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Characteristics of Lesser Spotted Woodpeckers *Dendrocopos minor* on irruptive autumn movement along the coast of southern Norway

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Abstract. The Lesser Spotted Woodpecker *Dendrocopos minor* is a facultative autumn migrant in Fennoscandia, but there is little published information about its migratory ecology. Analysing data from 26 years (1990–2015) of trapping at Lista Bird Observatory, southern Norway, we found that autumn migration varied in relation to sex and age in this species. Annual numbers of trapped birds fluctuated between 0 and 19 but there was no significant temporal trend in the numbers of birds trapped. However, the numbers were positively correlated with similar data from Falsterbo Bird Observatory in southern Sweden. Thus, the annual fluctuation of Lesser Spotted Woodpeckers at Lista probably reflects the situation across larger parts of the southern Scandinavian Peninsula. In total, 96% of the birds trapped at Lista (n = 136) were in their first calendar year, showing clear evidence for differential migration in the species. There was no sex bias in the material but the median arrival date was about 14 days earlier in males than in females. Wing length increased over the season in both sexes, although the explanatory value of this seasonal progression was low. Also, body mass was higher in males than in females and increased with date of trapping when body size (wing length) was controlled for. Our findings comply with the hypothesis that annual fluctuation in the number of migrating Lesser Spotted Woodpeckers is caused by varying breeding success in the source population(s), mediated by intra-specific competition (the competitive release hypothesis).

Key words: Lista Bird Observatory, migration, phenology, population fluctuation

INTRODUCTION

Bird migration strategies vary considerably both between and within species (Alerstam 1990, Berthold 2001, Newton 2008). Annual (obligate) migrants are characterised by the regularity of migration events in time and space, and a low variability between years and individuals. Such birds may be either short- or long-distance migrants, and annual migration seems to be largely, but not solely, controlled by intrinsic factors (Berthold &Terrill 1991, Pulido & Berthold 2003). In contrast, facultative partial migrants show a high variability in migratory movements both between years and individuals. Movements in this case are typically caused by shifting environmental conditions, such as reduced availability of fluctuating food resources. Timing and distance of migration may be controlled by competitive interactions resulting in sex and age differences in migratory strategies (review by Newton 2008), and such differential migration may be adaptive due to body size related differences in metabolism and fuel deposits (Heise & Moore 2003).

The Lesser Spotted Woodpecker *Dendrocopos minor* has a wide distribution throughout the Palearctic region, breeding in various types of woodland (Winkler & Christie 2015). During summer this small woodpecker species largely forages on surface-dwelling insects and populations may fluctuate in relation to the availability of such food (Winkler & Christie 2015, Selås et al. 2008). In Europe the species has declined in many countries due to habitat loss (Winkler & Christie 2015). Most populations are sedentary but at least in the northern parts of the breeding area there is a considerable southward movement of birds in autumn (Cramp 1985, Hågvar & Hogstad 1991, Hagemeijer & Blair 1997). The number of birds on the move in such cases may be highly variable between years (Haftorn 1971, Lislevand et al. 2009, Gohli et al. 2011). Although the Lesser Spotted Woodpecker is therefore probably best categorized as a facultative partial migrant (Gohli et al. 2011), little information has been published on migration ecology in this species. In a previous study, Gohli et al. (2011) showed that the numbers of Lesser Spotted Woodpeckers trapped at Lista Bird

Observatory, southernmost Norway, tended to increase during a period of 19 years. Also, correlations with breeding population indices suggested that birds trapped at Lista may come from an extensive area in Scandinavia, including the local region.

Here we use data from 26 years of trapping at Lista Bird Observatory to describe the migration in Lesser Spotted Woodpeckers. This data set is largely the same as used by Gohli et al. (2011) but contains information from several additional years. We therefore briefly provide an updated overview of the population trend. To see if the variable autumn occurrence of Lesser Spotted Woodpeckers at Lista is representative for a larger geographical region in Scandinavia we compared the trapping numbers from Lista with similar data from Falsterbo Bird Observatory in southernmost Sweden. Moreover, we investigated whether the species is a partial migrant, looking for sex and age bias in the material, and tested if sexes appeared at different times in the season. Finally, we checked if body size and body condition varied with sex, age and phenology as such relationships may be relevant for understanding basic aspects of migration ecology in birds (Yohannes et al. 2009).

MATERIAL AND METHODS

We analysed data from Lesser Spotted Woodpeckers trapped in mist nets at Lista Bird Observatory (58°06'N, 06°34'E) from 1990 to 2015. The bird observatory is located at a lighthouse surrounded by a generally flat and open landscape (predominately agricultural land) near the sea. Although there is a plantation nearby, Lesser Spotted Woodpeckers are rare breeding birds within a five km distance from the bird observatory (Gohli et al. 2011). Most birds were trapped in mist nets during periods of the day when a constant effort approach (Bairlein 1994) was applied, in which the total net area and net positions were held constant and playback was never used to increase trapping efficiency (Røer 1997, Edvardsen et al. 2004). From 15 July to 15 November each year mist nets were used on a daily basis as weather conditions permitted. Nets were opened 30 minutes prior to sunrise and closed no earlier than six hours later (the time limit for standardized trapping) unless weather conditions worsened. We note that data used by Gohli et al. (2011) included a few birds not trapped within the constant effort scheme. Apart from this, our data are the same in the period 1990–2008. Trapping data from Falsterbo Bird Observatory, southernmost Sweden (55° 23' N, 12° 49' E) were obtained from www.falsterbofagelstation.se. Also here trapping followed a standardized constant effort scheme with mist nets being used in the period 21 July–10 November each year since 1980.

Upon capture, all birds were ringed with a standard metal ring (Stavanger Museum). Ageing and sexing was done according to Baker (1993). Recorded morphological measurements included wing length (to nearest 0.5 mm), and body mass (to nearest 0.1 g). Sample sizes differ among analyses since measurements of full sets of biometric variables do not exist in all individuals.

Trapping totals were not normally distributed and we report median values as a measure of central tendency and interquartile ranges as a measure of dispersion for this variable. For biometric measures we report mean values ± SD. We modelled the variation in body condition by using an ANCOVA with body mass as response variable, wing length (proxy of body size) as covariate and sex of the bird as factor. We tested for the possible effect of seasonal progress in the model by including the relative trapping date which is the number of days before or after 11 October; the median trapping date across all individuals (relative date = 0). We report the minimal adequate model in which the possible interactions between sex and wing length ($p = 0.82$) and between sex and season ($p = 0.60$) were excluded sequentially (interaction with highest p-value removed first). Statistical analyses were done in R (v. 2.15.3; https://cran.r-project.org).

RESULTS

Autumn trapping totals of Lesser Spotted Woodpeckers varied considerably between years at Lista, from 0 to 19 individuals (median = 4, quartiles = 1.25–6.75, n = 26 years; Figure 1). Totally 136 birds were caught, of which 65 were females, 57 males and 14 not sexed. The great majority of individuals (96%) were found to be juvenile (n = 131), only one bird was adult and the remaining four birds were not aged. The number of trapped birds did not show any significant temporal

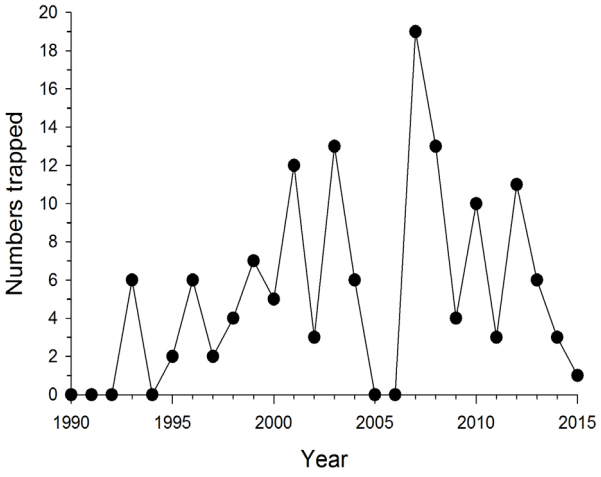

Figure 1. The number of Lesser Spotted Woodpeckers trapped between July and November at Lista Bird Observatory during 1990–2015 (total n = 136).

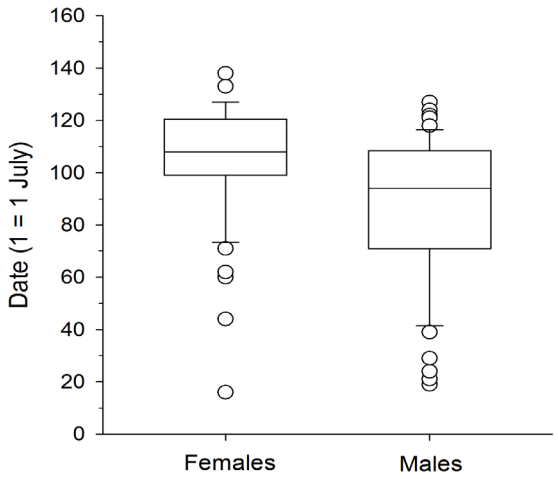

Figure 2. Sex differences in migratory phenology in Lesser Spotted Woodpeckers trapped at Lista Bird Observatory during autumn in the period 1990–2015. Trapping date is shown as days from 1 July (day 1). Median arrival date is 14 days later in females (16 October) than in males (2 October). Boxes show inter-quartile ranges where the median date is shown by the horizontal line within the box. Whiskers show 5 and 95 percentiles and open dots show extreme values.

trend over the 26 year period (r^2 = 0.11, n = 26, p = 0.10, Figure 1) but was positively correlated with the autumn trapping totals at Falsterbo, southern Sweden (r_S = 0.60, n = 26, p < 0.001).

Overall, birds were recorded during a wide time window from 16 July to 15 November, but occurrence was unevenly distributed over the autumn months with a marked peak in October (median date = 11 October, quartiles = 19 September–23 October; see also Gohli et al. 2011). Median annual arrival dates did not show any significant trend over the study period (r^2 = 0.09, n = 20, p = 0.19), nor were they related to the numbers of birds trapped each year (r^2 = 0.10, n = 20, p = 0.17). However, median arrival date was 14 days earlier in males (median = 2 October; quartiles: 12 September–16 October, n = 57) than in females (median = 16 October; quartiles: 7 October–28 October, n = 65; Mann-Whitney U-test: U = 1042, p < 0.001, Figure 2).

Overall, males were heavier than females (male mean = 23.7 ± 1.6 g, n = 44, female mean = 22.8 ± 1.3 g, n = 56, t_{98} = -3.2, p = 0.002), but there were no sex differences in wing length (male mean = 95.3 ± 2.0 mm, n= 50, female mean = 95.4 ± 2.7 mm, n = 59; t_{107} = 0.21, p = 0.83). Body condition (mass controlled for wing length) increased with relative trapping date, and was higher in males than in females (Table 1, Figure 3).Wing length increased over the season ($F_{1,106}$ = 5.78, p = 0.018), although the explanatory value of relative trapping date was low (r^2 = 0.06). When tested by ANCOVA, sex of the birds did not have a significant effect on this relationship (p = 0.27), nor did the interaction between sex and relative trapping date (p = 0.82).

Table 1. Body mass of migrating Lesser Spotted Woodpeckers at Lista, southern Norway, in relation to relative trapping date, wing length (as a proxy of body size) and sex. Results from ANCOVA treating body mass as response variable. Relative date is the number of days from the overall median date in the sample (11 October).

	Estimate	SE	t	p
Intercept	5.15	6.39	0.81	0.42
Wing length	0.17	0.07	2.6	0.012
Relative date	0.01	0.01	2.6	0.012
Sex	1.17	0.28	4.1	<0.001

DISCUSSION

In addition to showing a high annual variation in numbers characteristic of an irruptive migrant (Cramp 1985, Gohli et al. 2011, Winkler & Christie 2015), we found that Lesser Spotted Woodpeckers trapped at Lista Bird Observatory did not represent a random sample from the source population(s). Our study therefore provides evidence for differential migration (Terrill & Able 1988) in this species. Moreover, in contrast to previous findings (Lislevand et al. 2009, Gohli et al. 2011) the extra years included in our analyses showed a recent decline in trapping numbers. Hence, to the extent that data like these could be used for evaluating population changes (Silkey et al. 1999), our results may indicate that the population is no longer increasing in Norway or Fennoscandia. The positive correlation between trapping data at Lista and Falsterbo bird observatories suggests that the fluctuation in autumn numbers of Lesser Spotted Woodpeckers at Lista may reflect the situation across larger parts of the southern Scandinavian Peninsula.

Our material was almost exclusively made up of first-year birds (96%), and the overall likelihood of occurrence was similar in males and females. Several hypotheses have been proposed to explain differential migration (Smith & Nilsson 1987). First, smaller individuals may be more likely to migrate since they would be less able to store enough bodily energy resources to cope with periods of food shortage. However, this possibility seems unlikely in Lesser Spotted Woodpeckers netted at Lista, since their mean body sizes are similar to what has been reported in the literature (Haftorn 1971, Cramp 1985, Winkler & Christie 2015). Second, individuals may differ with regard to benefits of staying at or close to their breeding grounds due to competition for resources (e.g. breeding sites). This could explain why juvenile birds were over-represented in our material, if adults stay near the breeding sites while juveniles spread out to search for places to settle. Third, since dominance hierarchies are typically related to sex and age in birds, individual variation in migratory strategies may be caused by social relationships (Rogers et

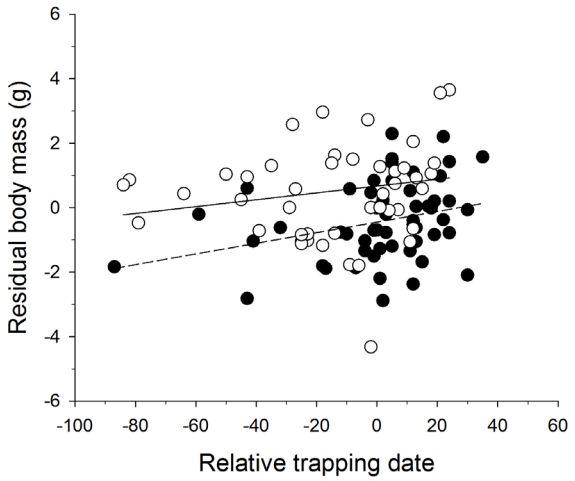

Figure 3. The relationship between body condition and migratory phenology in Lesser Spotted Woodpeckers trapped at Lista Bird Observatory during 1990–2015. Body condition is defined as the residual body mass from a linear regression between body mass (response) and wing length. Relative date is the number of days from the overall median date (zero), with later dates shown as positive values and earlier dates as negative values. The relationship is plotted for the purpose of visualization only (see Table 1 for results of the full model). Open dots show males (continuous line), filled dots females (broken line).

al. 1989, Helm et al. 2006). For instance, dominant individuals may force subordinates to move because the latter are out-competed for important resources (the competitive release hypothesis; Chapman et al. 2011, Gauthreaux 1982). In birds, males typically dominate females and adults dominate juveniles (Noble 1939, Smith & Nilsson 1987), although this is often assumed rather than measured (Newton 2008). It is therefore possible that the over-representation of juvenile Lesser Spotted Woodpeckers on autumn migration along the coast of southern Norway is caused by intra-specific competition and social dominance relationships.

We found no differences in wing length between sexes, but males were heavier than females, and both wing length and body condition increased with season. The results on sexual size dimorphism fit with earlier reports showing that sexes are similar in size in the nominate subspecies (Cramp 1985). The finding of a seasonal effect on body size might indicate that individuals in poorer condition migrate first because they are subdominant and hence forced to leave earlier. Alternatively, body condition might increase generally during the autumn so that birds are in poorer condition in late summer than in October when most birds migrate. We can only speculate on the causes of this pattern, but the nature of migratory irruption in Lesser Spotted Woodpeckers fits well with the expected if annual variation in occurrence is caused by density-dependent competition, increasing in years with a high reproductive output (Gohli et al. 2011). Migration in the Lesser Spotted Woodpecker seems to be largely parallel to that of the closely related Great Spotted Woodpecker *Dendrocopos major*, which also shows irruptive autumn movements in Fennoscandia (Eriksson 1971).

Although there was a large overlap in timing, male Lesser Spotted Woodpeckers appeared significantly earlier than females at Lista during autumn migration. Assuming that males dominate females (see above), social dominance relationships and competitive exclusion seem improbable to explain the pattern of phenology, since females would then most likely be forced to move before males. There may be a high selective pressure for earlier arrival in the sex competing for breeding sites, mates or territories (Francis and Cooke 1986, Myers 1981). Although nothing seems to be known about when migrating birds settle down, it is possible that young males compete for access to the best available breeding territories. If so, males should be subjected to a high selective pressure for early dispersal away from their natal areas, which would explain why they to a great extent move earlier than females.

More studies are needed on the migratory movements of Lesser Spotted Woodpeckers to sort out the details of both the migratory propensity in various populations and years, migratory routes, non-breeding areas and timing for when migrating young individuals establish a breeding territory. Increased ringing effort in this species, especially of birds from known populations, could potentially produce data useful for such analyses. Also, new technology may in the future provide exciting opportunities to track the migration of birds in much greater detail. For instance, the development of miniature light-level geolocators (McKinnon et al. 2013) makes it possible to follow the movements of individual birds much smaller in size than we could only dream of a few years ago. However, such devices are not suitable for tracking Lesser Spotted Woodpeckers or any other irruptive migrants since they require that birds are re-trapped after movements have taken place in order to acquire the data. This is not realistic in young birds which are typically less philopatric than adults (Greenwood 1980), so a remote tracking system where transmitters are of suitably small size (Wikelski et al. 2007) would therefore be required.

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