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Premigratory moult in the Lesser Kestrel *Falco naumanni*

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Abstract – Moult is one of three major energy-demanding life-history events in the annual cycle of birds but unlike breeding and migration it is poorly studied. Most of the long-distance migratory raptors suspend moult during migration and then finish it in their wintering quarters. However, detailed information on moult at staging or premigratory sites is rather scarce. In this study, 280 shed feathers collected from communal roosts were used to investigate the moult of a migratory falcon, the Lesser Kestrel *Falco naumanni* during the premigratory period. The results suggest that there are several differences regarding the pattern and timing of moult between sex classes during the premigratory period, with females showing a more advanced moult stage than males. In addition, Lesser Kestrels and especially females seem to perform a complete moult of wing and tail feathers prior to migration. Birds engage in an intense moult as soon as they arrive in the premigration areas whereas such moult strategy could be considered as an adaptation for exploiting superabundant food resources available in the area during late August.

Key-words: Greece, moult strategy, moult variation, premigration.

INTRODUCTION

Moult, along with breeding and migration, is one of the three main energy-demanding life-history events in the yearly cycle of birds (Newton 2008). In most species it occurs at a different time period from breeding and migration: some migratory birds moult in their breeding grounds as soon as nesting is complete, others moult at a staging area during migration, while others moult in their wintering grounds. However, some species exhibit a split moult, replacing part of their plumage in one area and the rest in another, while moult is arrested during migration (Newton 2009).

Long distance migratory raptors typically avoid moulting during migration to retain their flight efficiency. However, replacement of some primaries before migration can happen to enable the birds to exploit food resources (Newton 1979). Smaller raptor species can normally finish their moult before the post-breeding migration as the time required to grow a new feather is about 2-3 weeks, but larger ones, which take longer to grow their feathers, arrest moult during migration, and continue after reaching their winter quarters (Zuberogoitia *et al*. 2018). Regarding falcons (*Falconidae*), moult is completed in either one moult cycle (starting late in the breeding season and finishing in the autumn) or two seasonal moult cycles (shedding few feathers when on the breeding grounds, arrest moult and then finish moulting in the wintering grounds) depending on the species. In any case, wing moult starts by shedding the 4th primary feather (P4) and progresses from P3 to P1 and from P5 to P9. P10 is the feather to be shed last and is usually the one to be arrested in incomplete moult (see Fig. 1 in Zuberogoitia *et al*. 2018).

The Lesser Kestrel *Falco naumanni* is a small migratory falcon that breeds in southern Europe, with its wintering grounds located in sub-Saharan Africa (Cramp & Simmons 1980). The species often does not migrate directly to Africa but exhibits a premigratory behaviour that lasts several weeks; thus migration is separated in two parts, and is termed a split migration (Newton, 2008). In premigratory areas, birds exploit the temporal abundance of food resources, mainly insects and must build up the appropriate fat reserves and moult, at least partially, before the autumn migration (De Frutos & Olea 2008, Sarà *et al*. 2014, Bounas & Sotiropoulos 2017).

Although obtaining comprehensive information on the moult state of a bird requires its capture (even more than once), this can be very difficult with many species, especially birds of prey (Bird & Bildstein 2007). In this study, data from standardized collection of shed feathers were used to investigate the moult of the Lesser Kestrel during the premigratory period. This study aims to: a) examine any temporal and sex-specific patterns of wing and tail moult during the premigratory period and b) provide insights on the timing of moult in regard to energetic demands and the onset of autumn migration.

MATERIALS AND METHODS

Study area

The study was carried out in the city of Ioannina (39.66° N, 20.85° E; ~100,000 inhabitants; 470 m altitude), which is the largest city of the Epirus Prefecture located in Northwestern Greece (Fig. 1). The city is located on the shore of Lake Pamvotis and is included in a Special Protection Area (SPA) for the avifauna (GR2130012). About 60 breeding pairs of Lesser Kestrels occupy nests in the buildings of the city centre, whereas from July to September the city holds a large premigratory roost with almost 2,500 birds congregating annually (Bounas *et al*. 2016). During this period, birds exploit the high numbers of Orthoptera in the areas surrounding the city, that are mainly covered by open areas with wood pastures while the agricultural landscape consists of a mosaic of annual crops around the lake including arable land, extensive cereal cultures and rotation cultures with regular fallowing. In addition, the highlands surrounding the city are covered by low vegetation areas (dry grasslands, alpine and subalpine grasslands, scrubland and heath).

Figure 1. Map of the study area, Ioannina city, Greece including the transect line followed for feather collection. Black dots show the three main Lesser Kestrel premigratory roosts in the city center.

Data collection

From July 17th to September 13th, Lesser Kestrel shed feathers were collected every 5-7 days. A transect line of 1400m length that passed below the three main roosts in the city was walked in the morning (07:00) while actively searching for feathers. All feathers found were kept in paper envelopes. Both wing and tail feathers were identified by direct comparison to a reference collection that includes the full plumage of both male and female individuals of the species. Primaries were numbered descendently, from the carpal joint (P1) outwards to P10. The rectrices (tail feathers) were numbered in 6 pairs, from the central tail feather (T1) outwards to T6 (Baker 2016). The side of the wing or tail (right/left) was not included in the dataset, as moult tends to be symmetrical between both wings and tail at least in those species that develop a simple moult pattern consisting of one moult cycle (Zuberogoitia *et al*. 2018). Additionally, data from pellet analysis during the premigratory period were extracted from a previous study in the area. Specifically, a total of 108 pellets were collected along the same transect followed for feather collection, under Lesser Kestrel roosts, on a weekly basis. Only unbroken pellets were collected and stored separately in plastic bags to avoid mixing. Pellets were dry-dissected under a stereoscope and the total number of individual prey items in each pellet was calculated. All specimens were identified and assigned to the family level. For more details on the pellet analysis methods see Bounas & Sotiropoulos (2017).

Data analysis

To investigate the variation of wing and tail feather moult, two separate Linear Models (LM) were constructed using the number of moulting primaries as a dependent variable (from 1 to 10) in the first, and the number of moulting tail feathers (from 1 to 6) in the other. In both models, explanatory variables included Julian date (calculated as the number of the day from the beginning of the year) and the sex of the bird that the shed feather came from. The squared Julian date was used as a covariate to account for non-linear effects of the Julian date on shed feathers (Knudsen *et al*. 2007, Ramírez & Panuccio 2019). To evaluate the discriminatory ability of the models we used the area under the receiver-operated characteristic curve (AUC). AUC values range from 0.5 (no better than random) to 1 for a model with perfect fit. Finally, the number of collected feathers along with Lesser Kestrel consumption of Orthoptera (mean Orthoptera per pellet), were plotted against Julian date using smoothing interpolation through locally weighted regression. All statistical analyses were performed using R 3.5.1 (R Core Team 2018).

RESULTS

A total of 280 feathers were collected and unambiguously identified, 138 were wing feathers (primaries) and 142 tail feathers (rectrices). Regarding sex classes, most shed feathers belonged to female Lesser Kestrels (n=176) whereas 104 belonged to males. The most frequently found wing feathers of male birds were P7 (38.9%), P3 (16.7%) and P9 (11.1%). On the other hand the rarer feathers collected were P5, P8 and P10 with a collection frequency of 2.8% (Fig. 2). Contrastingly, female feathers with the highest frequency of collection were P8 (21.6%), P9 (18.6%) and P10 (14.7%), whereas P4 and P5 were found to be the feathers with the lowest frequency (1% and 2.9% respectively; Fig. 2). Regarding tail feathers, all six rectrices were found in similar proportions with the only exception of the central tail feather (T1) in male birds that appeared to be rarely shed (4.4%). A summarizing table of the frequency of collection for all feathers for both sexes can be found in the Table 1.

The LM on primary feathers had a reasonable discriminatory ability (AUC=0.71) and showed that both Julian date and sex class had a significant effect on the primary feather found (Julian date: $\beta = 0.09 \pm 0.01$, $p < 0.001$; Sex: Males, $\beta = -1.2 \pm 0.5$, $p < 0.05$). Outward primaries were more frequently found later in the premigratory period while females showed a more advanced moult than males (Fig. 3). The LM exploring the shed tail feathers performed worse than the previous model (AUC=0.59) but nevertheless showed a significant effect only for Julian date ($\beta = 0.03 \pm 0.01$, $p < 0.05$), with more outer tail feathers (T4-T5-T6) found during later premigratory period (Fig. 3).

Of the 108 pellets collected, Orthoptera were present in all of them, and constituted the 95.6% of the species diet during this season. The main bulk of shed feathers was found from late July to the beginning of August whereas the consumption of Orthoptera by Lesser Kestrels has been found to peak in late August (14.6 Orthoptera per pellet). The juxtaposition of both these trends (Fig. 4) showed that Lesser Kestrels start moulting as soon as they arrive on the premigratory grounds and then they actively feed on large amounts of Orthoptera prior to migration.

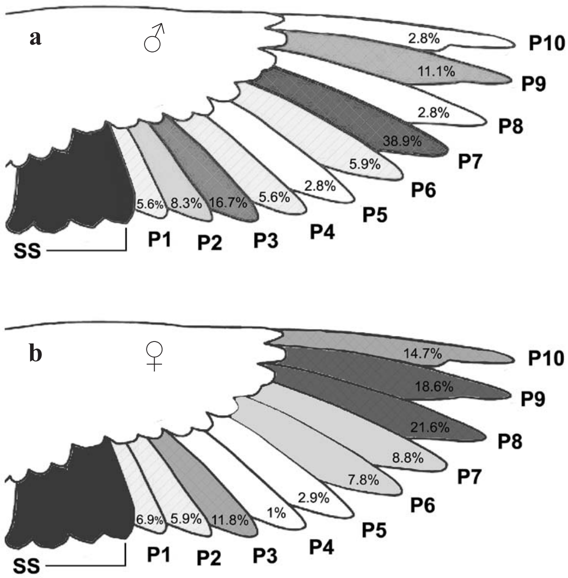

Figure 2. Proportion of shed primaries for male and female Lesser Kestrels, collected in the present study during the premigration period. SS = secondary feathers.

DISCUSSION

The results of this study suggest that Lesser Kestrels engage in an intense moult in the premigratory sites, with females showing a more advanced moult state than males. Nevertheless the collection of P10 of both sexes in the site, provide evidence that (at least some) of the individuals perform a complete moult before the autumn migration, rather unusual strategy for long-distant migrants. Previous studies of moult in the species, performed during the late breeding season, revealed that most individuals start moulting in June and females show more advanced moult stage than males (Forsman 1999, Corso 2001). It seems that this is also the case for other raptor species (Zuberogoitia *et al*. 2018, Ramírez & Panuccio 2019). Specifically, based on observations from Greece in June, (Forsman 1999) adult females showed two to three moulted primaries and males usually none (maximum two). In Matera, Italy (Corso 2001), females moulted 2-4 primaries and again males usually moult none (but occasionally up to three). These data are in agreement with the results of this study as very few P4 were found (P4 is the first feather to start wing moult), thus most of the birds arrive in the premigratory sites having already started the primaries moult and

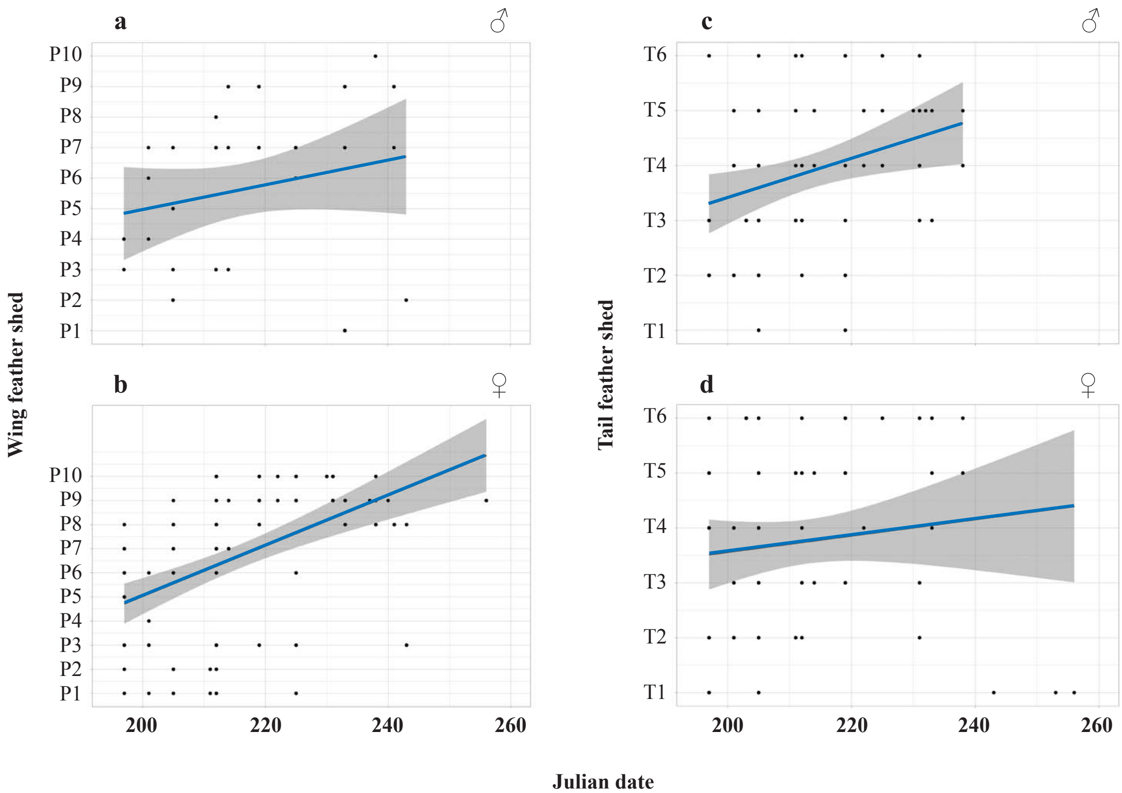

Figure 3. Moult of primary (a, b) and tail (c, d) feathers for male and female Lesser Kestrels respectively, in relation to Julian date during the premigratory period.

complete the wing moult there. Contrastingly to the results of this study, Forsman (1999) suggests that in Lesser Kestrel the moult is arrested before migration and is then completed in its winter quarters. However, these September observations were made in Kazakhstan, a population that winters in different areas from European birds (Wink *et al*. 2004, Rodriguez *et al*. 2009) and may as well show different moulting strategies.

There is limited information in the literature regarding tail moult. It seems that both female and male Lesser Kestrels do not moult any rectrices during the late breeding period, and when they do, the central tail feathers (T1) are the ones to be shed first (Corso 2001). The results of this study show that Lesser Kestrels roosting in Ioannina, engage in extensive moult of rectrices with all of the tail feathers (T1-T6) found shed in the area. This further suggests that individuals also perform a complete tail moult. But why engage in such an energy-demanding process since flight efficiency and control is mainly achieved by the wings (Hedenström 2002)? It has been shown that the tail can play a major role in maintaining stability and balance, generating lift at low speeds (Thomas 1996) and significantly contributes to yaw stability (Sachs 2007). Therefore, the tail could be rather important during migration and especially for individuals breeding in the central and eastern Mediterranean that perform sea-crossing to reach the wintering grounds. However, this remains to be investigated.

Like all biological processes, moult is subject to considerable variation even among populations of the same species (Newton 2009). Intraspecific variation in moult sequence and duration depends on various factors such as the breeding cycle, the age and sex of the individual bird, territory quality, latitude, local weather and climatic variation (Newton & Dawson 2011, Dietz *et al*. 2013, Zuberogoitia *et al*. 2018). The range of moulting strategies are subject to a wide range of selective forces thus moult is a trait that has evolved adaptively, in relation to the migratory requirements of species. For example, more southerly populations of raptors usually start to moult earlier than the more northerly ones (Forsman 1999). The premigratory concentration of Ioannina city is known to host individuals from several different populations (Bounas *et al*. 2018) whereas additionally, the method of shed feather

Table 1. Summary of the frequency of collection (number of feathers, F; proportion in the total of feathers collected, F%) for all feathers for both sexes.

	males		females	
	F	F%	F	F%
primary feathers				
P1	2	5.6	7	6.9
P2	3	8.3	6	5.9
P3	6	16.7	12	11.8
P4	2	5.6	1	1.0
P5	1	2.8	3	2.9
P6	2	5.6	8	7.8
P7	14	38.9	9	8.8
P8	1	2.8	22	21.6
P9	4	11.1	19	18.6
P10	1	2.8	15	14.7
total	**36**	**100**	**102**	**100**
tail feathers				
T1	3	4.4	10	13.5
T2	8	11.8	10	13.5
T3	17	25.0	14	18.9
T4	18	26.5	10	13.5
T5	13	19.1	15	20.3
T6	9	13.2	15	20.3
total	**68**	**100**	**74**	**100**

collection that was used here makes it impossible to quantify the findings among individuals and subsequently in regard to specific populations. This study offers more of a series of snapshots of the moult stage of the whole premigratory concentration in specific time points. However, keeping the above-mentioned in mind, this study could provide some inferences under an optimality perspective, which is essential to analyze and understand adaptations and behavioral strategies in bird migration (Alerstam 2011). Initiation of moult depends on the time of the year, the bird's energy reserves, its breeding status and its feather quality and location. It has been proposed that temporal and spatial variation of food resources has one of the most important influence on a migratory bird's annual cycle, thus the most optimal moult strategy is to engage in either summer or winter moult according to the abundance and seasonality of food resources (Barta *et al*. 2008). In fact, since the functional role of plumage is defined by environmental niches, moulting strategies are a function of environmental conditions (Beltran *et al*. 2018). Lesser Kestrels in Ioannina seem to moult as soon as they arrive and then exploit the local abundance of resources, not only for migratory fuelling but also to replenish their energy reserves after the extensive moult of flight and tail feathers that takes place. Although complete moult prior to migration may not be the pattern for all of the species' populations, it could be an adaptation of some, exploiting superabundant food resources available during August in the area, thus compressing an intense moult into a relatively short time in the autumn (Storer 1985).

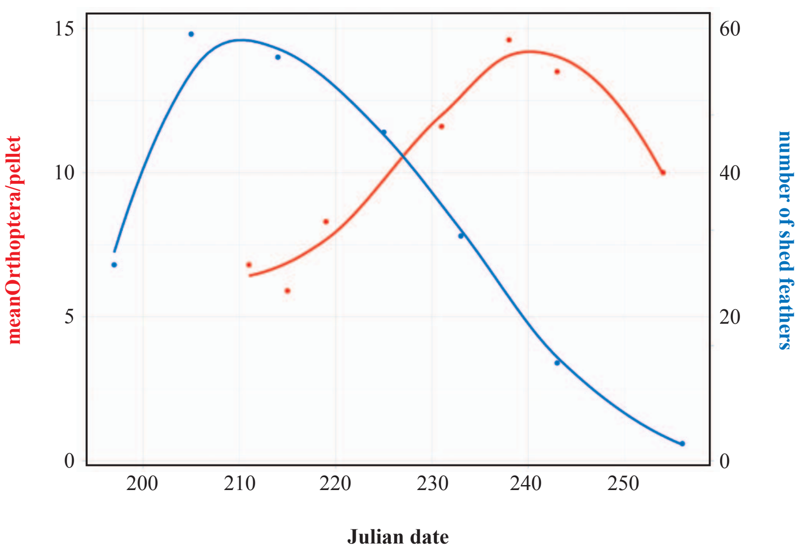

Figure 4. Number of shed feathers collected and mean number of Orthoptera included in Lesser Kestrel pellets in relation to Julian date. Julian date 200 = July 19th.

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