Home-range positions in a bird community from south-eastern Australia - questions and answers

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ABSTRACT

Territoriality in birds has been studied for almost 100 years, but a quantitative, simple and common unit which describes the position of a home range or territory on a study site, is lacking. Consequently it is difficult to assess, or to compare, any data that include for example, the putative movement of home-ranges between breeding seasons. The aim of this study of 11 species (18 species breed regularly on the study site) was to determine, using home-range centroids as the position of the home-range (a) the distance between the home-ranges of the male and female of a breeding pair, (b) the scatter of the home-range positions of a repeat (in different seasons) breeding male, and (c) the distance between the nest of a pair and the home-range centroid of the male. Over eight breeding seasons, all nests were found, and sightings of multiple individuals from each species were recorded and used to determine the centroid of the home-range of each individual. Nest positions and home-range centroids were used to investigate the three aims stated above. There are no differences between species for any of the three measurements. The male and female of a pair occupy home-ranges with similar positions. Repeat nesters return to similarly positioned home-ranges each season, and nests are not positioned in any particular relation to the centroid of a home-range. Other studies using centroids are rare, but we found some similarities between our data and those from one other study that used the centroid concept.

Key words: home-range, centroid, position, male, female, breeding pair, repeat nests, nest position

Published: 9 May 2024 DOI: https://doi.org/10.7882/AZ.2024.021

Introduction

In birds, there are many possible functions of both territoriality and a home-range, which relate for example to pair formation, food supply, nesting sites, predation, and population density. The search for evidence for these putative functions, as well as efforts to quantify their significance and to describe how their interactions determine the sizes and shapes of territories or home-ranges (the latter term will be used from now on), have been in progress for at least 80 years (e.g. Noble 1939, Seastedt and Maclean 1979, Schieck and Hannon, 1993, Adams 2001, Marshall and Cooper 2004, Yoon 2014). But despite the numerous studies over many years, a generally accepted and objective measure of the position of a home-range on a study site does not exist.

A measure that can be used to describe the position of a home-range is a home-range centroid, i.e. the average X and Y co-ordinates of multiple locations of an individual, from either sightings or tracking data. Home-range centroids, which are easily and objectively calculated, are unambiguous, high-resolution, numerical describers of home-range positions. They can be calculated in any study of home-ranges, and used in any subsequent analysis. It therefore follows that they can also be used to objectively compare data, its analysis, and the conclusions drawn from the analysis, between any studies involving home-range positions. Currently, such comparisons are often meaningless as the definition used to define the position of a home-range varies with the study. For example, the similarity between the home-ranges of the male and female of a pair have been assessed by measuring the overlap between the home-ranges (Osmun and Mennill 2011; Odom *et al.* 2019). Home-range fidelity is variously defined as a bird returning to 'essentially the same home-range in successive years' (Darley *et al.* 1977); or as the distance between nest boxes in successive years (Harvey *et al.* 1979); or as two home-ranges overlapping by at least 50% (Bridges 1994); or as repeat nests being within a certain distance of each other (Marchant 1982); or as a bird returning to the previous year's nesting area (an area encompassing a variable number of nest boxes (Hoover 2003)); or as two home-ranges with their centres (undefined) within 70 m of each other (Howlett *et al.* 2003); or as a bird that moved (undefined) less than 62 m; or as home-ranges which overlap (Sedgewick 2004).

A home-range centroid would also enhance the data from studies that attempt to determine the location of activities within a home-range, as the locations could be defined in relation to this centroid. An example is nest site selection. In some cases, e.g. species that nest in tree cavities, or in ground burrows or cavities, the choice of a nest site will be absolutely determined by suitable cavity positions, or soil character (Nyirenda *et al.* 2016; Camargos de Meireles *et al.* 2018). But for other (and in fact most) species there are many factors that could determine where a nest is built. For example, nest sites might be chosen as a compromise between distance from home-range boundaries, favourable environmental factors such as cover, and structure to support the nest. Numerous studies have addressed this issue in many species (e.g. Møller 1989; Schill and Yahner 2009; Goodenough *et al.* 2009; Slagsvold and Wiebe 2017; Fogarty *et al.* 2017; Chiaradia *et al.*2019; Rebollo *et al.* 2020; Perrella *et al.* 2021), but none of these studies included an assessment of where the nests were in relation to either the boundaries, or some sort of measurement of the centre of the home-range. Osmun and Mennill (2011) address the question of the position of singing sites in relation to nest position, but not the position of the nest in the home-range.

There are studies that have enlisted the centroid approach for the investigation of various aspects of home-ranges, but they are rare. To our knowledge, there are only three such studies, each involving only one species. Odom *et al.* (2019) used centroids to describe the position of the home-ranges of the male and female of pairs of Tropical Orioles, and as a measure of home-range fidelity over successive seasons. Schieck and Hannon (1993) used home-range centroids to describe the position of the nests of the Willow Ptarmigan. Butler *et al.* (2022) used home-range centroids of individual Whooping Cranes to assess the effect of age on the positions of home ranges, compared to the original position of the juvenile home-range.

We have previously used the average distance of multiple sightings of an individual bird from its home-range centroid to estimate home-range sizes (Guppy *et al.* 2023). In the current study we present further analysis of some of the centroid data and have addressed three questions. First, what are the distances between the home-range positions of the male and female of a breeding pair, and how do these compare to the distances between non-breeding pairs of birds? Second, what are the distances between the multiple home-range positions of an individual that breeds on the site in more than one season, and do these distances suggest that the same home-ranges are used in successive seasons? Third, is there any evidence to suggest that the 'centre' of a home-range is a factor when nest sites are chosen? For each of these questions we also test for species-specific differences. The centroid approach could provide a way to compare home-range data between studies, and could uncover principles that apply across species and habitats.

Methods

The Site

The study site (35°52'S, 150°03'E) was a 10ha woodland area (approximately 200 m x 500 m; 100 m above sea level), 6 km north-west of Moruya, New South Wales, Australia. Similar woodland is widespread for at least 5 km inland of a 150 km stretch of coast between Ulladulla and Bermagui, NSW (Austin 1978). The site adjoins State Forest and is situated in a mixed landscape of forest and cleared grazing land, with forest as the dominant component. Aerial photographs of the nearby State Forest (personal communication, Forestry Corporation of NSW, Southern Region) show that few and only small changes to the area of forested land have occurred since 1949. The site has been described in more detail previously (Guppy *et al.* 2021).

Field work and data collection

The field work has been described in detail previously (Guppy *et al.* 2021). The site was divided into 50 x 50 m squares by tracks running north-south and east-west. To identify breeding pairs of each species, all nests were found, individual birds (identified by colour-banding) were linked with each nest, and nests were monitored until the young birds fledged or the nest failed (usually by predation). Observations were made by two people (MG and SG) walking the grid, 25 m apart, on most (80-90%) days during the breeding season (August-January inclusive for the seasons 2007/2008-2014/2015), for a daily average period of 2.9 h. Walks covered 1.5-2.5 km, the entire grid was completed every 3-4 days and each home-range was monitored at least 45 times per season. Each time a banded bird was sighted, its position was recorded to the nearest intersection (on the 50 x 50 m grid). Recording to a finer accuracy was not realistic as the birds were often very mobile over the period the sighting was recorded. Duplicate sightings (sightings at the same grid reference) were not recorded within each month, but recordings for each individual started anew each month. Eighteen species regularly breed on the study site (Guppy *et al.* 2021). Data were collected from 11 of these (Table 1), representing nine genera, five families, and a range of different diets and nesting behaviours (Higgins *et al.* 2001, Higgins and Peter 2002). Data were analysed from (a) only birds for which there were at least four sightings for

Table 1. Species used in the analysis, and sightings data.
A: Average number of sightings per season for distance between centroids of pairs.
B: Average number of sightings of the male per season for nest to centroid distance.
[1] Weight ranges from the literature.

Species (abbreviation: weight range[1] (g))	A. Male (SE) Female (SE)	B. (SE)
White-throated Treecreeper (*Cormobates leucophaea*) (WTTC: 16-24)	20.3 (1.7) 19.8 (1.1)	21 (0.4)
Superb Fairy-wren (*Malurus cyaneus*) (SFW: 9-15)	13.6 (0.81) 12.3 (0.94)	15.2 (1.7)
Variegated Fairy-wren (*Malurus lamberti*) (VFW: 6-11)	14.7 (0.71) 17.3 (2.9)	14 (n = 1)
White-browed Scrubwren (*Sericornis frontalis*) (WBSW: 10-19)	10.7 (1.0) 7.1 (2.1)	21 (2.0)
Brown Thornbill (*Acanthiza pusilla*) (BT: 5-8)	15.3 (0.84) 12.3 (0.84)	14.2 (5.9)
Eastern Spinebill (*Acanthorhynchus tenuirostris*) (ESB: 8-16)	7.8 (1.6) 8.4 (2.3)	6 (n = 1)
Lewin's Honeyeater (*Meliphaga lewinii*) (LHE: 27-49)	7.8 (0.99) 9.8 (1.08)	10 (n = 1)
Yellow-faced Honeyeater (*Caligavis chrysops*) (YFHE: 15-20)	8.4 (0.76) 7.0 (0.68)	7.4 (1.0)
Eastern Yellow Robin (*Eopsaltria australis*) (EYR: 15-27)	21.1 (2.2) 12.6 (0.88)	14.6 (2.5)
Golden Whistler (*Pachycephala pectoralis*) (GW: 25-35)	11.1 (0.38) 12.9 (0.38)	11 (2)
Rufous Whistler (*Pachycephala rufiventris*) (RW: 18-32)	7.3 (0.75) 6.6 (0.95)	7 (1.8)

that season, (b) only birds that were colour-banded, (c) only birds whose sex was known, and (d) only birds that were associated with a nest that progressed to at least one egg. Note that not all eligible birds contributed to the data as there were not enough sightings for some banded and breeding individuals.

Calculations

The raw grid co-ordinates (X and Y in metres) of the sightings were entered into an Excel file that comprised one individual for one season (one individual could provide data for several seasons, and would therefore be represented by more than one file). These were used to calculate a home-range centroid (the average X and average Y of the sightings) for that individual for that season. The position of each nest was also recorded as an X-Y position on the grid in metres, to an accuracy of ± 2.5 m.

The centroid and nest-position data were then used in three calculations.

1. The distance between the home-range centroids of the male and female of a pair for one

season. Both male and female individuals could contribute more than once to this data set as they could be breeding on the site for more than one season, and individuals were not necessarily paired with the same mate in different seasons. These distances were compared to distances between home-range centroids of 'pairs' of birds that were definitely not breeding pairs. For this latter calculation we used the centroids of all male Brown Thornbills and all male White-browed Scrubwrens for one season only (the 2011/2012 season). All possible combinations of 'pairs' were used to calculate distances. The choice of species was limited as there were not sufficient data on all males of all species for each season. We chose two species which showed relatively large differences, even though this resulted in a low number of replicates for the Scrubwren.

2. The scatter of a male's home-range centroids (Repeat Centroids) when that male nested on the site in two or more seasons. This calculation was done by producing a Master Centroid, based on the home-range centroids from each season, then calculating the average distance of all home-range centroids from the Master Centroid.

3. The distance of each male's nest from that male's home-range centroid that season. If a male was associated with more than one nest in a season, each distance is recorded as a separate data point. For calculation 3, data from seasons in which the mate of a particular colour-banded male was not colour-banded, were included.

Statistical analysis

Analysis of variance (ANOVA) was used to determine whether there were differences between species for each of these measures. Probability plots showed that these measures were not quite normally distributed, but a square root transformation normalised them. However, ANOVAs using the transformed data gave the same conclusions as those using the raw data and only ANOVA results for the latter are presented.

Results

Distance between home-range centroids of pairs of birds.

The average distance between home-range centroids of the male and female of a breeding pair in one season ranged from 16 m to 44 m over the 11 species (Table 2; Figure 1). The mean ratio of these distances to the radius of each species' home-range is 0.46 (SE = 0.03; Table 2), and the mean overlap of home-ranges (using the areas of both male and female home-ranges) is 71% (n = 22, SE = 3.2; see Guppy *et al.* 2023 for home-range areas). There were significant differences between species ($F_{10,167}$ = 2.5, P = 0.007). However, pairwise tests (Tukey's HSD test) indicated that no differences between pairs of species were significant. It seems that for most comparisons there were no differences, but variation within certain species was sufficient to give an overall significant F value. The average distance between the home-range centroids of all Brown Thornbill males for which there was adequate data, in the 2011/2012 season, was 174 m (SE = 15.7; *n* = 28). For the White-browed Scrubwren the average distance was 169 m (SE = 53.8; *n* = 3). These distances are 8.3-fold and 4.5-fold larger than those between the centroids of breeding pairs of the same species, and 3.5-fold and 2.7-fold higher than the radii of the home-ranges of the same species (Table 2).

Home-range fidelity over multiple seasons

The average distance between Repeat Centroids and the master centroid for multiple season breeders ranged from 16 m to 51 m (Table 2) and there were no differences between species ($F_{10,42}$ = 1.9, P = 0.08). The average ratio of these distances to the radius of each species' home-range is 0.40 (SE = 0.12; Table 2). Generally these distances were less than or equivalent to the distances between the centroids of breeding pairs, but the Variegated Fairy-wren and Golden Whistler were exceptions with greater average distances between repeat centroids and the master centroid.

Position of the nest in relation to home-range centroid

The median distance between nest position and the associated male's home-range centroid, ranged from 32 m to 108 m and significant differences between species were evident ($F_{10,430}$ = 12.5, P < 0.001). Paired comparisons showed no differences, except when the Variegated Fairy Wren was involved. The average for the Variegated Fairy Wren was greater (108 m) than all other species (Table 2; Fig. 2).

Discussion

Most studies on the home-ranges of birds rely on some sort of multiple sighting data. We have demonstrated that it is a simple matter to transform these sightings into home-range centroids, which are objective and quantitative. They can therefore be used to investigate a range of questions and to produce conclusions that can be compared across studies.

Using our centroid data, we have answered the three questions posed in the Introduction. First, the average distance between the home-range positions of breeding pairs is at least four-fold less than the average distance between the home-range positions of non-breeding pairs of males. The distances are less than half of the

Table 2. Average distances (m) (A) between home-range centroids of the male and female of a pair in one season, (B) between home-range centroids and master centroid for multiple season breeders, and (C) between nest position and the associated male home-range centroid.

[1] See Guppy *et al.* 2023.

Species (Radius of home range)[1]	A. Average (number of pairs, SE)	B. Average (SE) (n, average number of centroids per individual, SE)	C. Average (n, SE)
White-throated Treecreeper (81.8)	43.9 (4, 10.9)	16.3 (1.0) (2, 2, 0)	64.3 (4, 30.2)
Superb Fairy-wren (54.2)	27.9 (41, 3.0)	20.2 (3.3) (12, 2.2, 0.1)	38.4 (96, 2.4)
Variegated Fairy-wren (105.3)	27.5 (3, 8.6)	51.5 (n = 1) (1, 2, 0)	108.4 (13, 10)
White-browed Scrubwren (62.3)	37.2 (9, 4.7)	16.3 (7.2) (3, 2, 0)	51.9 (18, 8.0)
Brown Thornbill (49.1)	21 (43, 2.0)	16.2 (3.2) (15, 3.2, 0.4)	35.2 (85, 2.1)
Eastern Spinebill (46.3)	16.3 (5, 2.2)	18.6 (n = 1) (1, 4, 0)	39 (15, 5.9)
Lewin's Honeyeater (80.1)	37.3 (5, 8.0)	33.7 (n = 1) (1, 3, 0)	51.7 (6, 15.3)
Yellow-faced Honeyeater (45)	26.6 (27, 3.6)	20.2 (3.6) (8, 2.8, 0.3)	32.4 (81, 2.9)
Eastern Yellow Robin (55.8)	18.6 (23, 3.2)	17.3 (2.3) (5, 1.6, 0.7)	47.2 (92, 2.4)
Golden Whistler (68.5)	26 (7, 8.2)	47.3 (33.3) (2, 2.5, 0.3)	61.9 (13, 11.3)
Rufous Whistler (60.1)	35.1 (11, 4.4)	30 (3.7) (3, 2.3, 0.3)	47.6 (21, 5.6)

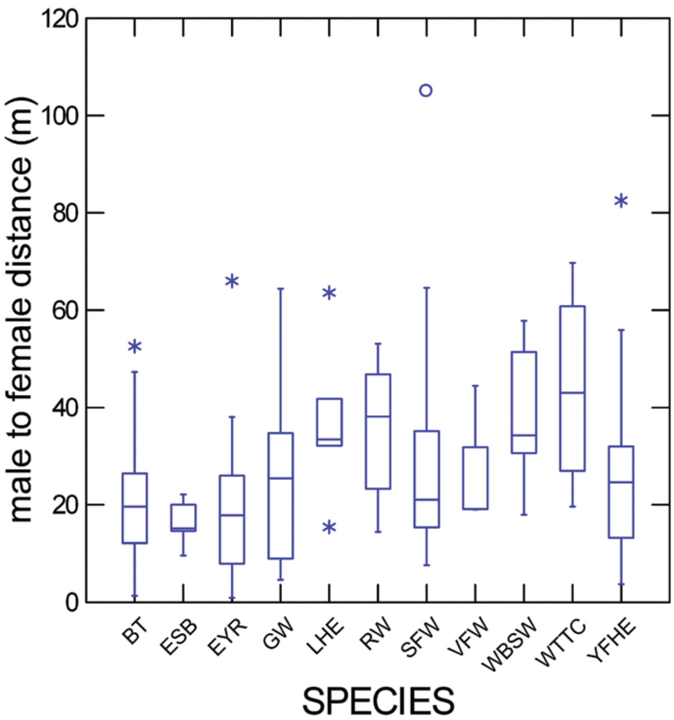

Figure 1. Distances between home-range centroids of the male and female of a breeding pair. Horizontal lines represent medians. Species abbreviations are explained in Table 1. Asterisks and open circle denote outliers.

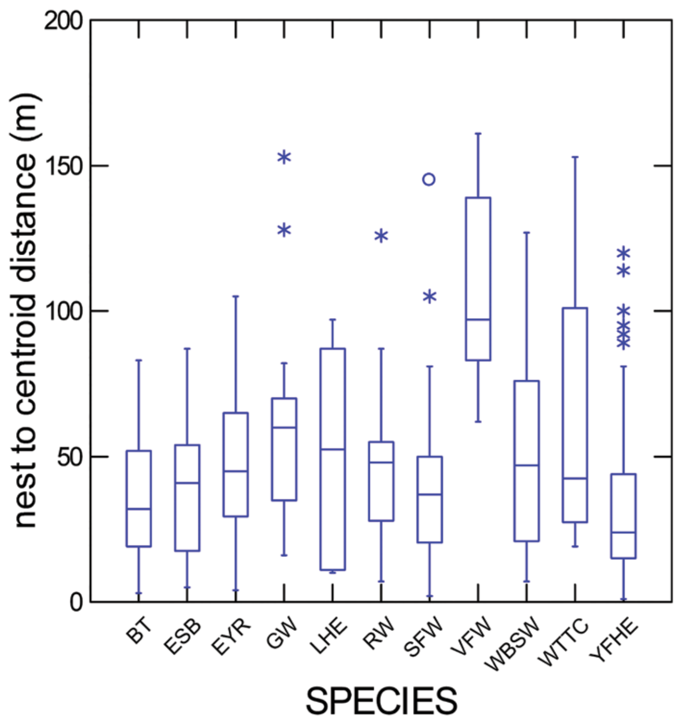

Figure 2. Nest to centroid distances. Horizontal lines represent medians. Species abbreviations are explained in Table 1. Asterisks and open circle denote outliers.

radii of the associated species' home-range, and the home-ranges of breeding pairs overlap by 70%. The simplest conclusion from these three lines of evidence, on this study site, is that the males and females of breeding pairs occupy the same home-range. There are no differences between species for this measure, despite the 11 species representing a range of genera, families, weights, feeding strategies, diets and nesting behaviours. This was also the case for home-range sizes of this group of species (Guppy *et al.* 2023), and in both instances is probably the result of inherent and unexplained variation (including individual variation between seasons) within each species.

There are two previous studies that have used centroids to investigate questions relating to home-ranges. The whooping crane study (Butler *et al.* 2022) is of a species and habitat that bear no relation to those of our study, and the home-range sizes of the whooping crane are at least five orders of magnitude larger than the species used in the study presented here. Due to these differences, a quantitative comparison with our data is not meaningful, but this study shows how flexible is the centroid approach across species and habitats. The study by Odum *et al.* (2019) on the other hand, is comparable to our study in that the data are derived from a medium-sized passerine in a forest habitat. They showed that the home-range size, shape and location were similar for the male and female of pairs of Tropical Orioles. The average distance between the centroids of the male and female of a pair was about 20% of the radius of the home-range, home-range overlap between mates was between 79 and 92%, and distance between home-range centroids of random pairs was 7.6-fold higher than those between breeding pairs. These numbers are similar to our data.

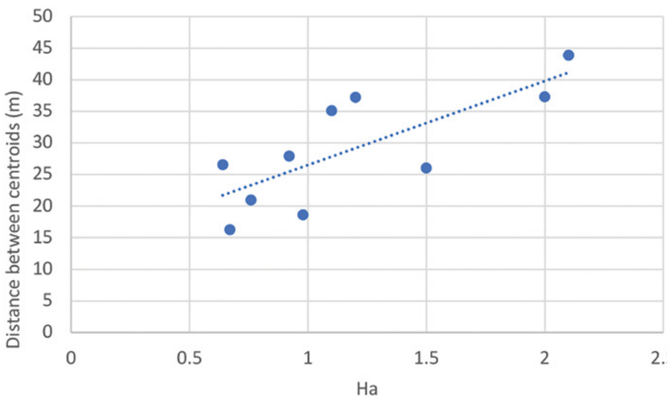

Figure 3. Average distance between home-range centroids of the males and females of breeding pairs of 10 species vs home-range size (from Guppy *et al.* 2023). r^2 = 0.58. The Variegated Fairy-wren has been omitted (Y = 27.5, X = 3.5). If the Variegated Fairy-wren data are included the r^2 = 0.16. For the Tropical Oriole, Y = 26.4, X = 7. (Odum *et al.* 2019).

Further analysis of our data shows a significant correlation between the separation distance of the centroids of pairs, and the size of the species' home-range (Figure 3). The variation in home-range size explains about half of the variation in the distance between centroids. The simplest explanation is that as home-ranges get larger, the male and female of a pair have more opportunity to forage or display in slightly different parts of the home-range, hence the greater distances between home-range centroids. The data from both the Variegated Fairy-wren and the Tropical Oriole do not conform to this correlation, and both have significantly larger home-ranges than the 10 species represented in Figure 3. This suggests that the increase in the distance between centroids reaches a plateau at some unknown size of the home-range.

Second, individuals that are repeat nesters have similar home-ranges in successive seasons, according to the centroid data. With the exception of the Golden Whistler, home-range centroids over multiple seasons are located within an area (taking this area as a circle) with a radius that is never greater than half the radius of the home-range (Table 2). The radius for the Golden Whistler is larger (69%), but there is no obvious explanation for why this species differs from the other 10. The value for the White-throatedTreecreeper is one of the lowest, but choices for nest location are limited to the few tree holes on the site for this species. So as for the first question (above), the simplest conclusion is that repeat nesters occupy the same home-range in different seasons, and the fact that there are no differences between the very different species is probably due to multiple levels of variation. In the Tropical Oriole (the home-range size is large compared to our species, about 7 ha vs an average of 1.4), home-range positions shifted by an average of about 100 m between seasons, approximately 67% of the home-range radius (Odum *et al.* 2019). So again, this result for the Oriole is similar to our data.

Returning to the final statement in the Introduction, these two comparisons show that the centroid approach is effective, informative and useful, for comparing home-range data between different studies and species. In addition, there is evidence (as yet scant) that this approach may uncover principles associated with breeding ecology and territoriality that are common across species and habitats.

The final question we addressed using home-range centroids was nest placement. The data were expressed as distances of nests from the associated male home-range centroid (Table 2) and again, there are no differences between the species. As stated in the Introduction, nest placement is considered to involve complex choices in which many factors

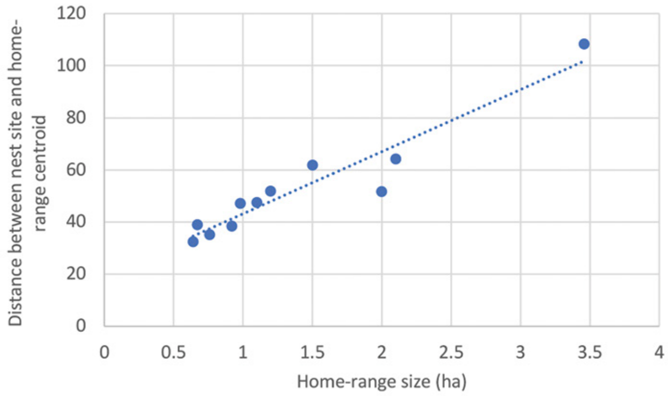

Figure 4. Average distance between nest position and the associated male home-range centroid vs home-range size (from Guppy *et al.* 2023) for the 11 species. R^2 = 0.91.

are taken into account. We were looking for any indication that nest placement was influenced by the position of the home-range centroid. There is a strong correlation between nest to centroid distance and the size of the home-ranges, the size of the home-range explains 91% of the variation in nest to centroid distance (Figure 4). Figure 5 shows some example plots for some of the species, of the sightings used to determine home-ranges, the home-range centroid and the nest sites. We interpret these data as evidence that the birds are selecting nest sites according to a variety of considerations. So in a bigger home-range there are more options for a nest site at a greater distance from the centroid. Proximity to the home-range centroid appears not to be given priority. This conclusion is in contrast to the only other study that has used centroids to address this question. The nests of the Willow Ptarmigan are located closer (but only by 12%) to the centroids of the home-ranges (median = 80 m) than to sites selected at random (median = 95 m) (Schieck and Hannon 1993).

Acknowledgements

This study was done under Scientific License number SL100520.

We were helped immeasurably by a group of dedicated bird banders led by Anthony Overs, operating under banding licence numbers 2195 and 2857. We also thank the Australian Bird and Bat Banding Scheme for the supply of numbered metal bands.

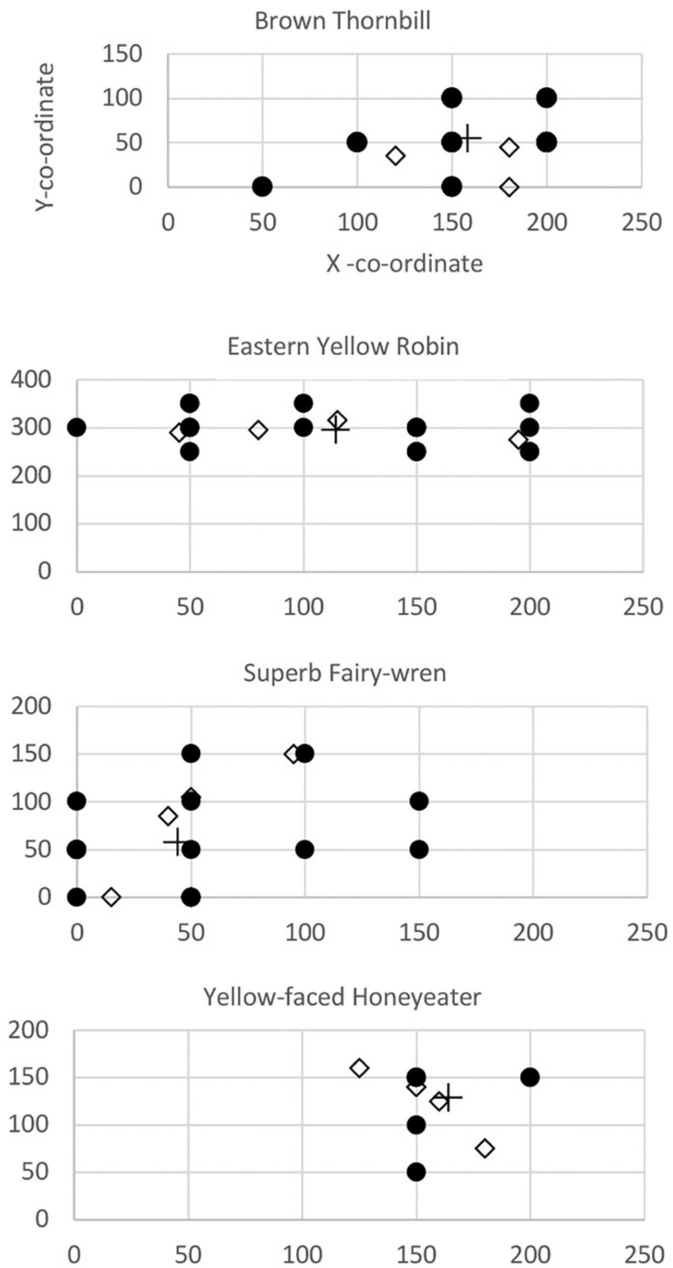

Figure 5. Plots for one season, for one male of each species, showing the sighting data used to determine the home-range, the centroid calculated from the sighting data, and the position of the nests. Filled circles: sightings; open diamonds: nest positions; cross: centroid. Number of sightings for each individual: Brown Thornbill, 19; Eastern Yellow Robin, 18; Superb Fairy-wren, 18; Yellow-faced Honeyeater, 7. Note that multiple sightings at the same point show as one point.

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