6. Home range and movements of adult Asiatic houbara (*Chlamydotis [undulata] macqueenii*) in Mahazat as-Sayd Reserve, Saudi Arabia

Abstract

I determined the home ranges of Asiatic houbara in Mahazat as-Sayd Reserve, Saudi Arabia, from the post-breeding period in 1995 to the breeding season in 1998, by locating the position of all adults of a radio-tagged population approximately twice weekly. Male and female use of home ranges and site fidelity were compared in different seasons using two home range indices. I found that individuals sometimes occupied overlapping home ranges, and inferred that they interacted with each other. Home ranges of males described using 70 % Bivariate Normal Ellipses were greatest in size during the pre-breeding season (mean = 19700 ha) and smallest during the breeding season (9650 ha), whereas female home ranges were greatest during the breeding season (22050 ha), and smallest during the pre-breeding period (9820 ha). Differences in home range size between the sexes were not significant except in the breeding season in 1996, when female home ranges were larger than male ranges. Core ranges described using 70 % Hierarchical Incremental Cluster Analysis were multi-centred (1 – 4 cores), and were similar in size for males and females (630 – 1000 ha). Distances between sequential locations were large (mean = 2.2 – 7.4 km), indicating that individuals frequently used all parts of their core ranges, regardless of its size, and there was moderate site fidelity by individuals for their core range areas: 47 – 50 % of observations over nine four-month observation periods were of individual houbara within the same core range. Similarly, repeated use of pre-breeding, breeding and post-breeding ranges by an individual was recorded for 36 – 53 % of observations, and therefore there was some degree of seasonal site fidelity. However, the area of overlap in seasonal ranges was generally low (60 – 80 % had < 25 % overlap). Home range areas were not exclusive, and the centres of home ranges overlapped with neighbouring individuals in most seasons, when compared with randomly generated nearest neighbour distances. Analyses of dynamic interactions using Jacob's Index showed that houbara were positively associated with each other on 9.4 % of all occasions. Associations were not spread randomly amongst the population: in the breeding season females associated with males. In pre- and post-breeding periods more associations occurred, and most were of birds of the same sex, whereas mixed-sex associations were rare. Female-male associations in the breeding season are likely to be breeding interactions, but the biological significance of single sex associations in non-breeding seasons is unclear. I discuss four non-exclusive hypotheses for differences between sexes in breeding season home ranges: mate, nest-site or food searching by females, and contraction of range by males during display, and suggest future directions for research on houbara movements.

Introduction

Understanding the behavioural ecology of an animal is greatly enhanced if detailed information is collected on the location and pattern of movement of the animal within its environment, and relative to other animals. These locations and movements collectively make up an animal's home range (White & Garrott 1990). Home ranges have been defined as "the area traversed by the individual in its normal activities of food gathering, mating and caring for young" (Burt 1943), but this definition lacks objectivity because "normal" activities are subjective measures (White & Garrott 1990). As a refinement, Robertson *et al.,* *(*1998) described home ranges as "an area within which lies a specified proportion of an animal's trajectory over a specified period".

There has been much debate about the value of home range analyses in describing anything meaningful about the activities of an animal (see Harris *et al.,* 1990, White & Garrott 1990, Robertson *et al.,* 1998). This debate centres mostly on the range of techniques available to analyse locations, and their appropriateness. There are three primary issues. First, because every site at which an individual is located is joined to every other one of its locations, then these locations are not independent i.e., they are autocorrelated (see Swihart & Slade 1985, Worton 1987, Harris *et al.,* 1990, de Solla *et al.,* 1999). Second, there is a lack of quantitative evaluation of the plethora of techniques available (e.g., Dixon & Chapman 1980, Alldredge & Ratti 1986, 1992, Worton 1989, Seaman & Powell 1996, Robertson *et al.,* 1998), and third, regardless of the effort put into collection of large samples of locations, most techniques provide only descriptive measures of an animal's movements, and therefore the usefulness of comparisons within species among studies, or between species, is severely limited (White & Garrott 1990, Aebisher *et al.,* 1993). Recent work by Robertson *et al.,* *(*1998) provides a comparison of seven of the most commonly available techniques at 11 different core estimates, and they concluded that the techniques ranged from those that describe a high density of trajectory points, but have low outline stability and are highly sensitive to sample size (i.e. Hierarchical Increment Cluster Analyses, "HIC"), to those that have low trajectory point densities, but have high outline stability and are relatively insensitive to sample size (i.e. Bivariate Normal Ellipses, "BNE"). Therefore, they recommend that a combination of techniques be used, depending on the analyses required.

Most studies on Asiatic houbara (*Chlamydotis [undulata] macqueenii*) have focussed on surveying population status (e.g., Mian 1984, 1989, Surahio 1985, Seddon & van Heezik 1996, Gubin 1996), migration (e.g., Osbourne *et al.*, 1997, Launay *et al.*, 1999), habitat use (e.g., Combreau & Smith 1997, Osbourne *et al.*, 1997, van Heezik & Seddon 1999), or population restoration (e.g., Gubin 1992, Seddon *et al.*, 1995, Saint Jalme *et al.*, 1996b). Home range size and details of local movements have been reported only three times in the literature. Van Heezik & Seddon (2002) tracked one sub-adult female houbara for 11 months in Harrat al Harrah Reserve in northern Saudi Arabia. That houbara used three patches of 20 $- 203$ km^2 in area (Kernel method, outline size not given), and spent one period of 49 days between February and April roaming widely (14.3 $-$ 59.1 km between successive sightings). Osbourne *et al.*, (1997) used satellite signals to find three houbara on the ground during one winter in Abu Dhabi. Those birds also used patches, and these had areas averaging about 40 km^2 (75 % BNE, N = 3 $-$ 21 locations cluster), that were 14 $-$ 34 km apart. Combreau *et al.*, (2000) reported on movements of mostly 1 $-$ 2 year old houbara in Mahazat as-Sayd Reserve, immediately after their release. In that study houbara had not yet established stable range areas, and home ranges were strongly and positively correlated to time in the reserve after release. Values given for 100 % Minimum Convex Polygons (MCP) were 116 $-$ 997 km^2 for all birds. Three of these birds (1 male and 2 females) were considered to be breeding, but evidence for breeding by the male is unclear. These three birds had small ranges during the breeding season (100 % MCP, 3 $-$ 11 km^2).

Undoubtedly, little detailed study of the movements, home range and interactions of houbara has ever been attempted because they are difficult to catch and follow (Launay *et al.*, 1999, Seddon *et al.*, 1999, Maloney 2001), and because they range over very large and remote tracts of desert and semi-desert (del Hoyo *et al.*, 1996). One method of studying a population of houbara is to breed birds in captivity and tag them before release. This technique has been used by the National Commission for Wildlife Conservation and Development in Taif, western central Saudi Arabia, and has enabled researchers to release and establish a wild population of houbara in the Mahazat as-Sayd Reserve (Seddon *et al.*, 1995, Combreau & Smith 1998). All houbara released into Mahazat as-Sayd Reserve have been fitted with solar-powered backpack transmitters, and coupled with detailed data on breeding status (Chapter 4), the population offers a unique opportunity to study closely the movements, interactions and home ranges of free-living houbara.

In this chapter, I aim to describe the movements of a population of adult houbara, and compare these movements between males and females, and between seasons. Specifically, I compare home ranges, distances between successive locations and between range centres, home range overlap, site fidelity and dynamic interactions of male and female houbara in Mahazat as-Sayd Reserve, from the post-breeding season in 1995 to the breeding season in 1998.

Methods

Sampling programme

I used a standardised sampling programme, where I searched for each bird for two to four times per week, by vehicle or by air. However, because not all birds were found during every search the number of locations collected from each bird varied. All houbara that were adults (one-year-old or greater) in 1995 or thereafter, and were regularly located in the reserve, were included in the analysis. These birds were the surviving subset of those released as sub-adults between 1992 and May 1995 by previous researchers, or by myself after June 1995 (Chapter 3). All were fitted with back-mounted solar-powered radio-transmitters (Telemetry Systems Inc., Mesquon, WI, USA; or AVM Instrument Co. Ltd., Livermore, CA, USA) at the time of release.

For Hierarchical Cluster Analysis (HIC, below) I selected 18 locations per annum, based on the collection of six locations per month, for each individual in each of three seasonal periods. The three seasonal periods were January to April (breeding season, wet and warm), May to August (post-breeding, dry and hot), and September to December (pre-breeding, cool and wet). These periods were determined by dividing each calendar year into three equal periods of four months each, and they reflect approximate changes in both climatic conditions and breeding status for houbara (see Chapter 4, Appendix 1). Where more than 18 locations were available, I sub-sampled points in a stratified random manner to ensure that at least one location was included for each week of the sample period. Where fewer than 18 locations were available, the individual was excluded from the analyses for that period. Individual houbara were the sample unit of interest, thus sample size (N of houbara) varied

between, but not within, time periods (Table 6.1). For BNE analyses, all sample points from each bird were included.

Table 6.1: Sampling periods (nine season-years and three seasons), number of male and female houbara, total and mean locations by sex for BNE, and total locations for HIC home range analyses.

Season-year	N females	N males	N female BNE locations	N male BNE locations	Mean BNE locations per female	Mean BNE locations per male	Maximum total N locations for HIC
Jan-Apr 96	12	9	315	236	26.3	26.2	378
Jan-Apr 97	14	10	421	265	30.1	26.5	378
Jan-Apr 98	12	8	321	184	26.8	23.0	378
May-Aug 95	10	9	303	265	30.3	29.4	378
May-Aug 96	14	9	429	267	30.6	29.7	378
May-Aug 97	13	10	477	358	36.7	35.8	378
Sep-Dec 95	10	9	255	213	25.5	23.7	378
Sep-Dec 96	14	8	314	169	22.4	21.1	378
Sep-Dec 97	13	9	282	195	21.6	21.7	378
All breeding seasons	15	14	1057	685	82.0	56.4	1134
All post-breeding	15	12	1209	890	80.6	74.2	1134
All pre-breeding	15	12	851	577	56.7	48.1	1134
Total locations			3117	2157			3402

Exceptionally, seven houbara released into Mahazat as-Sayd Reserve were located on different occasions at a second site, more than 100 km east of the reserve. Four of these birds returned to the reserve, of which two were later recorded as breeding adults. Because inclusion of these two adults during the breeding season in 1996 when they travelled to and from the reserve would have greatly inflated home range measures, these birds were excluded from data during that season. A list of all houbara that travelled to this site, and the

dates of their departure to and return from the eastern site are given in Appendix 6. All other houbara remained as residents within the reserve or in its immediate vicinity.

Tracking methods and accuracy of locations

I tracked houbara on the ground by scanning for signals on a Teleonics TR4 scanning receiver attached to a 5 m high four-element yagi aerial that was mounted on a 4WD vehicle. Location of houbara on the ground was rapid. I would drive towards the direction of the signal at speeds of 50 – 80 km/h, while continuously monitoring the strength and direction of the signal, until I had pinpointed the bird or patch of vegetation where it was hidden. I verified movement of houbara during my approach many times by following footprints back to display sites, feeding areas and when taking footprint measurements (Maloney 2001, and see other chapters). Generally, houbara would run away during my approach, or sit and freeze. The distance between my fix of a houbara's location and the last site where it was walking or feeding (as indicated by the spacing of its footprints, Maloney 2001, Appendix 3) was usually 5 – 100 m. Most often I would circle a small patch of vegetation, and the houbara would stay within the cover of the same patch. I rarely pursued birds to the extent that they flew. Where a bird was not seen it was considered alive if the signal was erratic during my approach, and if consecutive locations were in different sites. All driving locations were recorded using Garmin 50 or 75 model Global Positioning System (GPS) units. Birds were located from the air using a single-engine Maule aircraft flying at 300 m a.g.l., fitted with two side-mounted two-element yagi directional aerials. I used the same pilot for almost all flights and together we developed and used a modified flight technique that increased my ability to rapidly locate transmitters without the loss of accuracy. The technique relied on the ability of the observer to assess the relative strength of the signal from each side of the plane, then ask for the appropriate multiples of 10 degree incremental changes in the flight path that the pilot then made rapidly and accurately. These course changes were repeated as often as necessary, and on occasions when signals were overrun 180 degree on the spot turns were employed. Thus the plane was quickly lined up in the direction of the signal without the need to follow the "360 degree circle" or "90 degree angled" flight paths frequently used (White & Garrott 1990, Beaty & Tomkiewicz 1997). Sources of error for ground and aerial tracking are discussed in Appendix 2.

Comparison of home range areas

All home range data were analysed using RANGESV (Kenward & Hodder 1996). I used Bivariate Normal Ellipses (BNE; Jennrich & Turner 1969) to compare home range areas between sexes and seasons because BNE give the most stable estimates of range utilisation (Robertson *et al.*, 1998). Incremental plots of houbara ranges show that range size increases occur slowly using the 80 % of all locations nearest the range centre before greatly increasing in area for the remaining 20 % of locations, and with little variation indicating that most houbara follow this pattern. Therefore, I arbitrarily chose 70 % BNE as the ellipse that represented a large core area, but excluded outlying points. All locations were included because range size is not dependent on the number of locations when using BNE analyses (Jennrich & Turner 1969, White & Garrott 1990).

I further described home range use by measuring distance moved between successive locations. I compared mean distances moved between males and females, and between seasons. Because movement is dependent on the number of locations taken and time between each one, I used N = 18 samples per individual per season, as described above, and therefore I calculated 17 inter-location distances for each houbara per sample period.

Utilisation of core areas

Preliminary plots of locations show that houbara frequently have multiple centres of activity, and therefore techniques that are able to describe these centres separately should provide more realistic appraisals of houbara activity and spatial utilisation. Three indices are commonly used: Harmonic Mean Contouring (HAR; Dixon & Chapman 1980), Kernel Contouring (KER; Worton 1989), and Hierachical Incremental Cluster Analyses (HIC; Kenward 1987). Of these techniques, HIC is considered the most effective technique at describing core centres of activity (i.e., the sites of greatest trajectory density, Robertson *et al.*, 1998). I selected a maximum edge of 70 % to exclude the few outlying locations that greatly increased home range area. Like most other home range indices, HIC is sensitive to the number of locations collected per sample period. Recent work has indicated that none of the above indices gives stable area measures with fewer than 500 locations (Robertson *et al.*, 1998). Because home range area increases as the number of locations increase, the most critical factor for comparative studies is to ensure that sample size is even among individuals over the same time period (Boulanger & White 1990, Aebischer *et al.*, 1993, Swihart &

Slade 1997, Robertson *et al.*, 1998). I used N = 18 locations per sample period for HIC analyses, as described above.

I compared mean HIC areas for each individual between sexes, for each season, using Mann-Whitney U-tests. I used non-parametric U-tests here because home range data are non-independent, and there is no non-parametric equivalent of two-way ANOVA for unrelated data (Siegal & Castellan 1988). Because I undertook multiple comparisons of the same hypothesis, I divided alpha (0.05) by the number of pair-wise comparisons (N = 9 season comparisons) using the Dunn-Bonferroni procedure (Marascuilo & McSweeney 1977). Therefore, the adjusted significance level for these tests was P = 0.0055.

Site fidelity of individual houbara

I considered whether individual houbara utilised the same area of the reserve over time (i.e. showed strong site fidelity), by comparing an individual's core home ranges over nine season periods, and over three years. For each individual, their home range could either overlap with home ranges from previous seasons, or be separate (non-overlapping). The proportion of home range areas between seasons that either overlapped or did not overlap between seasons, and for all seasons between years, were compared using Chi-square contingency table analyses. Home range overlap was assessed by generating overlap matrices based on 70 % HIC ranges for each individual in each of nine periods (summer 1995 to the breeding season in 1998), and in each of the three seasons (pre-breeding, breeding, post-breeding). HIC ranges were used because they best represent core areas of range utilisation (Robertson *et al.*, 1998).

Analyses of interactions between individuals

I used three measures (level of home range overlap, spacing of home range centres, and occurrence of dynamic interactions) to determine whether houbara have overlapping home ranges, and hence were likely to interact actively with one another. As for site fidelity, I used Chi-square contingency table analyses to examine whether home ranges overlapped for each season-year group and for breeding, pre- and post-breeding groups. Significant levels of home range overlap indicate timing of possible interactions, whereas significant levels of non-overlap indicate periods of avoidance. Home range overlap values were determined by

generating overlap matrices based on 70 % HIC ranges for every possible pair combination in each of the nine season and year groups.

Spacing of home range centres was determined using nearest neighbour analysis (Clarke & Evans 1954). I used 70 % BNE values for comparisons of home range centres of houbara in each of three seasons, from summer 1995 to the breeding season in 1998. BNE indices were used because cluster analysis techniques (e.g., HIC) do not describe home range centres (Kenward & Hodder 1996), and because BNE gives more stable results than polygon methods (Robertson *et al.,* 1998). Boundary settings used were half of mean N – N distances (Kenward & Hodder 1996). Resulting observed t-test values were compared to an expected t-value generated from a sample of 1000 random locations using critical values of $t_{0.05(2)}$ given in Zar (1996, Table B.3).

I examined dynamic interactions (Macdonald *et al.,* 1980) between individuals to gauge the level of social interaction. I used the dynamic interaction function of RANGESV (Kenward & Hodder 1996) for the analyses, which does not require either independence between locations, or parametric distribution of the data (Kenward 1992, Aebisher *et al.,* 1993). Dynamic interaction occurs either as "association", where locations from two individuals were recorded at the same location at the same time, or "avoidance", where individuals use the same range at different times (Macdonald *et al.,* 1980, Kenward & Hodder 1996). The program calculates mean, geometric mean and median distances between each pair of individuals recorded at the same time and day, then compares this observed distance with all possible distances calculated when each pair member was at each of its other locations. Comparisons were made using Jacob's Index (Jacobs 1974 in Kenward & Hodder 1996). Index values approach +1 if two animals are associated, and –1 if they are avoiding one another. I report the Jacob's Index scores for the geometric mean values because they provide the greatest consistency (Kenward & Hodder 1996). I considered Jacob's Index scores of > +0.5 as indicating that animals were associated, and scores of < -0.5 as indicating animals that were actively avoiding one another. I calculated the proportion of interactions that were between same-sex (F-F; M-M) or different-sex (F-M) pairs in each season, and tested for a difference in the number of interactions between same- and different-sex pairs by season using a Chi-square test.

Autocorrelation

Autocorrelation among locations was not specifically measured in this study, for two reasons. First, movements of houbara were not restricted. Houbara are excellent flyers that are international migrants, are capable of movements of several hundred kms in one or two days (Osbourne *et al.*, 1997), and could easily cross the length of the study area (50 – 70 km) in a single flight. Second, I chose a sampling regime that set the minimum time between two successive samples as one day, and collected most samples at two to four day intervals. Third, all points on a trajectory of movement are valuable in that they represent where an animal moved. Where appropriate I sub-sampled data sets to give even sample sizes for comparison amongst individuals within time periods. I included all data where analytical techniques did not require independence between locations (e.g., BNE; Jennrich & Turner 1969).

Results

Home range area

For all seasons and years combined 70 % BNE home range area (mean ± 95 % C.I.) was similar between females (16660 ± 4040 ha) and males (13250 ± 2950 ha). There were no significant differences in home range size by sex for any of nine season-year comparisons (Mann-Whitney U-tests, Dunn-Bonferroni adjusted rejection level was P = 0.0055, all values were > P = 0.05, except in the breeding season 1996, P = 0.009, pre-breeding 1996, P = 0.041). Generally, patterns of mean home range size was similar between years: in all three summers, and in two of three breeding seasons, female home ranges were larger than males, and in all three pre-breeding seasons, male ranges were greater than those of females (Table 6.2, Fig. 6.1). Male 70 % BNE home ranges were significantly smaller in size in the breeding season compared to their pre- and post-breeding ranges, whereas there was no significant difference in the size of female ranges between seasons (Kruskal-Wallis tests; males, H = 11.72, D.F. = 2, N = 81, P = 0.0029; females, H = 3.88, D.F. = 2, N= 112, P = 0.14)
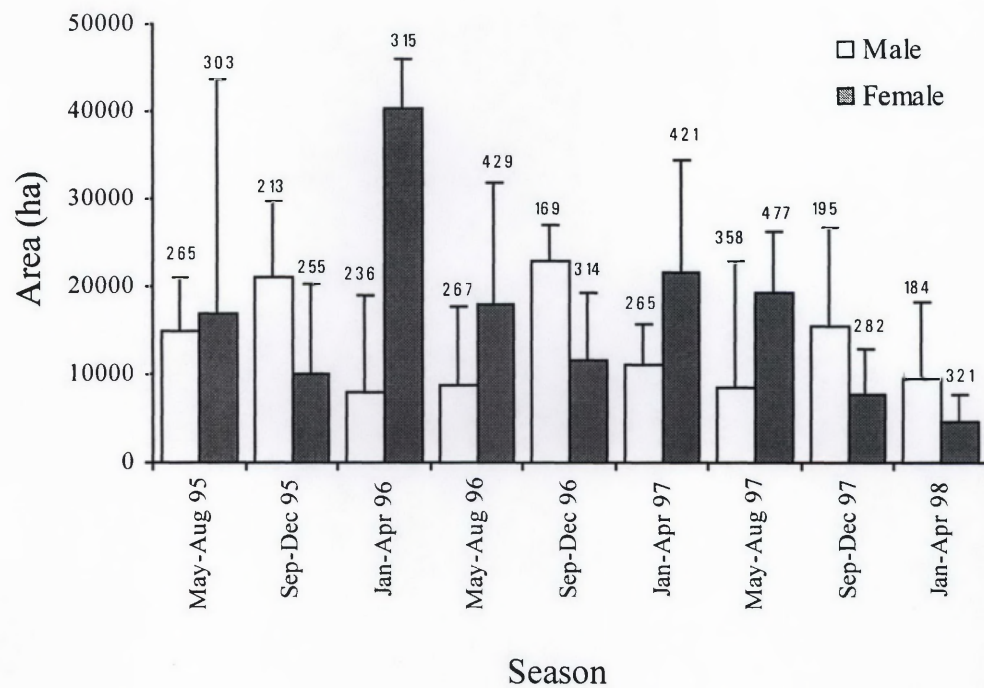
Figure 6.1: Mean (± 95 % C.I.) home range areas calculated using the 70 % Bivariate Normal Ellipse method for male and female houbara in each of nine seasonal periods from May 1995 to March 1998. Breeding season is Jan-Apr, post-breeding is May-Aug, and pre-breeding is Sep-Dec. Numbers above bars = total number of locations per period. N values for males and females are given in Table 6.1.

Comparisons of core areas using 70 % HIC showed similar patterns to elliptical ranges. For all seasons and years combined core home ranges were similar in size for females (870 ± 230 ha) and males (800 ± 190 ha). Female core home range was significantly greater than males in the 1996 breeding season (Mann-Whitney U-test, $P < 0.01$), otherwise there were no significant differences in seasonal core range size between the sexes (all other comparisons, $P > 0.05$). As with BNE ranges, the general pattern over the three study years was for core home ranges to be larger for males during the pre-breeding period (Table 6.2, Fig. 6.2). Within sexes, male core (70 % HIC) ranges were smaller during the breeding season compared to post-breeding, with pre-breeding ranges intermediate in size (Kruskal-Wallis test, $H = 12.94$, D.F. = 2, $N = 81$, $P = < 0.01$). Female core ranges were not significantly different in size between seasons, with a trend towards smaller core ranges during breeding and larger ranges post-breeding in 1997 and 1998, but not in 1996 (K-W test, $P > 0.05$, Fig. 6.2).

Houbara used 1 – 4 (mode = 2) core areas within a season. The number of cores was similar in the breeding and post-breeding seasons, and although more houbara had three cores and fewer had one core in the pre-breeding season, these differences were not significant (K-W tests, P > 0.05; Fig. 6.3).
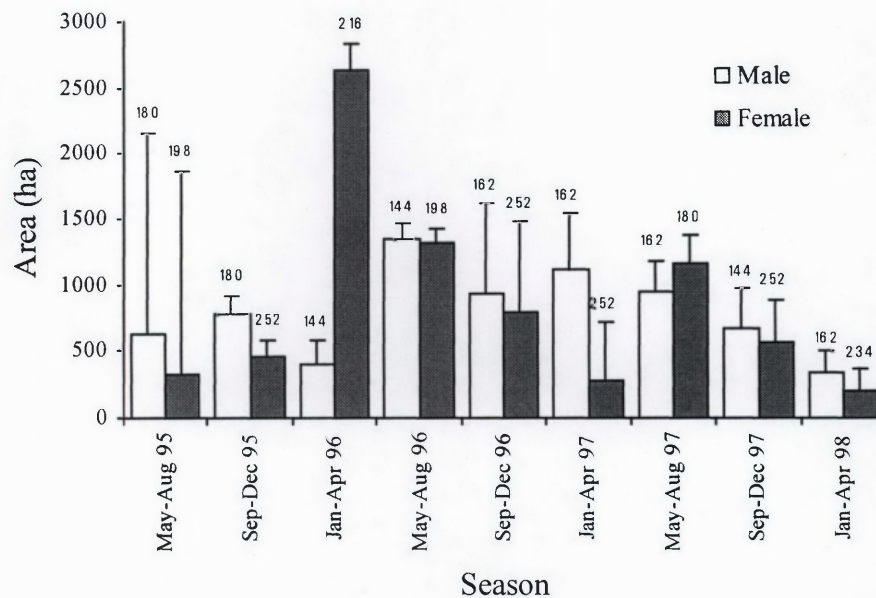
Figure 6.2: Mean (+ 95 % C.I.) core home range areas calculated using the 70 % Hierarchical Incremental Cluster Analyses method for male and female houbara in each of nine seasonal periods from May 1995 to March 1998. Season periods as per Fig. 6.1. Numbers above bars = number of males or females from Table 6.1 multiplied by 18 (the fixed number of locations).

Table 6.2: Mean home range (ha) and 95 % C.I. values for male and female houbara in the breeding, pre- and post-breeding seasons (N = 3 years combined) as determined using BNE and HIC home range indices. Data rounded to nearest 10 ha. Sample sizes are as per Table 6.1.

	Males		Females	
70 % BNE	Mean	95 % C.I.	Mean	95 % C.I.
Breeding	9650	4340	22050	8840
Post-breeding	10600	3740	18120	6610
Pre-breeding	19700	6940	9820	2910
70 % HIC				
Breeding	640	940	1000	520
Post-breeding	970	990	990	340
Pre-breeding	790	630	630	160
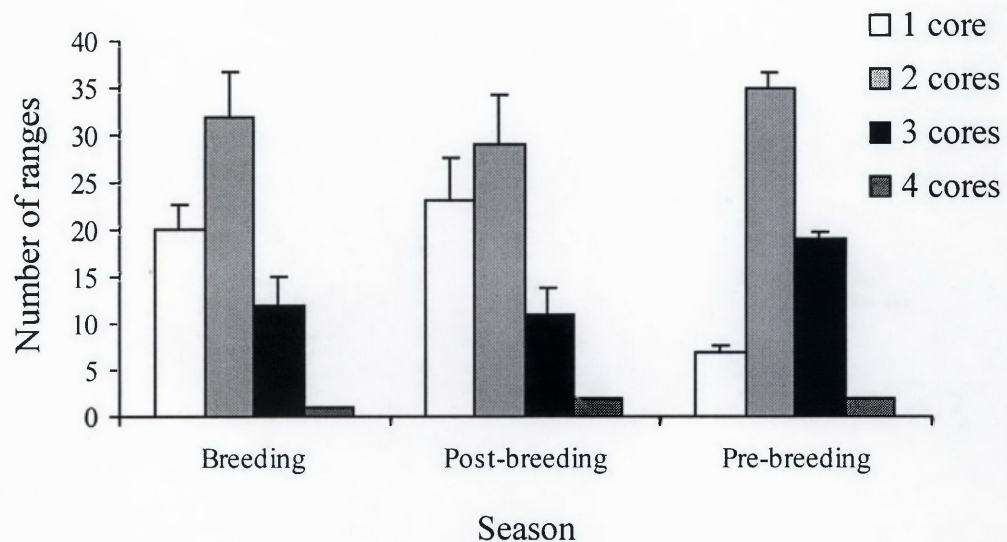
Figure 6.3: Mean (+ 95 % C.I.) number of home range core areas per houbara per season over three years. Season periods as per Fig. 6.1.

Distances between locations and patterns of movement

Mean distance moved between successive locations was 2.2 – 7.4 km throughout the study, and seasonal comparison of inter-location distances showed similar patterns to area analyses. Mean distance between successive locations was significantly greater for females than males in the 1996 breeding season (U-test, P < 0.0001; rejection level P = 0.0055). No other inter-sex seasonal comparisons were significant, and except for the breeding season in 1998 (P = 0.035) and the 1995 and 1997 pre-breeding periods (P = 0.021, P = 0.012, respectively), P was > 0.05 (Fig. 6.5).

Movements of individual houbara frequently followed a similar pattern. Within each season, each bird stayed in one small core area for a few weeks then moved quickly to another core area where it again stayed for another few weeks, and so on. Up to four of these cores were discernible within a four-month period. During time spent within a core, there would often be short rapid flights to and from neighbouring vegetation patches, as if the bird was sampling available habitat prior to moving to a new location. Core areas were frequently separated by several km, meaning that mean inter-location distances were usually long, as houbara traversed unused space between feeding sites. Typical movement patterns for three male and three female adult houbara are shown in Figure 6.4.

Site fidelity

Houbara showed moderate site fidelity between sample periods. A total of 47 % of female and 50 % of male core ranges (70 % HIC) from each four month long period overlapped with a core range from the same individual in a different time period (N = 209 possible range overlaps for 13 males, N = 378 possible overlaps for 15 females). However the area of overlap was small; 76 % of observations of males and 73 % of females were of ≤ 25 % overlap. There was a moderate level of year-to-year site fidelity among individual houbara. Between 36 – 53 % of core home ranges (70 % HIC) were used at the same time of year in different years by the same bird. The proportion of use was not significantly different between sexes within each season (Yates corrected χ^2 tests, P > 0.05), or between seasons for each sex (χ^2 tests, P > 0.05; Fig. 6.6). The trend was for a greater proportion of females to have overlapping core ranges compared to males, with more use of the same range by females in pre- and post-breeding seasons than in the breeding season.
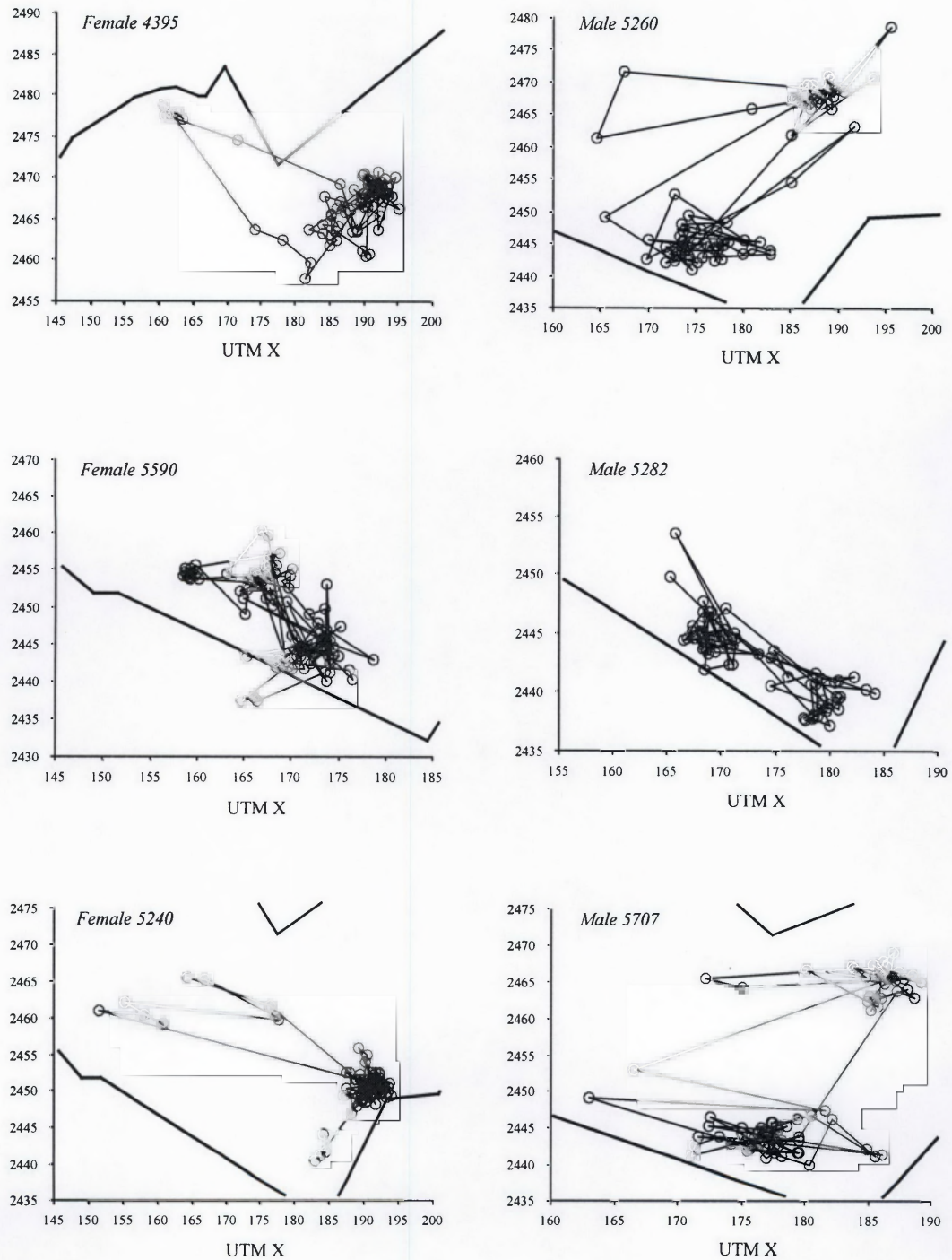
Figure 6.4: Movement patterns for three male and three female adult houbara (tx frequencies given) over a one-year period in Mahazat as-Sayd Reserve in 1997. Time between locations is 1 – 4 days. Dark line is reserve boundary. Scale is in km, and differs between graphs. UTM co-ordinates as per Figure 3.3.

Although core ranges often overlapped, the area of overlap was usually small. Overlaps of ranges in all three seasons by both sexes represented 1 – 25 % of the core range area for between 50 – 100 % of all overlap observations. There was much variation between individual houbara; some male and female houbara used the same core areas in multiple seasons, whereas others never used the same areas (Fig. 6.7). The proportion of overlapping area tended to be greater (more than 50 %) in the post-breeding season when core ranges were overlapped for 21 % of male and 22 % of female observations, compared with < 15 % of observations during the breeding and pre-breeding seasons. Males never used more than 25 % of their pre-breeding ranges in more than one year, whereas females often re-used a large proportion of core pre-breeding areas; 34 % of female overlaps in the pre-breeding season had areas > 25 % (Fig. 6.7, Fig. 6.8).
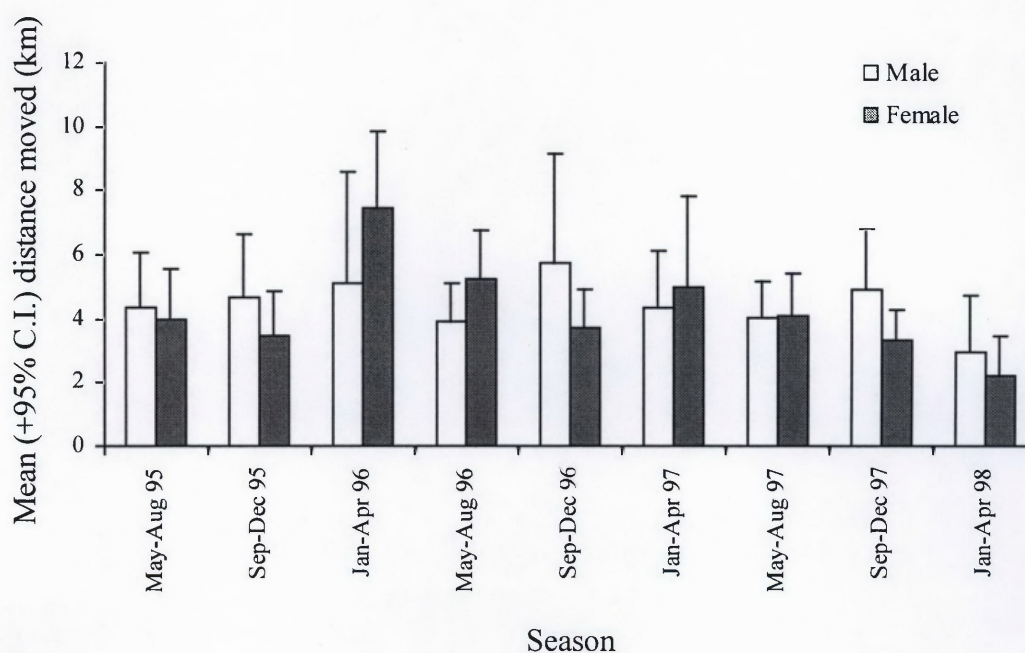
Figure 6.5: Mean (+ 95 % C.I.) distance (km) moved between successive locations for male and female houbara in each of nine season-year periods from May 1995 to March 1998. Inter-location distances are based on a sub-sample of N = 18 locations per season-year per houbara. N of houbara and locations are given in Table 6.1.
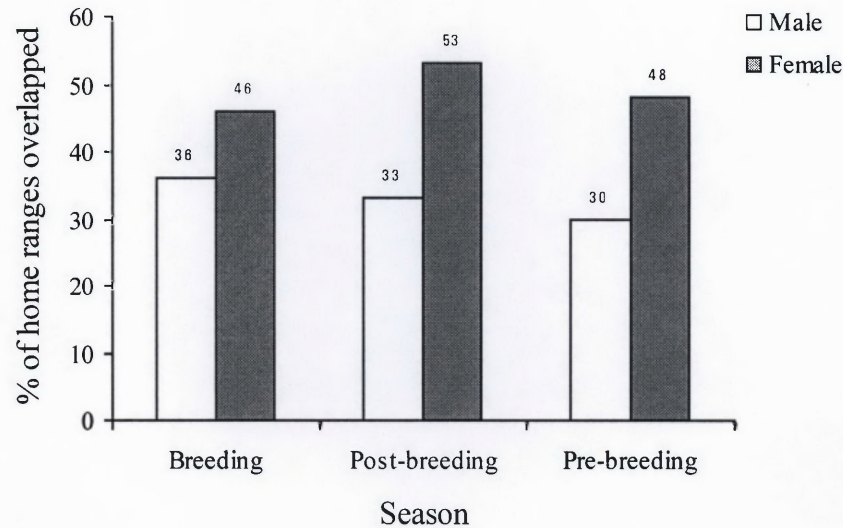
Figure 6.6: The proportion of individual houbara home ranges (70 % HIC) that were overlapped with at least one other of its own core ranges from another season, for males and females in the breeding, pre- and post-breeding seasons. Numbers above bars are the total N of possible overlaps for all individuals per season. N individuals available are given in Table 6.1.

Interaction analyses

Overlap of 70 % HIC core ranges occurred for 11 – 45 % of all possible paired combinations among individuals (Table 6.3). The number of paired combinations with overlapping home ranges differed among seasons and years (χ^2 = 115.1, D.F. = 8, P < 0.0001), because there were significantly fewer overlaps in the breeding season than in pre- and post-breeding periods (χ^2 = 88.1, D.F. = 2, P < 0.0001). For combinations that overlapped, the mean size of the overlap did not differ significantly between seasons (Kruskal Wallis test, H = 1.69, P > 0.05, Table 6.3). Most houbara had home ranges that overlapped with at least one other individual, but nine females and four males had exclusive core ranges for at least one season-year comparison. Over the three seasons and three years (i.e. nine periods) there were 20 occasions (15 in the breeding season, two in post-breeding and three in pre-breeding) when home ranges were exclusive: 16 of these were female ranges, and four were male ranges. One female (tx5240) maintained an exclusive home range for five of the nine periods

measured, and this female, as well as female tx4412, were the only females that had exclusive ranges in pre- and post-breeding seasons (Table 6.4).

Table 6.3: Total number of possible home range (HR) combinations of any two individuals ("pairs"), the percentage of combinations that overlapped, and the mean, and 95 % C.I. values for those combinations that overlapped, for each of nine season-year groups. Jan-Apr = breeding season, May-Aug = post-breeding, Sep-Dec = pre-breeding.

Season-year	N birds	Total N of pairs	% of overlapped pairs to all possible pairs	Mean % HR area overlap	± 95 % C.I.
Jan-Apr 96	21	210	31.4	17.5	3.5
Jan-Apr 97	24	276	13.4	19.4	7.6
Jan-Apr 98	20	190	11.0	7.7	3.2
May-Aug 95	19	171	21.6	17.1	1.9
May-Aug 96	23	253	45.0	23.2	3.1
May-Aug 97	23	253	34.8	24.6	4.7
Sep-Dec 95	19	171	39.8	12.8	2.1
Sep-Dec 96	22	231	44.2	17.7	2.3
Sep-Dec 97	22	231	39.0	19.1	2.7

Table 6.4: Transmitter frequencies of houbara that had exclusive 70 % HIC home ranges (i.e., no home range overlap) for each season-year comparison. Frequencies in bold are males. Normal text are females. Seasons as per Table 6.3.

Season	Season-year	Tx Frequency
Breeding	Jan-Apr 1996	5131
	Jan-Apr 1997	5026, 5113, 5240, 5441, 5358
	Jan-Apr 1998	**4060, 4282, 5385, 5547,** 5026, 5240, 5441, 5496, 5515
Post-breeding	May-Aug 1995	5240
	May-Aug 1996	-
	May-Aug 1997	4412
Pre-breeding	Sep-Dec 1995	5240
	Sep-Dec 1996	-
	Sep-Dec 1997	4412, 5240
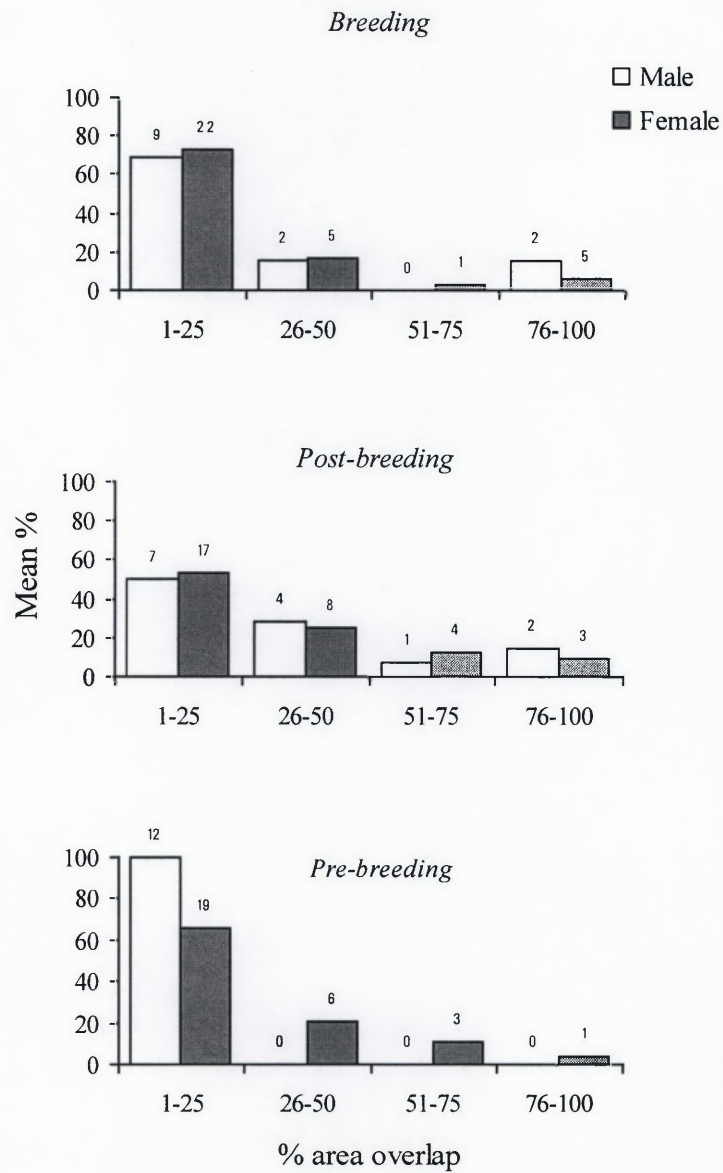
Figure 6.7: Area of overlap categories for individual houbara home ranges (70 % HIC) for males and females in the breeding, pre- and post-breeding seasons. Numbers above bars are the total N of overlapping ranges for each sex in each season.
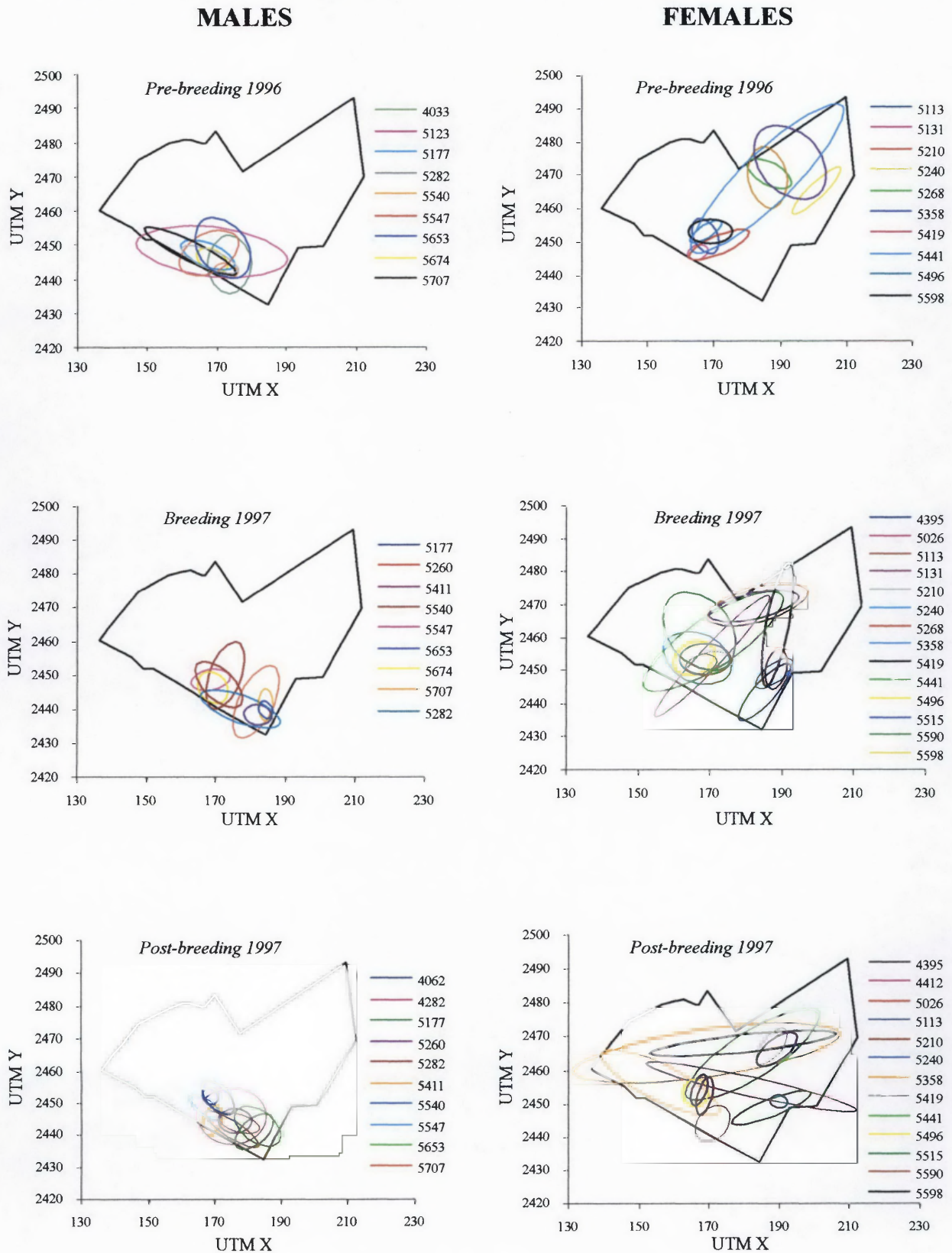
MALES **FEMALES**

Figure 6.8: (A) 70 % BNE plots of representative home ranges of houbara in Mahazat as-Sayd Reserve. Data are from Sept – Dec 1996 "pre-breeding", Jan-Apr 1997 "breeding" and May-Aug 1997, "post-breeding" seasons, for males and females separately. See Figs 6.1 and 6.2 for home range areas for these plots. Bird identifiers are transmitter frequencies. Scale is in km. UTM co-ordinates as per Fig. 3.3.

MALES　　　　　　　　　　　**FEMALES**
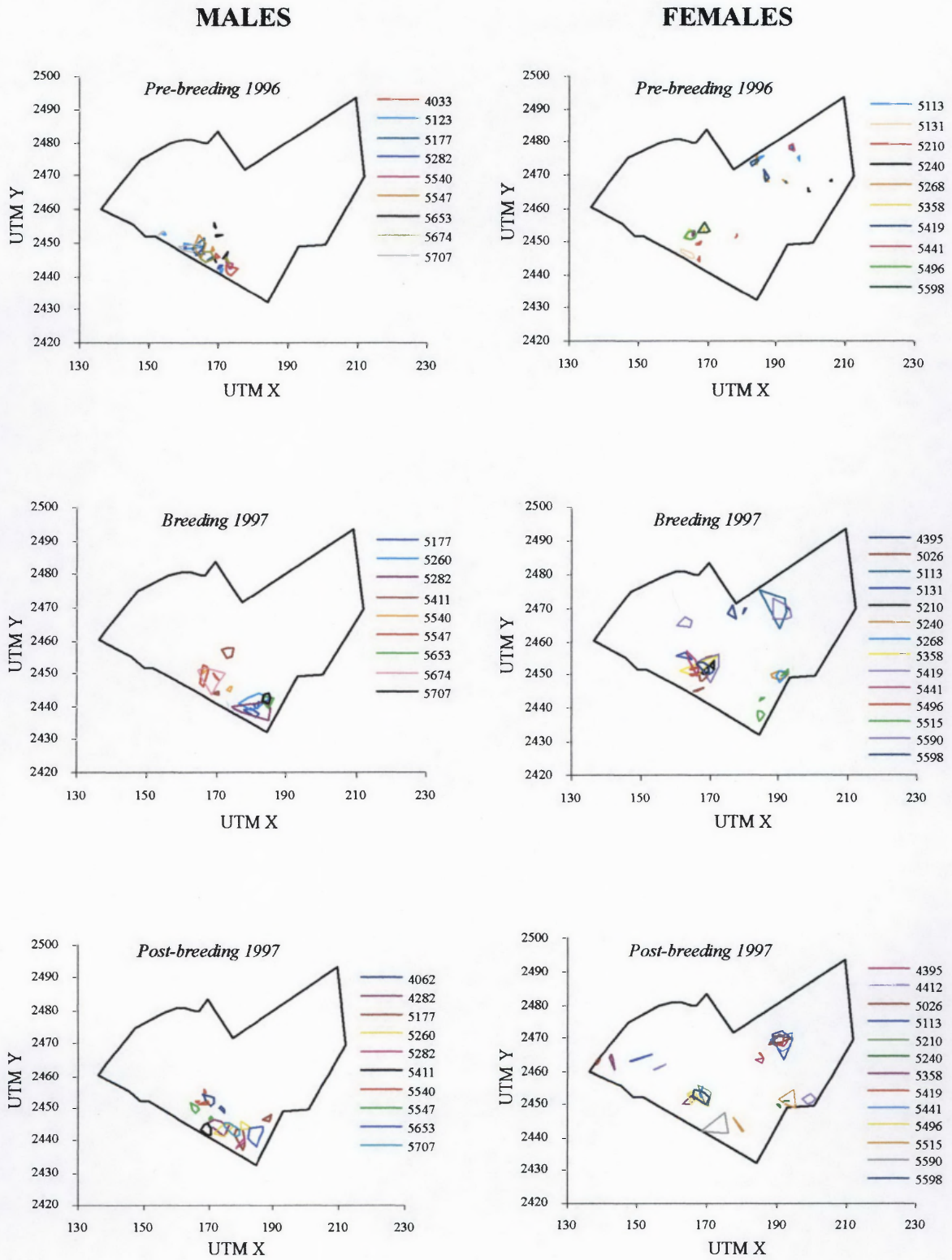
Figure 6.8: (B) 70 % HIC plots of representative home ranges of houbara in Mahazat as-Sayd Reserve. Data as for Figure 6.8(A). Scale is in km. UTM co-ordinates as per Fig. 3.3.

Range centre spacing

Mean range centres were significantly closer than randomly generated spacings in all seasons except the 1997 breeding season, and the 1995 pre-breeding season, when spacings were more regular (t-tests, Table 6.5).

Dynamic interactions

Of 1108 possible pair interactions over three season periods, houbara were positively associated on 104 (9.4 %) occasions. There were no observations of avoidance (Jacob's Index scores < -0.5). The majority of home range overlaps occurred when one or other of neighbouring birds were nearby but not associated (Jacob's Index scores between – 0.5 and + 0.5). Positive associations between houbara (Jacob's Index scores > +0.5) were significantly related to time of year, with fewer associations in the breeding season (N = 16) than in post-breeding (N = 36) or pre-breeding seasons (N = 46; χ^2 = 17.7, D.F. = 2, P < 0.0001, Table 6.6). Within each season patterns of association also varied: in the breeding season the greatest proportion of associations were males with females; in pre- and post-breeding seasons most were females with females. However, differences in numbers of associations within and between sexes per season were not significant (χ^2 = 8.42, D.F. = 4, P > 0.05; Fig. 6.9).

Table 6.5: Observed and random mean and S.E. distances (m) between neighbouring pairs of home range centres, and observed and critical Students t-values, for each season-year group. NS = non-significant, P > 0.05. N = number of houbara included in the analysis each season. Distances rounded to nearest 10 m.

		Observed		Random				
	N	Mean	S.E.	Mean	S.E.	t	Critical t	Significance
Jan-Apr 96	21	2230	510	4600	90	4.55	2.080	P < 0.001
Jan-Apr 97	24	3650	980	5370	100	1.74	2.064	NS
Jan-Apr 98	20	3310	1360	6170	120	2.10	2.086	P < 0.05
May-Aug 95	19	2690	870	6260	110	4.04	2.093	P < 0.001
May-Aug 96	23	2010	250	4050	80	7.64	2.069	P < 0.001
May-Aug 97	23	2060	420	4380	90	5.47	2.069	P < 0.001
Sep-Dec 95	19	3090	760	4500	90	1.84	2.093	NS
Sep-Dec 96	22	2180	590	4710	90	4.24	2.074	P < 0.001
Sep-Dec 97	22	1990	490	3870	70	3.83	2.074	P < 0.001

Table 6.6: Total number of positive associations (Jacob Index scores > +0.5) between houbara in each season, the number of possible associations and the % of observed to possible associations. The number of possible associations is the sum of all permutations of all individuals with each other. Total numbers of houbara available were 29 individuals in the breeding season (N = 15 females, 14 males) and 27 in each of the pre- and post breeding seasons (each N = 15 females, 12 males).

	Female-female	Female-male	Male-male	N observed	N possible	% total to possible
Breeding	5	9	2	16	406	3.9
Post-breeding	20	6	10	36	351	10.2
Pre-breeding	21	14	11	46	351	13.1
Total	46	29	23	104	1108	$X = 9.4$
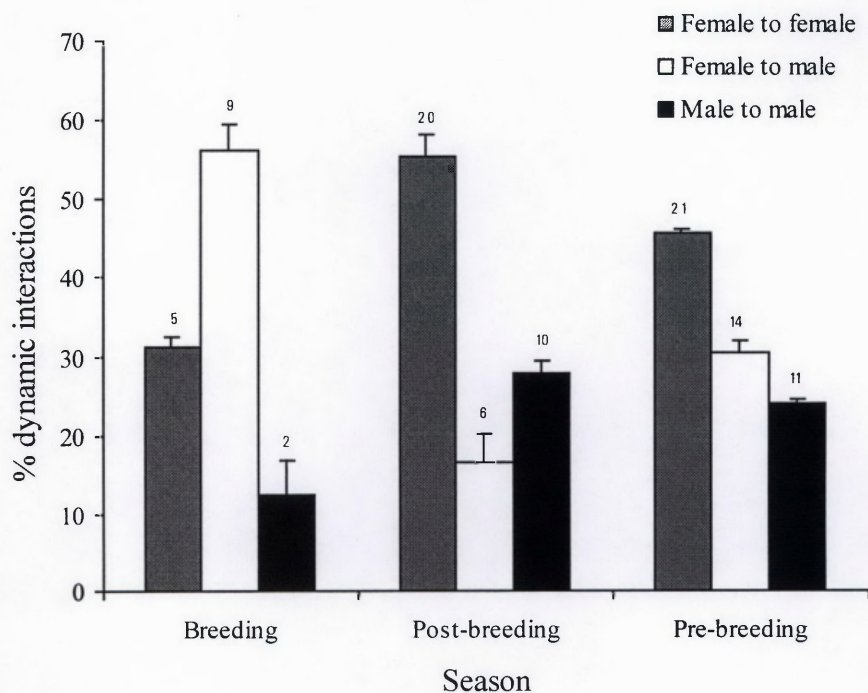
Figure 6.9: Proportion (± 95 % C.I.) of interactions that were female-female, female-male and male-male positive associations per season, for each of three seasons. Numbers above bars are the number of positive associations recorded for each comparison per season.

Discussion

Home range size

Houbara in Mahazat as-Sayd Reserve had large home ranges that were similar in total size for males and females. Only males had seasonally different home range areas, where, relative to pre- and post-breeding season ranges, males had smaller mean home ranges and smaller core ranges in the breeding season. This difference is probably because male ranges contracted during the breeding season when males spent almost all of their time at display arenas. In comparison to males, mean female home ranges were similar in size at all times of year, even though females spend much of the incubation period at or near their nest sites. Breeding females may have been expected to have small home ranges over this period, but female breeding was asynchronous, and when raising precocial chicks, after nest failure and during visits to male lek arenas, female home ranges were large, offsetting the smaller range sizes of nesting females.

Possibly, home range sizes may be smaller for males than females in the breeding season because they had different dietary requirements from females, or lived in different habitats, and therefore could utilise a locally abundant food source that was not accessible to females. In support of this hypothesis, I have showed that both home range overlap and positive associations occurred less frequently in the breeding season than in other seasons, i.e., males and females tend to live in different places in the study area when breeding. However, there are no data available on differences in food requirements for males and females (Cramp & Simmons 1980, del Hoyo *et al.,* 1996), and males and females were inter-dispersed across similar areas of habitat. Therefore, I conclude that the small size of male home ranges relates to display activity, rather than focussing on a rich food source.

Patterns of movement

Individual houbara had a pattern of short movements in core areas over several weeks followed by brief exploratory movements, then large movements to new core areas, and this was similar to the pattern of houbara of movement described by van Heezik & Seddon (2002) for a single wild caught sub-adult houbara in northern Saudi Arabia. In that study, the houbara used a single large patch for a period of three months, moved to another patch for five months, was very mobile for two months followed by another period at another patch.

Movements between patches were preceded by short exploratory movements to and from each patch. All of the single patches (20 – 203 km^2) were much larger than the largest mean patch size of male houbara in Mahazat as-Sayd Reserve (70 % BNE ellipses, ~13000 ha, 11 km^2), probably because vegetation, and therefore food, is more abundant in Mahazat as-Sayd Reserve (Combreau & Smith 1997) than it is in northern Saudi Arabia (van Heezik & Seddon 1999), or because the Harrat al Harrah bird may have been moving large distances in search of other houbara. However, it is difficult to compare the movements of this bird to the general pattern of the houbara I studied, primarily because van Heezik & Seddon (2002) used different methods to analyse home range, their bird was a sub-adult, and their study area was massively disturbed by people at the time the houbara became very mobile. Similarly, Osbourne *et al.'s* (1997) "winter" data on three houbara followed sporadically for 58, 26 and 13 days in April-May, mid-October to mid-November, and October, respectively, offer few meaningful data on range size, movements and interactions at a population level. Data from Combreau *et al.,* (2000) provides more detail on houbara ranges, but their data were mostly from young houbara that had not yet settled into established range areas, and they used minimum convex polygons in their analyses which limits the value of this work (Robertson *et al.,* 1998, Burgman & Fox 2003, and see introduction to this Chapter). Combreau *et al.,* (2000) related the minimum distance moved daily to rainfall, and concluded that rainfall stimulated movements by houbara. However, during their two year study (1994 – 1995) rainfall fell only February to May (mostly March-April), and thus, movements of houbara may have been related to changes in behaviour related to the breeding season (e.g., young males searching for suitable lek sites, young females searching for future breeding sites or males). Except for two females, no breeding activity was reliably recorded during that study.

No other studies have described home range size or detailed local movements of marked individual houbara. Of the other bustards, the great bustard (*Otis tarda*) has been studied in the most detail. Female great bustards in Spain had four different types of movement pattern, partial migration (where individuals move short distances only), sedentary, large-scale migration, and movement from a year-round home range only to mate (Alonso *et al.,* 2000), and this contrasted to the usual commentary for the species as being migratory or sedentary (e.g., Cramp & Simmons 1980, Johnsgard 1991). Alonso *et al.,* (2000) suggested that such partial migration may be common among other bustards, including houbara. Indeed,

movement of houbara females fit well within a pattern of local movements or partial migration to breeding sites. In two of three years of study, home ranges of females were smallest in the pre-breeding season and largest during the breeding season, indicating that there was a seasonal element to movements. These movements were very local in size (< 50 km), and the population is resident year round in the reserve, in contrast to other Middle Eastern houbara that migrate 3000 – 12000 km to Asia to breed (Launay *et al.,* 1999).

Partial migration has been described for other lekking species (Cade & Hoffman 1993, Schroeder & Braun 1993), indicating that there may be a general relationship between breeding systems and movement patterns. However, further evidence is required to clearly show that movements of houbara fit a partial migration pattern. There are several other alternative hypotheses that may explain the patterns of movement described here. Movements of houbara within the reserve may be because food in the reserve is temporally and spatially patchy, and houbara may be merely adjusting their home ranges to suit conditions, i.e., they may have a flexible home range strategy that will vary over longer time periods than this study. In addition, where populations are at low density, houbara may be moving unusually large distances to find mates or for social interaction. Further, regular movement of houbara to other sites may be masked in the Mahazat as-Sayd Reserve population, because the reserve is effectively an island, completely surrounded by land that is over-grazed and hunted. Thus, houbara that leave the reserve may have little chance of living for long periods, and will not have the opportunity to establish regular movement patterns that include areas beyond the reserve boundaries.

Site fidelity

Home range overlap

Overall, overlap in home ranges was high. Mahazat as-Sayd Reserve is approximately 2250 km^2 in area, and houbara home ranges were 11 – 12 km^2. If houbara were distributed evenly over all of the reserve, there would be space for a minimum of 187 home ranges without overlap, and with core ranges of around 0.8 km^2, Mahazat as-Sayd Reserve has space for more than 2600 core ranges without overlap: therefore there is more than enough space for the 30 – 40 resident houbara to live in discrete locations. However, I have shown that core

ranges frequently overlapped within seasons, and distances between nearest neighbours were less than expected by random. This strongly indicates that houbara were selectively using the same parts of the reserve and were under-utilising other parts. A simple plot of all adult houbara locations throughout the reserve shows that houbara were not evenly distributed in all areas of the reserve (Fig 6.10), but were clustered in two main regions to the south, and north east of the reserve. These clusters are more than 10 km from the release site. Locations of breeding (nest site, display arena) sites are discussed in Chapters 4, 5, 7, and 8.
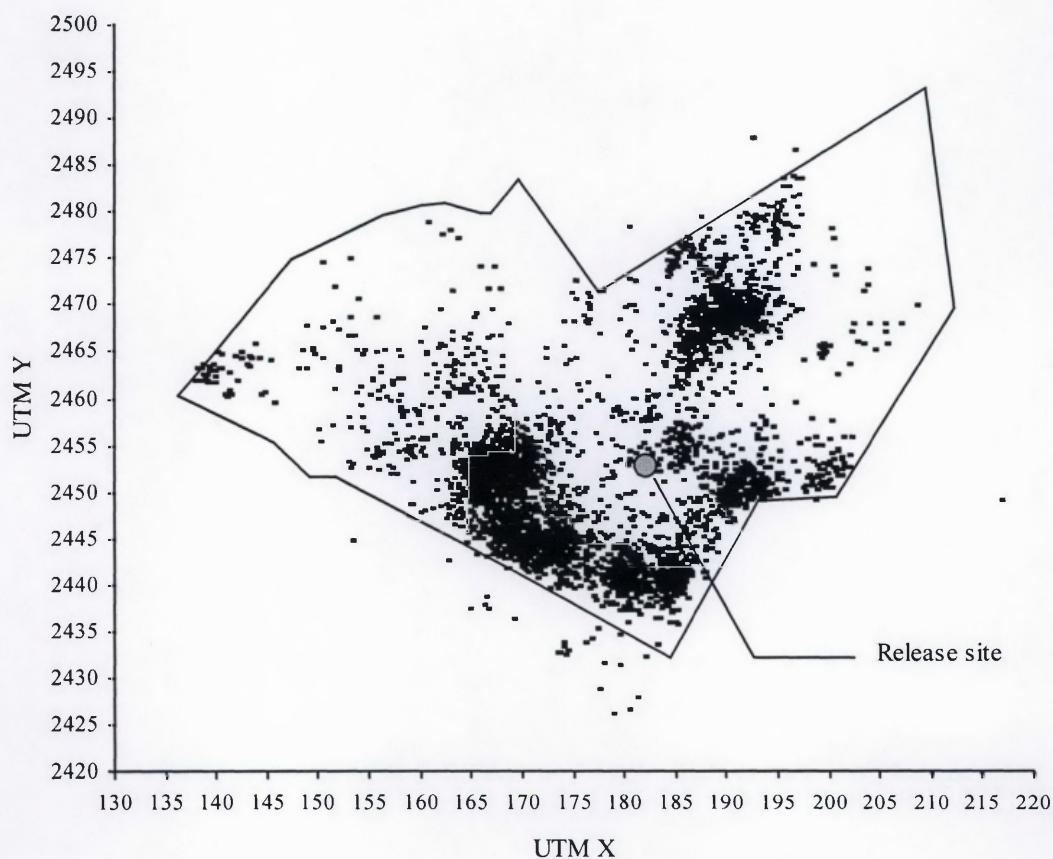
Figure 6.10: Plot of weekly locations of adult houbara in Mahazat as-Sayd Reserve from July 1995 to March 1998, showing pattern of use of the reserve over the three years. N = 5078. UTM co-ordinates as per Fig. 3.3. Scale is in km. Weekly locations are used here, because some birds were visited on a daily basis during the breeding season, and therefore these individuals are over-represented in location data. All areas of the reserve were searched by air or on the ground twice per week from July 1995 to March 1998, and therefore search effort was even over the reserve.

Why did these clusters form? Although my results for home range overlap show that many houbara utilise common areas, the area of overlap was small (< 20 %) relative to total core areas. This indicates that houbara in Mahazat as-Sayd Reserve are not gregarious, and in fact, were rarely found in groups, at any time of year. I suggest that there are two explanations for this clustered distribution. These are: first, the presence of patches of preferred or available food or habitat, and second, social interactions between individuals that attract houbara to common focal areas within the reserve.

Houbara in other populations are considered to flock to sites with an abundance of favoured food that is usually found in very small, discrete patches (e.g., *Capparis spinosa* in northern Saudi Arabia, van Heezik & Seddon 1999). The apparently high likelihood of encountering houbara at these *Capparis* patches means that they are often used as sites for capturing houbara using lines of nooses and several birds can be flushed at the same time from these sites (Seddon & van Heezik 1996, Seddon *et al.*, 1999). However, Mahazat as-Sayd Reserve has few such patches of "favoured" food. *Capparis* was very rare in the reserve (Combreau & Smith 1997, S. Collenette pers. comm., Chapter 5), and houbara almost never used two sites in the reserve that were rich in salt bush (*Haloxylon spp.*), a species often listed as a preferred food (e.g., Surahio 1985).

Where houbara did occur in the same area of the reserve, there was little positive association between individuals. That is, they used the same sites, but they rarely did so at the same times as when other houbara were present. Possibly, this lack of interaction may be because patches were often large in scale, and densities of houbara in the reserve were low, and therefore, there was sufficient space for several houbara to forage at patches without overlap. However, despite differences in rainfall and run-off that frequently lead to a patchy mosaic of green flushes and dry vegetation throughout the reserve, many houbara were found in the same small area over several seasons and years, and showed no propensity to move to new areas of the reserve as food resources changed. From this, I conclude that houbara in Mahazat as-Sayd Reserve do not form groups and that when clustering does occur, it is not a function of food availability or distribution.

Alternative to a distribution based on food supply, houbara may be clustering at preferred sites of the reserve based on habitat types (i.e., structural components of the environment).

Few houbara were recorded in the north east, north west and western regions of the reserve (Fig. 6.10). Small patches of salt bush (Hammada, *Haloxylon salicornicum*) that make up 2.3 % of the reserve area (Chapter 5, Table 5.1) are found in the north east and north west, whereas the north west has no tall shrubs and trees (10.4 % of the reserve), and much of the western region has large areas of basalt (32.5 % of the reserve), with either low or high densities of trees. But, houbara are commonly located in the south of the reserve where trees are present, in the south east where basalt is common, and in the north where basalt is absent and tree density is low. Thus, although habitat differences do occur throughout the reserve, the presence or absence of trees, shrubs or different substrate types does not explain the distribution or grouping behaviour of houbara in the reserve.

I suggest that the few occasions when houbara groups form have a social or behavioural function. Associations between houbara were not random events involving all birds in the surrounding area. There was a tendency for associations to have a gender-based social context. In the breeding season, associations were rare, but those that occurred were mostly between males and females. Outside the breeding season, more associations were recorded and most were single sex groupings: usually females with other females, or less frequently males with other males, and mixed-sex groups were recorded less often. I conclude that male-female associations in the breeding season are related to breeding activity, but further work is now required to understand the function of male and female houbara associations in the non-breeding season.

Site fidelity of individuals

Houbara appear to be very flexible in their habitat requirements and use. Some individual houbara were very settled, and had overlapping home ranges between most seasons, whereas others never used the same sites within the reserve in more than one season. There was no clear pattern here. Individuals that had high site fidelity overlapped with those that had low site fidelity. Therefore, both had access to similar resources, yet some chose to stay in these sites while others moved on. Differences were not related to gender, although females tended to have more overlapping home ranges than did males. While both males and females showed similar levels of variation in fidelity, it was usually females that maintained exclusive ranges, mostly during the breeding season. This may be because females actively chose sites away from other houbara when nesting, or alternatively because in the non-

breeding period, male home ranges increased in size and numbers of female-female associations increased.

Even for houbara that used parts of the same range repeatedly, there was much variation in the degree of overlap. Some individuals included all previously used areas within their home range, but for most individuals the areas they used between seasons and years overlapped very little (< 25 %), indicating an attachment to the general area, but not to a specific site. This fits well with observations that food and habitat within Mahazat as-Sayd Reserve are patchy but widespread, both temporally and spatially (Combreau & Smith 1997), and flexibility is undoubtedly a key survival strategy in this environment. In addition, the reserve is almost certainly not at carrying capacity for houbara, and perhaps only < 20 % of available home ranges are occupied. Thus, houbara may have abundant resources spread over all parts of their range, and therefore, they need not restrict their activities to smaller core areas. In general, birds that live in desert environments tend to be nomadic rather than sedentary because food supply is dependent on irregular rainfall (Serventy 1971, MacLean 1976). Andersson (1980) has shown that nomadism increases where food is cyclic in occurrence rather than random, and nomadic habitats are expected to increase as the time between successive good year's increases. The strong site tenacity of individual houbara in Mahazat as-Sayd Reserve is in contrast to predictions of movements based on the patchy and low rainfall in this desert area, and indicates that habitat may have been generally favourable for the species in the reserve at the time of this study, particularly when compared to the severely over-grazed habitat available immediately adjacent to the reserve.