Territory size variations in wintering Finsch's Wheatears, *Oenanthe finschii*

(Aves: Passeriformes)

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Abstract. Finsch's Wheatear, *Oenathe finschii*, is a widespread winter visitor in Jordan, primarily in arid – semi arid hilly areas with a mean annual rainfall of 100-300 mm. The average territory size in winter varied among the different study areas from 1.6 to 3.4 ha. This variation was not related to productivity and food density, but may have been caused by differences in habitat structure and interspecific territoriality by the Mourning Wheatear, *Oenanthe lugens*, which was present in half of the study areas. Territory size variations were not sex-related although females were apparently excluded from more productive habitats by dominant males.

Key words. Territoriality, non-breeding season, social dominance, Jordan, Middle East.

Introduction

Wheatears (genus *Oenanthe*) are among many passerine birds which exhibit winter territoriality (HARTLEY 1949, SMITH 1971, CORNWALLIS 1975, PANOV 2005). Winter territoriality *per se* is recognized as the long-term defence of foraging areas which are rewarding in terms of food availability and energy intake (SNOW & SNOW 1984, DAVIES & HOUSTON 1983) and/or contain the best cover and shelter from predators (CUADRADO 1997).

The food value theory states that the size of a territory relates inversely to food abundance (HIXON 1980, ADAMS 2001), i.e. territories tend to be smaller when resources are more available. This appears to be valid for breeding and non-breeding territories in a variety of birds (MYERS et al. 1979, ENOKSSON & NILSSON 1983, TYE 1992, KHOURY & BOULAD 2010). For the proximate mechanisms that cause a variation in territory size, three hypotheses based on the food value theory have been suggested: (1) a territorial bird assesses prey density directly and accordingly adjusts territory size to include resources sufficient for its energy needs (MCFARLAND, 1986, TEMELES, 1987), (2) the bird uses cues, usually a structure within the habitat that correlates with prey density (SMITH & SHUGART 1987), or (3) according to the "contender hypothesis", territory size is constrained by intraspecific competition, i.e. when food is more abundant, more competitors will be attracted, making the area more costly to defend, hence the smaller territory sizes (MYERS et al. 1979, PONS et al. 2008, KHOURY & BOULAD 2010). It is becoming evident, however, that the proximate causal mechanisms responsible for these correlations are not always obvious. Limitations in other resource/habitat parameters may constrain territory size, e.g. the abundance of suitable nesting sites (DAVIS 1982) or of elevated perches (YOSEF 1993).

Finsch's Wheatear, *Oenanthe finschii* (Heuglin, 1869), is a short distance migrant inhabiting hilly to mountainous areas of western to central Asia (PANOV 2005). In Jordan, overwintering individuals usually defend territories against conspecific contenders (ANDREWS 1995). An unequal sex ratio has been reported with males usually dominant in more "favour-

Zoology in the Middle East 57, 2012: 35–43.
ISSN 0939-7140

able" areas (CORNWALLIS 1975, PANOV 2005). Male social dominance is known from a variety of bird species during the non-breeding season (e.g. MARRA & HOLMES 2001); however, very few attempts have been made to relate its effects to territory characteristics. In spite of the substantial literature on territory size, few studies focus on the possible effects of interspecific competition. Interspecific territoriality is well known among wheatears (e.g. CORNWALLIS 1975, KABOLI et al. 2006, RANDLER 2010, RANDLER et al. 2010), even in winter among migrant and resident species (LEISLER et al. 1983), and if it is intense, territory size may be inversely related to competitor density in a similar way to the conspecific contender hypothesis (PONS et al 2008). The aim of this study was thus to investigate determinants of territory size in the non-breeding season including the possible effects of male social dominance and interspecific territoriality.

Material and methods

Study species and areas. Finsch's Wheatear, *Oenanthe finschii*, is a small insectivorous passerine (22-30 g) which has a breeding range extending from Turkey eastwards to central Asia. Finsch's Wheatear exhibits a sexual dimorphism which is obvious in the field. The wintering grounds are generally located to the south of the breeding range in semi-arid and Mediterranean climates. The western subspecies *O. f. finschii* is found in Jordan during winter, as confirmed by the morphological data of 3 males and 2 females trapped in Jordan (cf. PANOV 2005, SHIRIHAI 1996). Breeding and wintering habitats are generally similar in being open, dry and undulating or hilly areas with scattered rock outcrops, often along shallow valleys, and in foothills adjacent to rocky slopes (PANOV 2005). Finsch's Wheatear is a common winter visitor in central and western Jordan (Fig. 1), with a few scattered birds also recorded in the eastern desert and along the rift margins and Jordan Valley. Its main distribution in Jordan roughly coincides with the semi-arid climate zones and includes the Irano-Turanian steppe and Mediterranean batha steppe phytogeographic zones (ALBERT et al. 2004), where the average annual rainfall ranges from 100 to 300 mm. Data on territories was collected in four different areas which had a high density of Finsch's Wheatears but varied in precipitation, productivity (Fig. 1.) and vegetation type.

The climate of all four study areas is generally Mediterranean, with hot dry summers and rainfall mostly in the cool winter months (NATIONAL ATLAS OF JORDAN 1984). All contained limestone hills and flat plains with low and scanty steppe vegetation, and some with rain-fed fields of wheat or barley. Grazing pressure (mainly sheep) was high in most areas and apparently led to degradation of the natural vegetation. Two study areas were in moderately arid climates with an average annual precipitation of 110-190 mm. They included the Hashemite University campus (hereafter HU) which is the most arid site studied and is located north-east of Zarqa (32°06'N 36°11'E, altitude approximately 590 m a.s.l.). Territories were studied in this area in the winter seasons of two successive years, 2008/2009 and 2009/2010, thus allowing analysis of annual variation in territory sizes. Furthermore, the proportion of female Finsch's Wheatear was highest (approximately 50% of all individuals) at this particular site. Um Al-Waleed is located east of Madaba (31°38'N 35°55'E, altitude c. 680 m a.s.l), where field work was carried out only during the winter season of 2011/2012.

Two study areas were semi-arid Mediterranean with an average annual rainfall of c. 290 mm. Marajem is located east of Jerash (32°15'N 36°02'E, altitude approximately 680 m a.s.l.). Male Finsch's Wheatears predominated in this area and their territories were studied only during one winter season (2009/2010). Hawiyyah is located south-west of Madaba (31°40'N 35°45'E, altitude approximately 780 m a.s.l.). Territories of Finsch's Wheatears were studied here only during the winter season of 2011/2012.

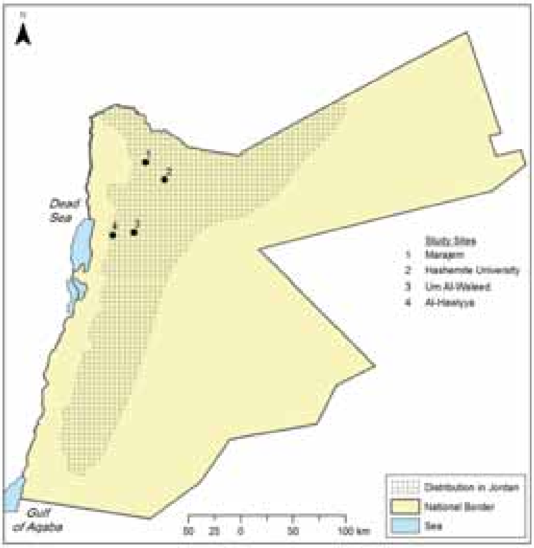

Fig. 1. Main distribution of Finsch's Wheatear, *Oenanthe finschii*, in Jordan during the winter season (late October – early March) and locations of the four study areas.

Field methods. Territories were studied during mid-winter only, i.e. between December and early February in three winter seasons 2008/2009 (HU), 2009/2010 (HU and Marajem) and 2011/2012 (Hawiyya and Um Al-Walid). For determining territory sizes, each territory was visited at least twice to collect the coordinates of not less than 12 peripheral points later used for delineating territories (GPS: Etrex-Garmin, accuracy 4-5 m). Peripheral points were determined by observing the locations of the birds as well as by 'driving' (KHOURY & BOULAD 2010). All observations were carried out during the morning hours (7:30–12:00 a.m.). Synchronized observations by two observers resulted in the avoidance of any confusion about the identity of the focal individual although Finsch's Wheatears are easy to observe in their open habitats. Individual marking was thus unnecessary, assuming that the same birds defended the same area throughout the season.

The presence/absence (0/1 values) of the following structures was recorded within the territories: large rock boulders, rock piles, small cliffs (1.5-3 m high), wadis / large water runnels. In addition, habitat variables were generally quantified as estimates of ground and vegetation cover (%) within territory boundaries. For further analysis, the cover of all types of vegetation (herbaceous and low vegetation, dwarf shrubs and shrubs) was pooled in one variable (total vegetation), which relates directly to productivity (KHOURY & BOULAD 2010). To contrast food availability between arid and semi-arid habitats (Hawiya and Um Al-Waleed), arthropods were sampled using plastic cups (volume = 200 ml) as pitfalls; thirty pitfalls were distributed in each area, usually in three lines or clusters of 10 with a minimum of 5 m distance between pitfalls, along foothills, water runnels and in fields, i.e. where foraging wheatears were usually observed. These pitfalls were used simultaneously for 24 hours in February 2012 during a period of mild weather conditions (i.e. without rain and night frost and maximum temperature during the day of around 15°C). The arthropods were then counted in each cup and insects were identified to order level. Most trapped arthropods had sizes less than 10 mm and are thus considered potential prey for wheatears; arthropods were thus not classified according to body size.

Table 1. Means (± S.D.) of habitat variables and frequencies of habitat features, means (± S.D.) of territory sizes of *Oenanthe finschii*, average number of conspecific and heterospecific individuals (see text), and sex ratios in four study areas. Statistical analysis: Kurskal Wallis (KW) for multiple samples, chi-square for comparing ratios/frequencies (ridges, boulders, piles, runnels, female ratios) and t-test for comparing two independent samples.

	HU	Marajem	Hawiyya	Um Al-Waleed	statistics
Mean annual rainfall (mm)	110	290	280	190	
Total no. of territories	23	7	7	6	
Rock %	20.5±18.3	35.1±8.8	25.7±12.4	29.2±13.6	KW: χ^2_2=5.7 p=0.13
Stone %	14.0±6.3	21.4±4.7	25.7±9.8	22.5±11.7	KW:χ^2_2=18 p=0.006
Soil / gravel %	66.7±22.4	42.9±5.7	48.6±4.8	49.2±4.9	kW: χ^2_2=12 p=0.009
Shrubs%	0.80±1.0	0	0	0	
Dwarf shrubs%	14.0±6.3	4.7±2.2	4.0±1.6	7.8±2.5	KW: χ^2_2=29 p=0.001
Herbaceous %	1.7±1.1	27.9±7.0	21.3±2.9	7.2±2.4	KW: χ^2_2=35 p<0.001
Total vegetation %	16.6±7.7	32.7±8.0	25.0±4.0	15.0±1.9	KW: χ^2_2=60 p<0.001
Small cliffs %	8.7	14.3	86.0	67.0	χ^2_2=59.6 p<0.001
Large boulders %	87.0	100	100	100	χ^2_2=1, p=0.77
Rock/stone piles %	83.0	86.0	86.0	83.3	χ^2_2<1, p=0.99
Wadi/water runnels %	70	100	57	83	χ^2_2=13, p=0.004
Territory size (ha)					
2008/2009	3.4 ±2.1				
2009/2010	3.1±1.1	3.2±0.7			t=0.07, p=0.4
2011/2012			1.6±0.4	1.6±0.5	t=0.4, p=0.97
Conspecifics	1.8±0.5	3.2±0.7	2.0±0.6	1.7±0.8	KW: χ^2_2=15.4 p=0.002
Heterospecifics	0.6±0.9	1.3±0.9	1.9±1.1	1.8±1.3	KW: χ^2_2=11.6, p=0.01
Arthropods			11.80±7.36	6.70±4.49	t=3.1,p=0.003
Females%	56	10	20	44	χ^2_2=43, p<0.001

The number of neighbouring territories of members of the same species (contender pressure) was noted and these conspecific neighbours were considered competitors if visible within 100 m from the territory boundary. The number of territories of other wheatears (Mourning Wheatear, *Oenanthe lugens,* Isabelline Wheatear, *O. Isabellinus*) and other members of the thrush family (Blackstart, *Cercomela melanura*, Black Redstart, *Phoenicurus ochruros,* Stonechat, *Saxicola torquatus*) that bordered or overlapped with the studied territories of Finsch's Wheatear were also recorded. Five individuals were trapped at two sites using clap nets with live bait (mealworms) in order to take morphological measurements including weight and fat stores. The fat scores or size of visible, subcutaneous fat depots were determined and classified according to the 9-grade score (0–8) (BAIRLEIN 1995). The birds were then ringed and released on-site.

Data analysis. Territory size was calculated for 43 territories for which coordinates of 12 or more peripheral points were collected. Territory maps were drawn as minimum convex polygons (MCPs, Fig. 2) linking the outermost points. Territory sizes (= area of MCPs) were calculated using ArcGIS (9.3) and Hawth's Analysis for ArcGIS (www.spatialecology.com). We used parametric and non-parametric tests (Mann-Whitney/T-test, Kurskal Wallis and chi square) to compare means and frequencies. Multiple-regression analysis was used to evaluate the effects of habitat variables and competitor abundance on territory size.

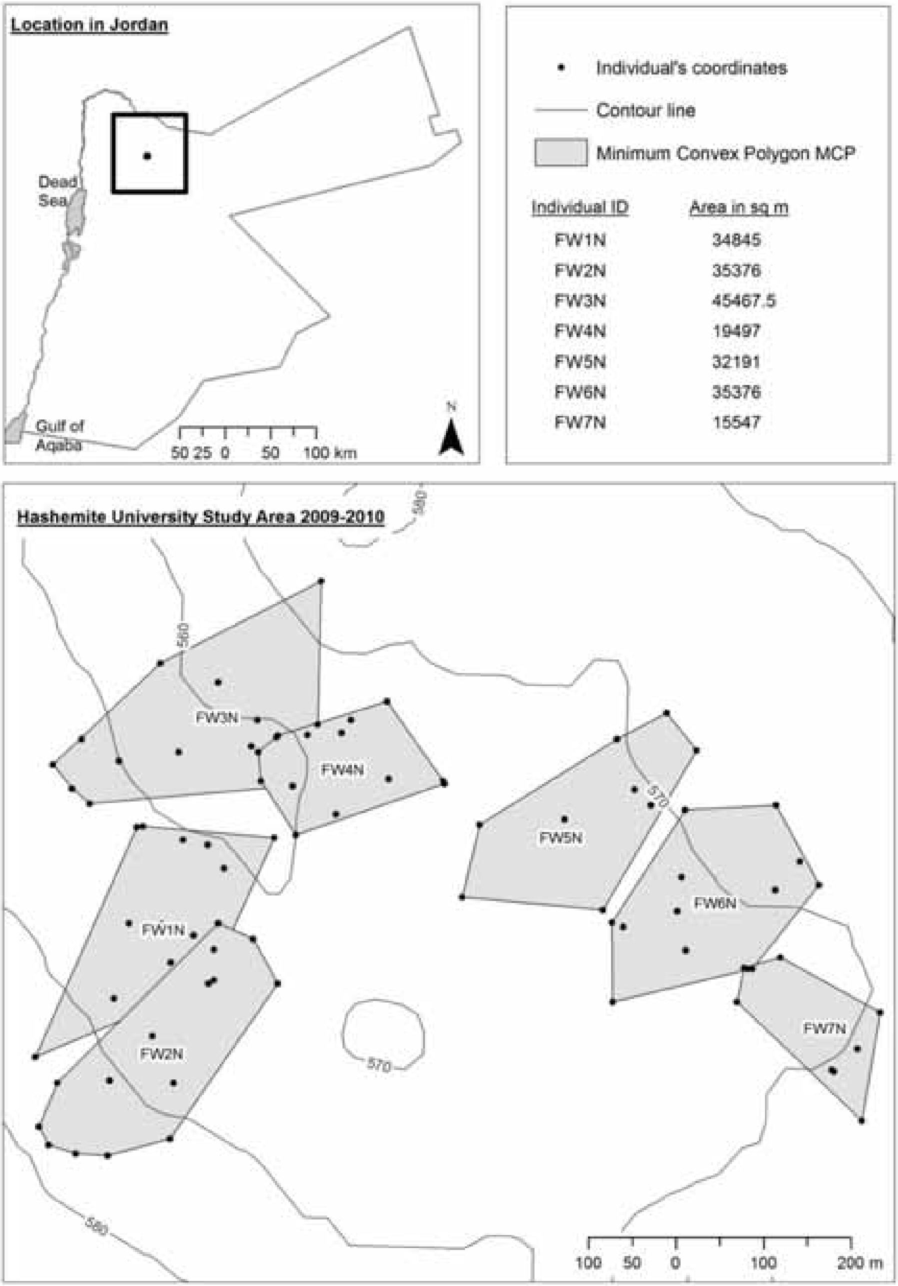

Fig. 2. Spatial arrangement of studied winter territories (minimum convex polygons) of Finsch's Wheatear, *Oenanthe finschii*, in the HU study site in 2009/2010, Jordan. Further territories that bordered these studied territories are not shown in the figure.

Results

The sizes of 34 territories in the four different study areas were determined during three winter seasons (Table 1). The mean territory size across all sites and years was 2.8±1.6 ha. Territory sizes ranged widely, e.g. from about 1 to 8 ha in the HU study area. Territories in HU were studied in two successive years, but the annual variation was not significant (T-test: t=0.4, p=0.73; sexes pooled as no sex-based variation was measured, see below). Territory sizes of arid and less arid areas located in the same geographic regions did not differ during the same years although there were significant differences in vegetation cover and prey density (productivity/prey availability). Table 1 provides comparisons between these study areas in habitat variables. Arthropod prey density was higher in Hawiyyah compared to Um Al-Waleed, and this difference was attributed to the significant difference in small coleopterans (t=-1.4, p<0.001) which contributed to 73% of all arthropods collected in the former site, while the number of Hymenopterans (mainly seed harvester ants *Messor* sp.) and other arthropods (e.g. spiders) did not vary significantly between both sites. As expected in dry environments, overall arthropod density was correlated with annual rainfall, but this did not appear to affect territory size, indicating another resource not related to energy intake which may be limiting the sizes of winter territories. The highest numbers of conspecific individuals were recorded in the Mediterranean study areas with fairly high productivity, particularly in Marajem (Table 1), indicating a high density of territorial birds; however higher contender pressure did not appear to affect territory sizes (Table 2).

The five trapped individuals (2 females, 3 males) did not show signs of starvation or other physical stress, as demonstrated by normal pectoral muscles and storage of subcutaneous fat. Three out of four individuals trapped in HU had a fat score of 3 while the fourth, a female had a fat score of 1. The single male trapped in Hawiyyah also had a fat score of 3.

The average territory sizes in the two sites studied in 2011/2012 (Hawiyyah and Um a-Waleed) were significantly smaller than the two other sites studied in previous years (HU and Marajem). This may have been caused by differences in habitat structure and/or in the presence of other competing wheatear species. Small cliffs on rocky hillsides appeared to be limited although often used by Finsch's Wheatears if available; such small cliffs were more frequent in Hawiyya and Um Al-Waleed where the rocky outcrops were partly steep and rugged. Multiple regression analysis including seven variables indicated a possible relationship between the presence of small cliffs and territory size (Table 2). Territories which contained small cliffs within their boundaries were significantly smaller than territories without small cliffs (Mann-Whitney – test, U = 32, p<0.001). Additionally, the occurrence of the Mourning Wheatear in Hawiyya and Um Al-Waleed probably constrained the territory sizes of Finsch's Wheatear. Spearman correlation analysis indicated a possible relationship between the number of Mourning Wheatears neighbouring or overlapping with Finsch's Wheatear territories and the territory sizes of the latter ($r_s = 0.5$, p=0.001).

The proportion of females in HU and Um Al-Waleed was 44-56%, decreasing to 10-20% in the less arid habitats of Hawiyyah and Marajem. However, there was no significant difference in the territory size of males (3.2±2.1 ha, n=8) and females (3.7±2.3 ha, n=8) in the HU study area during the winter season of 2008/2009 (Mann-Whitney U- test: U=27, p=0.65). When comparing (micro-) habitat variables between males and females within the HU study area (data from 2 years pooled), there were no significant differences (t- and χ^2 - tests, p>0.1), and thus there was no evidence of sex-related habitat segregation within the same area.

Table 2. Multiple linear regression model ($R^2 = 0.34$, $F_{7, 35} = 2.9$, $p=0.03$) to describe the relationship between territory size of Finsch's Wheatear and 7 independent variables in winter. P-values of independent values indicate their significance in contributing to the model (significance in bold letters).

Variable	**P - value**
Conspecifics (same species)	0.31
Heterospecifics	0.36
Total vegetation cover	0.78
Rock boulders	0.71
Rock piles	0.62
Small cliffs	0.004
wadis	0.61

Discussion

The considerable variations in territory size of Finsch's Wheatear in winter were not related to variation in productivity or prey availability. Prey abundance probably determines a lower limit for territory size as birds have to ensure a minimum amount of food to cover energy needs (ADAMS 2001). All study areas apparently had sufficient prey density during the study periods because even in the driest study area small territories (c. 1 ha) and birds with fat depots were found. Although sample size was too small to be conclusive, the storage of fat in five individuals generally indicates that birds did not experience long-term limitations in energy intake during mid-winter regardless of study area. Winter fattening is generally known from other insectivorous birds which spend the winter season in temperate climates (PILASTRO et al 1995). Resident or short-distance migrants from the non-tropics are exposed to low temperatures during the night and unpredictable adverse weather in their winter quarters. Such birds that are more likely to encounter food shortages may store fat in anticipation of energy deficits (BLEM 1990).

The unequal sex ratio in different areas indicates male dominance with a large scale exclusion of females from areas which are more productive and predictable in terms of food availability. It is not our intention to describe and explain here the intersexual spatial or habitat segregation of wheatears in the non-breeding season; rather our objective is to determine if territory size is related to male social dominance. The sizes of male territories were not different from female territories. Moreover, territory size did not vary spatially or according to variation in productivity, i.e. at a larger scale, the unequal sex ratio was not matched by a variation in territory size. There are two possible determinants of territory size in overwintering Finsch's Wheatears: the first is territoriality by the Mourning Wheatear which is socially dominant over Finsch's Wheatear (CORNWALLIS 1975, PANOV 2005). The occurrence of the Mourning Wheatear in Hawiyya and Um Al-Waleed in winter is attributed to their proximity to breeding grounds along the central and southern rift margins (KHOURY & BOULAD 2010) and possibly to the slightly more rugged terrain compared to HU and Marajem. To confirm the proposed role of interspecific interactions in determining the size of winter territories (cf. PONS et al. 2008), further studies on niche partitioning and possible interspecific encounters at the beginning of the season would be required (cf. LEISLER et al. 1983, RANDLER et al. 2010). Furthermore, small cliffs in the otherwise gently sloping, rocky hillsides are indicated as a possible factor enhancing habitat quality and affecting territory size. These structures may be regarded as additional resources which affect territory quality and size (e.g. YOSEF 1993). Small cliffs are elevated sections of rocky hillsides which provide a suitable vantage for territorial birds, and they contain numerous holes and crevices which may provide cover and shelter from predators and adverse weather conditions. However, the role of such habitat structures still has to be confirmed by detailed studies of habitat use.

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