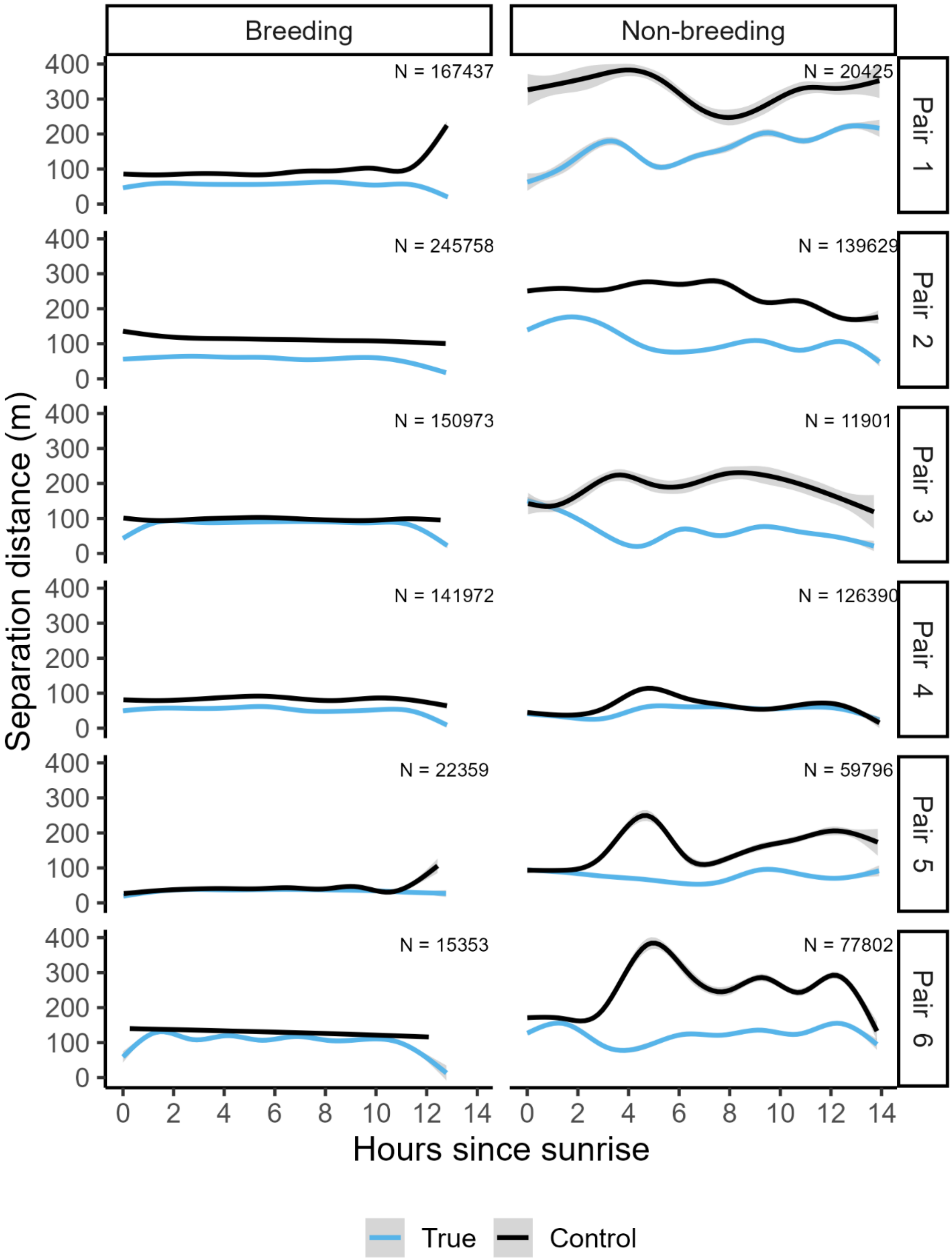
Figure 4.

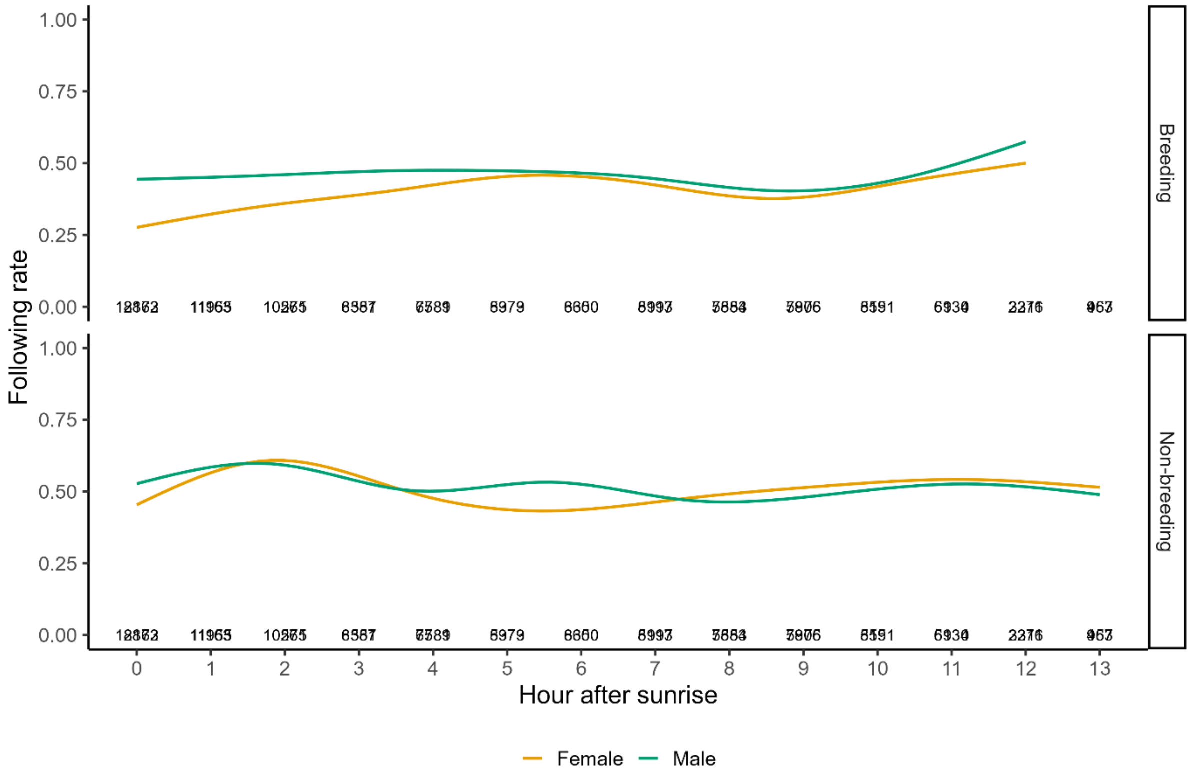

N = 60
N = 6
N = 60
N = 6
Home range overlap
1.00
0.75
0.50
0.25
0.00
Not pair-bonded
Pair-bonded
Breeding
Non-breeding

617 Figure 5.



618

Figure 6.


Following rate
1.00
0.75
0.50
0.25
0.00
Breeding
Non-breeding
0
1
2
3
4
5
6
7
8
9
10
11
12
13
Hour after sunrise
Female
Male