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Christos G. Vlachos[a], Dimitrios E. Bakaloudis[a], Kyriaki Kitikidou[b], Vassilis Goutner[c]*, Vasileios Bontzorlos[d], Malamati A. Papakosta[a] and Evangelos Chatzinikos[d]

[a]*Laboratory of Wildlife & Freshwater Fisheries, School of Forestry and Natural Environment, Aristotle University of Thessaloniki, Thessaloniki, Greece;* [b]*Department of Forestry and Management of Environment & Natural Resources, Dimokritos University of Thrace, Pandazidou, Orestiada, Greece;* [c]*Department of Zoology, School of Biology, Aristotle University of Thessaloniki, Thessaloniki, Greece;* [d]*4th Hunting Federation of Sterea Hellas, Athens, Greece*

Home range size and foraging habitat use in breeding lesser kestrels (*Falco naumanni*), a bird species of conservation concern, were investigated during the breeding season of the species in 2008 in an intensively cultivated area of central Greece, using radio-tracking. Grasshopper (the main prey) densities were measured at the most important habitats (cotton, cereals, grasslands and margins). Home ranges were not significantly different between sexes either as overall means or during incubation and nestling periods. Movements of both sexes were non-random during incubation but random during the nestling period. Habitats used by males during incubation ranked as: margins > other > cotton > corn > cereals and during nestling period as: cereals > margins > grasslands > corn > cotton. Female habitat use greatly differed ranking as cereals > cotton > grasslands during incubation and as grassland > cotton > corn > cereals > margins during nestling period. Female habitat use seemed to be in disagreement with the conditions generally favouring prey availability, probably for reasons associated with low and uniform distribution of grasshopper densities over the habitats.

Keywords: *Falco naumanni*; home range; foraging habitats; Greece

Introduction

The lesser kestrel is a small falcon with a relatively wide Palaearctic distribution ranging from southwest Europe, through the Middle East to central and western Asia (BirdLife International 2012). Up to the end of the 1990s, large population declines had been reported in most of the lesser kestrel's breeding range (Negro 1997) attributed to food shortage as a consequence of agriculture intensification and urban sprawl (Biber 1990). This had led to a decreased availability of natural open areas constituting foraging grounds of the lesser kestrel (Donázar et al. 1993). Formerly rated as globally endangered and vulnerable by the International Union for Conservation of Nature (Evans 1994), the lesser kestrel is now qualified as 'least concern' because of indications of stable or slightly positive population trends overall over the last three decades

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*Corresponding author. Email: vgoutner@bio.auth.gr

(BirdLife International 2012). Nevertheless, considerable declines still occur locally: the trend of the Greek population, which comprises *c*.15% of the European total, has been declining and is mostly concentrated in Thessaly, central Greece, in 98 colonies totalling 2900 pairs (Vlachos et al. 2004). In the study area, lesser kestrels start laying eggs from late April to early May (Bakaloudis et al. 2000). After clutch completion (one to six eggs per nest), both parents incubate the eggs for 28 days. Most eggs start hatching during late May (Bakaloudis et al. 2000), and nestlings spend 37 days in the nest (Bustamante and Negro 1994). During the nestling period, both parents bring food to the nestlings. This mostly comprises grasshoppers and locusts (Rodríguez et al. 2010), but occasionally small mammals are also provided for the young (Chatzinikos 2000).

Habitat selection in raptors is greatly affected by the habitat influences upon their prey, particularly in areas with low prey diversity or where prey abundance is unevenly distributed in habitats (Janes 1985; Bakaloudis 2009). In lesser kestrels, which traditionally live in association with human activities, the management of landscape around colonies is of great importance for their conservation (Donázar et al. 1993; Bustamante 1997; Tella et al. 1998; De Frutos et al. 2010). Once agricultural landscapes covered 60% of land in Europe (Pain and Dixon 1997), but agricultural policies and land use changes affect lesser kestrel populations by affecting their prey types and availability (Tella et al. 1998; Ursúa et al. 2005; Catry et al. 2012). Hence, knowledge of habitat use by local populations of this bird in Europe is of prime importance for its conservation.

Within the framework of the promotion of conservation of the lesser kestrel and its habitats in Greece, the objectives of the present study were (1) to estimate the home range sizes of males and females during the breeding season; (2) to quantify foraging habitat preferences using radio-tracking; and (3) to evaluate the observed habitat preferences in relation to the density of grasshoppers and locusts (their main prey).

Materials and methods

Study area

The study area is situated in the eastern part of the Larissa plain, Thessaly, central Greece (39°29′07″ N, 22°41′39″ E) and includes the lesser kestrel colony of *c*.120 pairs near the village of Armenio and the surrounding intensively cultivated agricultural land. The climate is thermo-Mediterranean, with mild rainy winter, dry and hot summer and a mean annual precipitation of about 465 mm. The composition of crops has been altered through long-term agricultural changes on Thessaly plain. Acreage of cereals and corn cultivations has been increased, whereas cotton production has decreased since 2005. The habitat types were: (1) Cotton (43.3%): it is sown in April reaching a height of *c*.20 cm in late May and *c*.60 cm at the end of June. (2) Corn (11.7%): sown in March and April, has a height of *c*.100 cm in late May and *c*.200 cm at the end of June. (3) Cereals (21.2%): sown the previous autumn, have a height of *c*.80 cm and dense ground cover in late May whereas they are harvested through June, depending on the crop type. (4) Grasslands (15.5%): natural areas dispersed in the study areas with low natural vegetation. (5) Margins (7.1%): the edges of cultivations including the dykes among them. (6) Other areas (1.2%): minor crops of vegetables, legumes, almond trees, sugar beets, etc. (hereafter 'other'). All aforementioned heights of cultivations were measured with a tape, and were expressed to the nearest decimetre.

Fieldwork

The study was conducted during the breeding period of the lesser kestrel in 2008 by radio-tracking five males and five females (five pairs). This method provides a useful technique for investigating habitat selection in birds and other animals (Harris et al. 1990; Aebischer et al. 1993; Donázar et al. 1993; Resources Inventory Committee 1998; Rutz 2006; Awa et al. 2009). All birds were captured within their nest boxes. No effect of radio-tagging on reproduction or survivorship of birds has been observed (Vekasy et al. 1996).

The backpack transmitters used were type TW4 single button celled tags (4.2 g, 2.8 cm long, 0.6 cm thick, 1.3 cm wide), operating with a battery life of 4 months, with a 22-cm linear antenna (Biotrack Ltd, Wareham, UK). Their size conformed to the need that the weight of the transmitter must be lower than 3% of the bird's total body mass (Kenward 2001).

All radio-tagged lesser kestrels were monitored for 4 days (once per week) during the incubation period (May) and for 5 days during the nestling period (June), and they were located from sunrise to dusk every 30 minutes (session period). The radio-tagged birds were located by two teams, each consisting of two people, using flexible three-element hand-held Yagi antennas (Televit Ltd, Televit International), in conjunction with Sika receivers (Biotrack Ltd, Dorset, UK) covering frequencies between 166 and 174 MHz. The teams were stably positioned at elevated points near the colony and the foraging ground, and were approximately 900 m apart. Each radio-tagged bird was scanned for 3 minutes every session period (Harris et al. 1990) and, when located, two compass bearings were taken while the second person tried to spot the bird with binoculars (8 × 40). If an individual was not located at the first scan of a session, a second trial was conducted after the completion of the session period and until the bird was found. Locations were first recorded on a 1 : 5000 map and then digitized using ArcView GIS 9.3 version. In addition, the habitat over which the bird hunted was noted when visually possible. Following this procedure, a total of 368 locations for hunting males and 271 locations for hunting females were obtained during the study sessions. Locations derived from incubating or brooding individuals from the colony were excluded from compositional analysis. Surveys were avoided on windy and rainy conditions. The locations data were uploaded using DNR Garmin 5.3 to ArcGIS, and were then analysed using the Home Range extension for ArcView GIS 9.3 (Rodgers and Carr 1998).

Data analysis

Home range areas were estimated for males and females during incubation and nestling periods using minimum convex polygon (Mohr 1947; Silverman 1986; Worton 1989; Harris et al. 1990; White and Garrott 1990; Wray et al. 1992; ESRI 1996; Rodgers and Carr 1998; Nilsen et al. 2008). Home range is defined as 'that area traversed by the individual in its normal activities of food gathering, mating and caring for young' (Burt 1943). The minimum convex polygon is a classical method of home range estimation, in which all data points are completely enclosed by connecting the outer locations in such a way as to create a polygon. Furthermore, it has no assumptions about the distribution of the data. Analysis of birds' movements was carried out to calculate foraging distances, and the distribution of circular data were checked by Rayleigh's test (Batschelet 1981; White and Garrott 1990; Rodgers and Carr 1998). The chi-squared approximation test for the Rayleigh probability value gives very accurate

results for sample sizes greater than 30 and fairly good estimates for smaller sample sizes. The home range analysis was carried out using ArcGIS 9.3 and statistical analyses with SPSS 19 software, respectively.

The habitat preferences of both sexes were estimated using compositional analysis consisting of a comparison of point habitat occurrence data to the habitats available within a home range boundary (Aebischer et al. 1993). This estimates the log-ratio differences of used and available habitat proportions to determine habitat use preferences. With use defined as the proportional occurrence within each individual's home range, availability is also defined as proportional occurrence within each individual's home range. Tests for overall selection are indicated by Wilk's Lambda statistic. Negative and positive values in the matrix of compared variable pairs indicate avoidance or selection of the numerator habitat type over the denominator habitat type. If selection was indicated, comparison of pairs of resource types was conducted using *t*-tests or randomization tests (Aebischer et al. 1993). Habitat ranking, with regard to their preference by lesser kestrels was evaluated by the formula [(used – available)/available] × 100.

In order to evaluate both the importance of each habitat type as foraging ground for kestrels and also a temporal prey availability, grasshopper and locust densities were estimated in cotton fields, cereals, grasslands and margins. Grasshoppers and locusts were sampled every 10 days in May and June 2008. On each visit, three randomly located transects were conducted within each habitat type. Each transect was sampled by a square plot 0.25 m^2 thrown eight times on locations approximately 10 m apart. When the square plot was located on the ground, firstly all flushed orthopterans were counted and then a careful search was carried out for the remaining individuals within the plot. In all statistical comparisons, densities (X) were transformed as $\sqrt{(X + 1)}$ (Zar 1996).

Results

Home ranges

Overall, estimated male home range was 70.51 ± 20.73 (SE) km^2 for 100% of the observations ($n = 343$) and 24.84 ± 6.06 km^2 for 95% of the observations (Figure 1). Females' home ranges were 49.60 ± 15.05 km^2 (100%, $n = 321$) and 16.55 ± 3.46 km^2 (95%), respectively. Nevertheless the difference between mean male and female home ranges was not significant (for 100%: $Z = -1.192$, $p = 0.233$; for 95%: $Z = -1.280$, $p = 0.200$, Mann–Whitney U-tests). In males, mean home range increased from 26.30 ± 2.03 km^2 in incubation (based on $n = 153$ locations) to 64.46 ± 4.41 km^2 in nestling period ($n = 190$) but the difference was not significant ($Z = -1.192$, $p = 0.050$, Wilcoxon test). In females, mean home ranges remained similar between the two periods, being 20.65 ± 1.45 km^2 ($n = 136$) and 24.46 ± 2.53 km^2 ($n = 131$) ($Z = -1.470$, $p = 0.142$), respectively. Additionally, there was no significant difference in home range sizes between sexes either during incubation ($Z = -0.557$, $p = 0.564$, Mann–Whitney U-test), or during nestling period ($Z = -1.149$, $p = 0.251$).

Movements and habitat preferences

Movements of both males and females were non-random during incubation ($p = 0.003$ and $p = 0.003$, respectively, Rayleigh test). In contrast, movements of
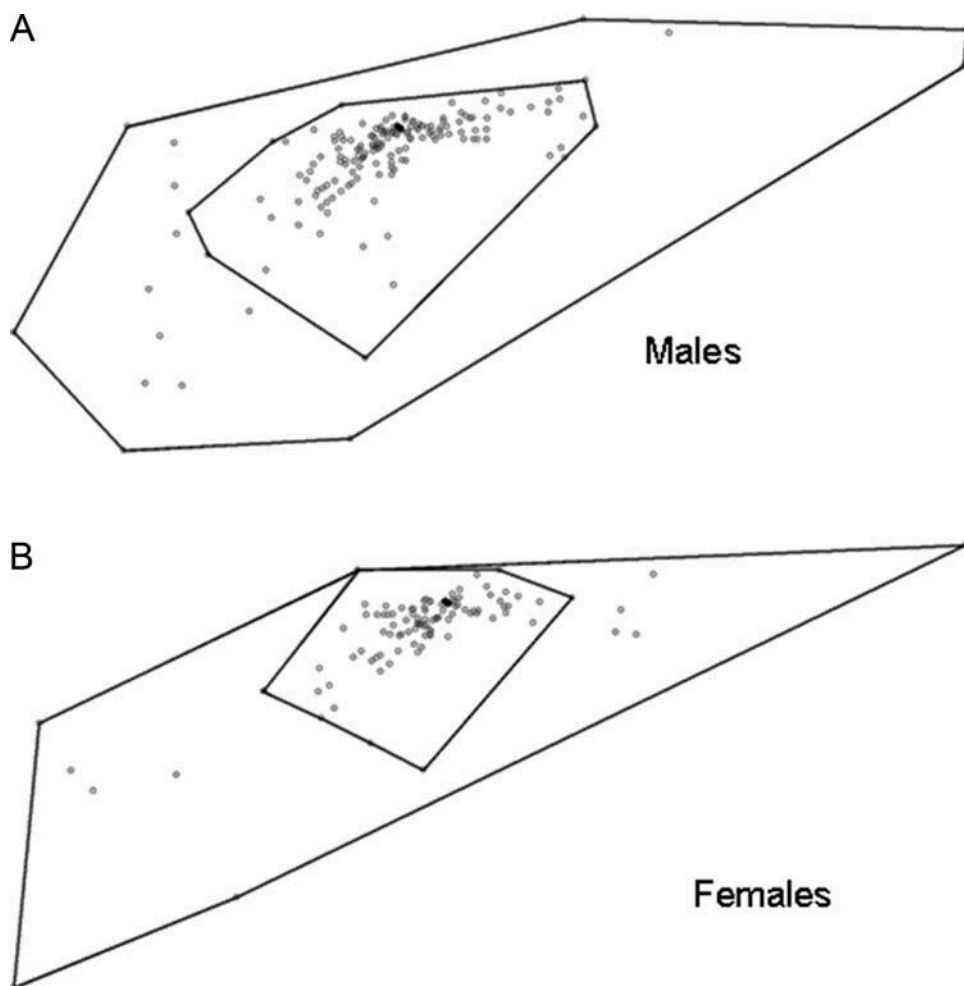
Figure 1. Minimum convex polygon home ranges (outer: 100%, interior: 95% of locations) of male (A) and female (B) lesser kestrels during the breeding season in central Greece, 2008.

both genders were statistically random during the nestling period ($p = 0.214$ and $p = 0.149$, respectively, Figure 2). The maximum distances of males from the colony during incubation and nestling period were 22.0 km and 24.5 km, respectively; and of females were 39.6 km and 23.7 km, respectively.

Generally, the habitats used by each sex during incubation and nestling periods were significantly different from those available (Figure 3). Margins, cotton fields and 'other' habitats were preferred by males during incubation, whereas cereals and margins were the most preferred habitats during the nestling period (Table 1). Females preferred cereals during incubation with a habitat rank as cereals > cotton > grasslands ('other' were not used), whereas the preference changed over grasslands and cotton during the nestling period, with a rank as grasslands > cotton > corn > cereals > margin ('others' were not used).
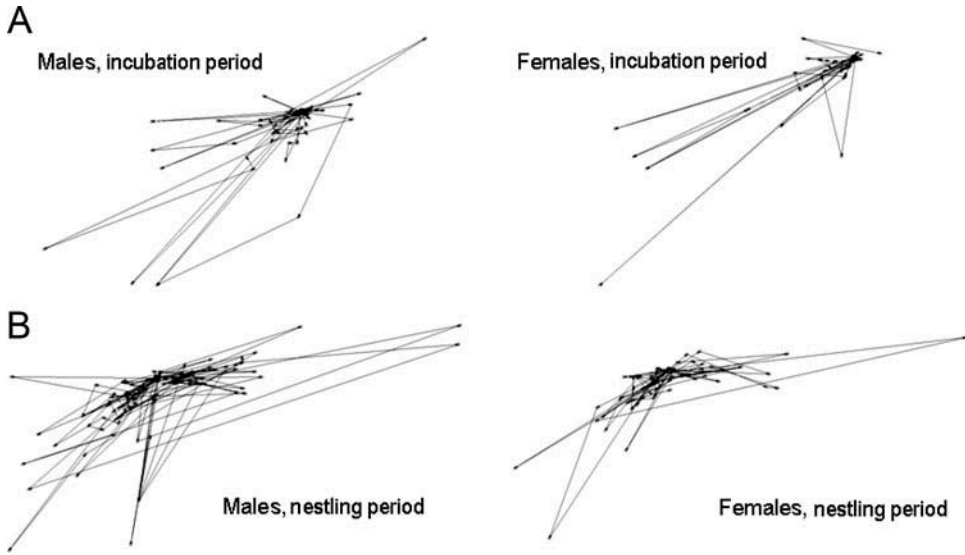
Figure 2. Direction of movements exhibited by radio-tagged male and female lesser kestrels during (A) incubation and (B) nestling periods in central Greece, 2008.
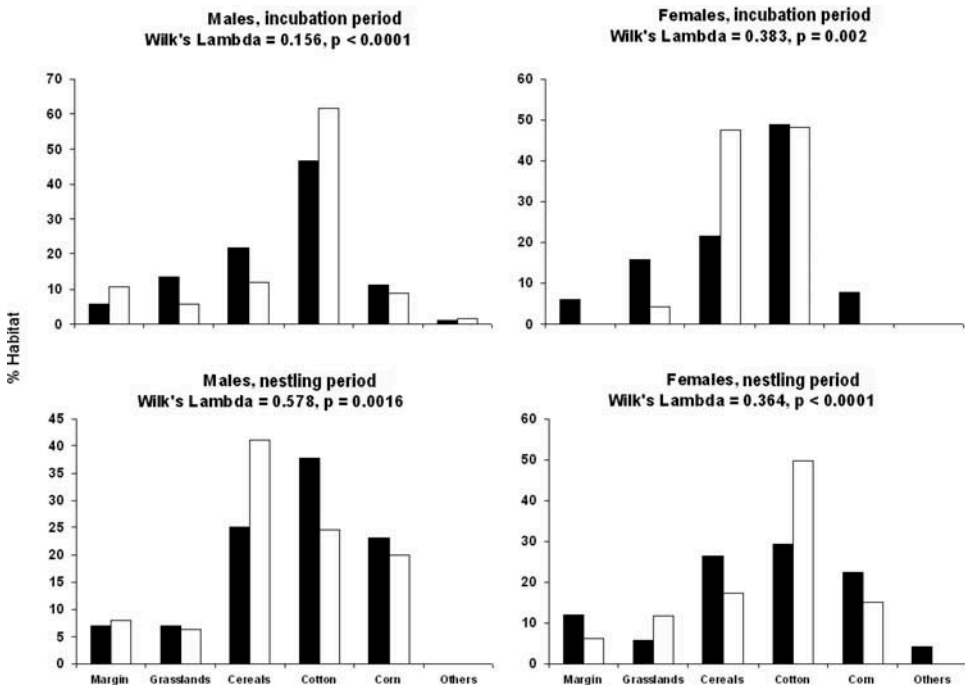

Figure 3. Percentage of foraging locations over used habitats (open columns) of radio-tagged male and female lesser kestrels in relation to habitat available (black columns) within home ranges, during breeding stages in central Greece, 2008.

Table 1. Ranking (0 = least preferred, 5 = most preferred) of habitats used by foraging male and female lesser kestrels during incubation and nestling periods in central Greece, 2008. Assessment based on compositional analysis (Aebischer et al. 1993), using habitat used at location points, compared with proportional availability of habitats within home ranges.

Habitat	Males, incubation	Rank	Males, nestling	Rank	Females, incubation	Rank	Females, nestling	Rank
Margin	82.05	5	15.26	3	−100.00	0	−47.60	1
Grasslands	−57.56	0	−7.86	2	−73.44	1	101.21	5
Cereals	−45.00	1	63.86	4	120.23	3	−34.27	2
Cotton	31.47	3	−35.12	0	−1.40	2	68.81	4
Corn	−21.57	2	−14.05	1	−100.00	0	−32.36	3
Other	54.60	4	0.00	0	0.00	0	−100.00	0

Table 2. Mean ($\pm$ SE) number of grasshoppers per 0.25 m^2 in different habitats during breeding stages of lesser kestrels in central Greece, 2008.

Habitat	Incubation	Nestling	Statistic*	p
	Mean $\pm$ SE	Mean $\pm$ SE		
Cotton	0.00 $\pm$ 0.00	0.42 $\pm$ 0.09	−4.58	<0.001
Cereals	0.42 $\pm$ 0.08	0.50 $\pm$ 0.09	−0.67	0.506
Margin	0.60 $\pm$ 0.09	0.68 $\pm$ 0.10	−0.47	0.639
Grasslands	0.49 $\pm$ 0.08	0.56 $\pm$ 0.08	−0.62	0.538

Sample sizes: 72 replications in each habitat type every breeding stage.
*Differences are based on two-sample *t*-test.

Grasshopper densities

Grasshopper densities were low in all habitats, averaging from 0.00 to 0.68 per 0.25 m^2 (Table 2). In cotton fields grasshoppers increased significantly in densities during nestling. In the other three habitats densities were similar during incubation and nestling period (Table 2). The differences in densities among habitats during incubation were overall significant (analysis of variance, $F_{3,284} = 13.804$, $p < 0.001$) but the difference was located only between cotton and the remaining habitats (Duncan's multiple range test). Finally, no difference in densities among the four habitat types were observed during the nestling period ($F_{3,284} = 1.56$, $p = 0.200$).

Discussion

Home ranges

The overall average home range (males 70.51 km^2, females 49.60 km^2), as well as home ranges during incubation and nestling periods of lesser kestrels in our area were much larger than those reported for 22 radio-tracked lesser kestrels at Los Monegros (Ebro Valley, northeastern Spain) being 12.36 $\pm$ 8.28 km^2 and smaller in males (10.80 km^2) than in females (13.67 km^2) (Tella et al. 1998). Nevertheless, in seven of the nine pairs

that were tracked, home range did not differ from a 1 : 1 proportion (Tella et al. 1998). The findings from radio tracking from four males and four females in Mainera del Alcor, southern Spain, indicated large home ranges from 27.12 km^2 to 68.75 km^2 in males and 51.5 km^2 to 91.25 km^2 in females (Negro et al. 1993). Although these home ranges are generally greater than those found in our area, they indicate similarities within the spectrum of range sizes reported. The large home ranges of lesser kestrels according to Negro et al. (1993) are due to their colonial habits and communal hunting, because they do not defend restricted foraging areas (Newton 1979). In Spain, the habitat types around colonies also affect home range sizes, the latter being much larger for birds breeding in intensively cultivated areas than those in traditional agro-grazing systems (63.65 km^2 versus 12.36 km^2, Tella et al. 1998). This is probably due to the irregular distribution of prey resources as a result of the intensive biocide treatments (Tella et al. 1998). The maximum distances travelled by both sexes seem to fit this model and are supported by foraging theory as well (Stephens and Krebs 1986): the intensification of agriculture around lesser kestrel colonies force the birds to fly longer distances to exploit food resources in contrast to areas with low-intensity agriculture (16 km versus 3 km, Bustamante 1997). Maximum distances in our area for the first mentioned category, were even greater than those reported in Spain.

Habitat preferences

Considerable differences were found in the foraging habitat preferences between sexes in both incubation and nestling period. These findings are in disagreement with those of Tella et al. (1998) whose radio-tracked male and female lesser kestrels used similar habitats at pseudo-steppes in Spain. In contrast, different habitat use by each sex is known to raptors such as the wintering American kestrel (Koplin 1973; Ardia and Bildstein 1997) and sparrowhawks (Marquiss and Newton 1982). In other raptors, even when both sexes use similar habitats, differences occur either in the habitat time budgets (Preston 1990) or in hunting success (Toland 1987). Although it was assumed that, in a species with a reversed sexual dimorphism, size-related differences evolved due to differences in foraging ability, it seems unlikely to be the case (Mueller 1990). Size dimorphism may have initially evolved for reasons other than differential habitat use (Bildstein 1992; Ardia and Bildstein 1997). The lesser kestrel has a strong plumage dimorphism and females are 24% heavier than males (Negro et al. 1992). Nevertheless, in insectivorous raptors the evolution of dimorphism may have been inhibited because insects of sufficient size to provide worthwhile food for a raptor are available in only a very limited range of sizes (Mueller 1990). Therefore differences in habitat use by lesser kestrels should rather be sought in the local ecology of the species.

The reported distribution of male lesser kestrels over foraging habitats during incubation seems reasonable as margin, 'other' habitats and cotton are expected to be used in preference to corn and cereals because of the considerable height of the latter making potential prey inaccessible (Toland 1987; Donázar et al. 1993; Vlachos et al. 2003; Bakaloudis 2010). Again, during the nestling period, when cereals have been harvested and margins and grasslands still retain low-height vegetation, potential prey seems to be reasonably available (Donázar et al. 1993; Vlachos et al. 2003; Rodríguez and Bustamante 2008). Also in this period, cultivated land is intensively irrigated so prey tends to assemble at the marginal habitats rather than in cultivations

(Ursúa et al. 2005). Falcons cue on human-related disturbances in managed grassland habitat (Toland 1987) and probably use a combination of habitat features as cues to select suitable hunting sites (Bakaloudis 2010; De Frutos et al. 2010). The random movements of both sexes during the nestling period may be associated with a foraging strategy with local enhancement, which is expected in insectivorous birds such as the lesser kestrel (Negro et al. 1993).

Nonetheless, the habitat distribution of females exhibited an almost inverse tendency to that found for males, as their activity was concentrated in habitats generally avoided by males. Differences in habitat use may have been enforced by competition for resources due to prey depletion around the colony (Colwell and Futuyma 1971; Cody 1974; Marquiss and Newton 1982; Ardia and Bildstein 1997; Bonal and Aparicio 2008). The higher maximum distances travelled by female lesser kestrels during incubation may support this idea. Within the framework of these flights, different prey types may have been taken by males and females: the diet of these birds in Thessaly includes coleopterans (up to 47% by number during incubation and 33% in nestling period) and also small mammals (3% and 0%, respectively) (Chatzinikos 2000). Additionally, males are still involved in female feeding during the early nestling period (Donázar et al. 1992; our observations) making females less dependent on foraging effectiveness compared with males, and probably leading to a drop in the maximum distances travelled during the nestling period.

In conclusion, this study is a preliminary approach to foraging habitat selection of the lesser kestrel and the first of this kind carried out in Greece. Evidently, use of radio-tracking alone seems inadequate for fully clarifying the reasons for habitat preferences of males and females. Therefore a more thorough study is planned on the foraging ecology of both sexes during incubation and nestling periods using a combination of methods (cameras, observations and collection of prey remains at nests) combined with prey sampling at the habitats used.

Acknowledgements

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