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Dispersal and age at first breeding in Norwegian Northern Lapwings (*Vanellus vanellus*)

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Dispersal and age at first breeding were studied in Northern Lapwings from south Norway. In total, 40 adult birds (two males) and 114 chicks were colour-ringed. There were no sex differences in returning rates of birds ringed as chicks (n = 10 males and 14 females). Nor were there sex differences in natal and breeding dispersal distances. When sexes were pooled, natal dispersal was longer than breeding dispersal (median distances 160 m and 62 m, respectively). Also, colour-ringed females were more likely than males to breed in their second calendar year. Analyses of a separate data set of regular ring recoveries largely confirmed the relatively low degree of natal dispersal in Norwegian Northern Lapwings. In total, 72% of birds reported during the breeding season (total n = 104) were found within 10 km from their natal site. Dispersal distances observed in Norway are similar to those reported from a comprehensive British study, and from Europe in general.

1. Introduction

Dispersal patterns can have a great impact on life histories, population structures and behaviour in birds and vary considerably both interspecifically and in relation to sex and age (Greenwood 1980, Gauthreaux 1982, Greenwood & Harvey 1982, Lindberg *et al*. 1998). Within species, dispersal may be more extensive in migrating than in sedentary populations (Berthold 2001, Forero *et al*. 2002). This pattern is similar for migratory and sedentary species (Paradis *et al*. 1998).

The Northern Lapwing (*Vanellus vanellus*) is a Palaearctic shorebird that typically breeds on farmlands and pastures across Europe (Cramp & Simmons 1983). Breeding dispersal distances of British and Central European Lapwings are shorter than natal dispersal distances in both sexes (Thompson *et al.* 1994, Glutz von Blotzheim 2001). In addition, yearling breeders in Britain were equally common among males and females (Thompson *et al.* 1994), although a difference in this respect was later reported by Parish *et al.* (2001).

In northern Europe, Northern Lapwing populations are mostly migratory, wintering in Britain and south-western Europe (e.g., Cramp & Simmons 1983, Appleton 2002, Bakken *et al*. 2003, Lislevand 2006, Shrubb 2007). Little is known about dispersal patterns in these northern populations (but see Berg *et al*. 2002). Based on national ringing data, Grimeland (1966) suggested that na-

tal dispersal would be higher in Norway than in other European populations. However, the difference was marginal, i.e., 68% of Norwegian birds stayed within 10 km as compared with 72% that did so elsewhere in Europe, and the difference was not statistically tested (Grimeland 1966).

Here, we present observations of natal dispersal, breeding dispersal and age at first breeding in Norwegian Northern Lapwings. We estimated distances between nests from year to year for individual Lapwings, and examined differences between sexes and age classes. Our colour-ringing study (see Material and methods) was limited to a small study area which made long-distance movements unlikely to be discovered. Hence, we also analysed regular ring recoveries of Lapwings ringed as chicks in Norway and later recovered in the breeding season.

2. Material and methods

We studied Northern Lapwings in an agricultural grassland area at Gimramyra, south-western Norway (Rogaland county; 58°47' N, 05°37' E), at two sites about 1.5 km apart. The area is situated in a shallow depression, formerly a lake, drained in the 1920s. It is used for hay and silage production and interspersed with some spring-sown crops. The study fields are partly bordered by woodlots and are still quite wet due to poor drainage. This region of Rogaland is one of the national prime agricultural areas; hence, the study sites are surrounded by vast farmlands in which some ringed birds may have dispersed without us being able to detect them.

We carried out the field work during five breeding seasons (mid March–May) between 1998 and 2002. We identified individuals between seasons by their colour-ring combinations and opportunistically observed the Lapwings during other studies of their breeding behaviour (Grønstøl 2001, Lislevand 2003). The total size of the study area varied between 20 and 33 ha/year according to requirements of other parts of the study. Median egg-laying date was the 31st March, and the study period included the time from territory establishment to hatching in most nests. The average density of Lapwings, in suitable habitat at Gimramyra, was 1.45 ± 0.11 SD territorial males/ha (n = 5 years). Across years, 33%–48% of males were polygynous, 43%–64% were monogamous, and 2%–13% remained unmated throughout the season (see Byrkjedal *et al*. 1997 for methods).

Table 1. The number of colour-ringed Northern Lapwings in relation to age per year and the numbers of these birds re-sighted within the study area in subsequent breeding seasons. Only two of the individuals ringed as adults were males (one in 1998 and one in 1999).

	n ringed	*n* re-sighted/year			
Year	(ad/pull)	1999	2000	2001	2002
1998	13/45	6/2	4/6	2/6	1/3
1999	10/35		6/3	4/4	4/4
2000	2/31			2/5	2/5
2001	15/3				9/0

Between 1998 and 2001, we ringed 38 adult females, 2 adult males and 114 chicks with one metal ring and three plastic colour-rings of individually unique combinations (Table 1). Incubating adults were trapped on their nests. Compared with females, males were much more reluctant to enter nests with traps; hence the low number of adult males ringed. We ringed chicks with a metal ring just after hatching, and added colour-rings when they were from two to four weeks old (mean body mass = 113 g ± 27 SD, n = 60). Each year after 1998 all territorial birds within the study fields were checked for colour-rings using binoculars and telescopes. Adults could be sexed based on plumage characters (Cramp & Simmons 1983) but we did not determine the sex of chicks unless they were re-sighted as adults. We marked locations of nests on maps (scale 1:500) and assigned ringed birds to their respective nests if possible. When a chick's nest of origin was unknown we used the ringing location instead.

Distances between an individual's nests in subsequent summers were measured on maps. In cases of nest predation and subsequent clutch replacement we used the first nest location. As a measure of natal dispersal we used the distance between the first known own nest and the nest where a bird hatched or, if this was not known, its ringing location (see above). We estimated breeding dispersal as the distance between an individual's own nests from one season to the next. If a bird was

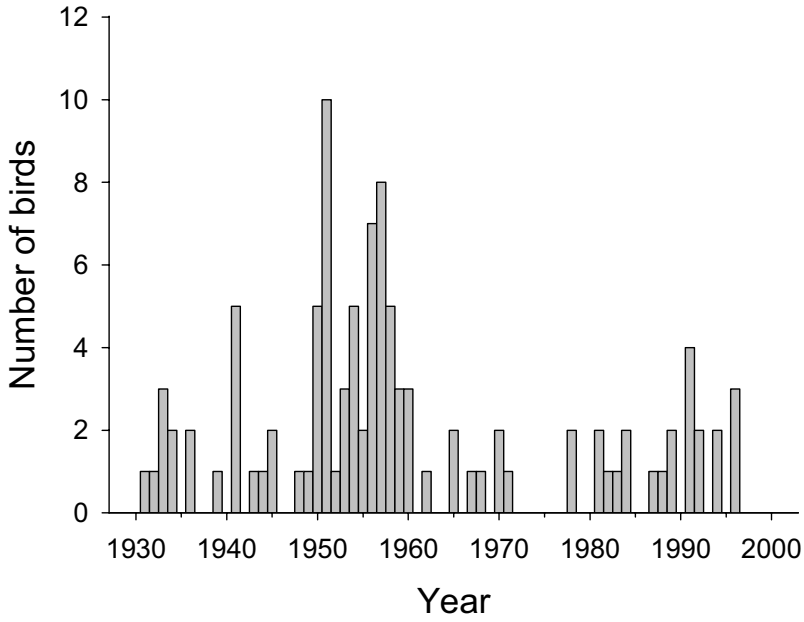

Fig. 1. The temporal distribution of Northern Lapwings ringed as chicks in Norway and recovered in their second calendar year or later. Number of birds refers to the year of ringing in the period 1931–2002. Only birds recovered during the breeding season (April to May) were included (n = 104).

found breeding in more than two seasons we used the mean moving distance. For polygynous males we used the midpoint between all nests on the territory as measuring points. For four males (unmated) and one female no nests were found, although they appeared to be territorial. In these cases, we used the approximate centre of the respective territories as measuring points for dispersal distances. Excluding these individuals from the analyses did not affect our conclusions. Non-territorial birds were omitted from all analyses of dispersal and age at first breeding.

To investigate the dispersal patterns of Lapwings across southern Norway, we analysed a separate data set acquired from the national ringing scheme (i.e., excluded our colour-ringed birds). In total, this material consisted of 678 birds ringed and subsequently recovered between 1931 and 2002. The accuracy of dispersal distances in these data is one km. To estimate dispersal from regular ring recoveries, we included only birds ringed as chicks and recovered in a different year in April and May, which is the main breeding season of Lapwings in southern Norway. Further, we omitted from the analyses individuals with uncertain date of recovery. The temporal distribution of these recoveries is shown in Fig. 1; see Bakken et al. (2003) for the distribution of ringed Lapwings. All recoveries used in the analyses were of individuals ringed from Sør-Trøndelag county southwards. The majority (72%) came from Rogaland county.

3. Results

In total, we re-sighted 24 Lapwings colour-ringed as adults (60%) and 24 ringed as chicks (21%) at least once in the subsequent breeding seasons. Among birds ringed as chicks there were no sex differences in rates of return to the study area; 10 were males and 14 were females (Binomial test: P = 0.42). The median natal dispersal distances were 175 m and 144 m for females and males, respectively, and did not differ between sexes (Mann-Whitney U-test: $n_{\text{males}} = n_{\text{females}} = 9$, $U = 34$, P = 0.57). The median breeding dispersal distances in females were 60 m and in males 109 m and did not significantly differ among sexes ($n_{\text{females}} = 25$, $n_{\text{males}} = 5$, $U = 41$, $P = 0.23$). With sexes pooled, natal dispersal (range 18–1,540 m, median = 160 m, quartiles = 87 and 248, n = 18) was higher than breeding dispersal (range 11–710 m, median = 62 m, quartiles = 44 and 155, $n = 30$; $n_{\text{natal}} = 18$, $n_{\text{breeding}} = 30$, $U = 152$, $P < 0.015$; Fig. 2).

As with the pattern revealed by the colour-ringing data, ordinary ringing recoveries of Lapwings from southern Norway (n = 104) also

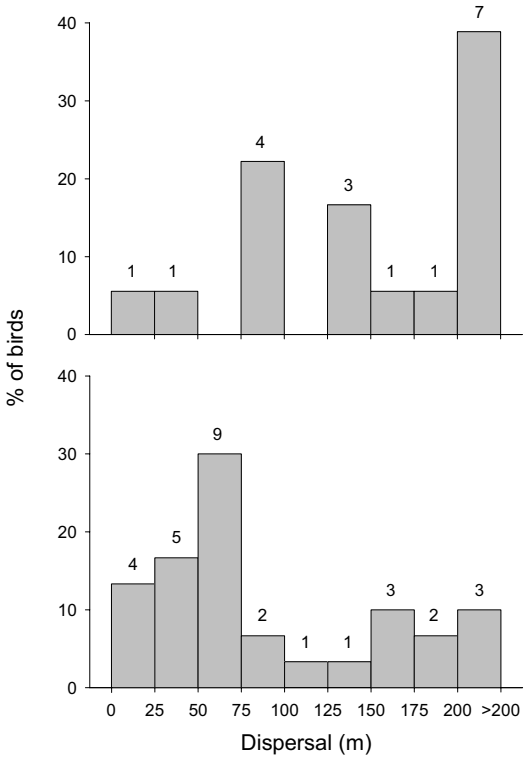

Fig. 2. Natal dispersal distances (top; n = 18) and breeding dispersal distances (below; n = 30) of colour-ringed Northern Lapwings within the study area in south-west Norway (in m). Sexes were pooled. Distances were binned using 25-m intervals up to 200 m. Numbers of birds in each interval are shown above bars.

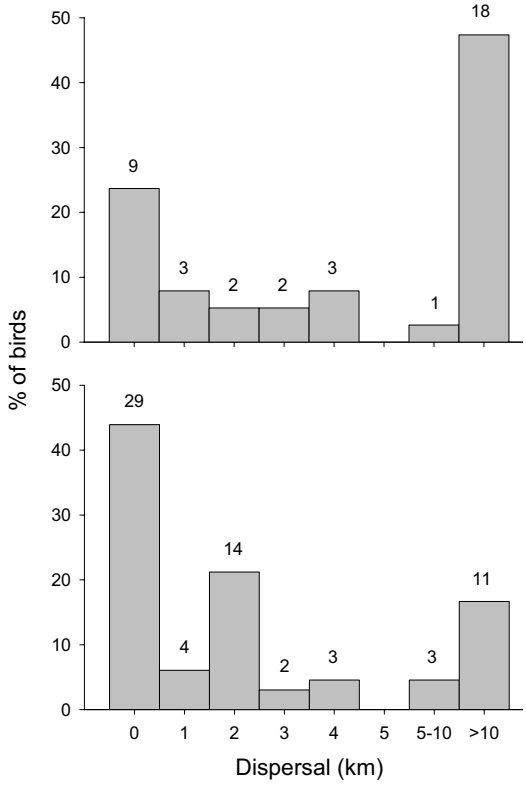

Fig. 3. The distribution of dispersal distances in Norwegian Northern Lapwings ringed as chicks and recovered during a subsequent breeding season (April–May). The geographical resolution of the data is 1 km. Data from the second calendar year birds are shown on the upper figure (n = 38) and older birds below (n = 66). For birds that were observed returning to areas >5 km away from their ringing site, percentages are binned using the intervals 5–10 km and >10 km. Numbers of individuals in each interval are shown above bars.

showed a high degree of site fidelity. In total, 37% of birds recovered in the breeding season were reported at 0 km, 68% within 5 km and about 28% farther away than 10 km, from the site they had been ringed as chicks (Fig. 3). Birds in their second calendar year were found between 0 and 1369 km from the ringing locality (median = 6 km, quartiles = 1 and 88.5, n = 38), whereas older birds were reported between 0 and 2363 km away (median = 1.5 km, quartiles = 0 and 3.75, n = 66). Dispersal distances were significantly longer for Lapwings reported in their second calendar year compared with older birds ($n_{\text{second year}} = 38$, $n_{\text{older birds}} = 66$, $U = 829$, $P = 0.003$). The two longest dispersal distances were of a young bird recovered in Russia (distance = 1,369 km) and an adult in Portugal (distance = 2,363 km).

Among the colour-ringed birds, females were more likely to appear on the study site as yearlings: seven of nine females attempted breeding, while only one of eight males defended a territory within the study area in their second calendar year (Fisher's Exact test: $P = 0.015$).

4. Discussion

A major problem in many studies attempting to estimate animal dispersal distances is that of limited survey areas (Koenig *et al.* 1996). Our observation procedures were not comprehensive enough to

identify colour-ringed birds returning to areas more than a few hundred meters from the natal site. Because 63% of regular ring recoveries were located 1 km or more from the ringing location, our colour-ringing study almost certainly underestimated natal dispersal. However, estimates of breeding dispersal are better, as a higher proportion of the birds colour-ringed as adults returned to the study area in at least one subsequent season compared with those ringed as chicks (60% vs. 21%, respectively). We observed no sex differences in (1) returning rates to the natal area, (2) natal dispersal distances, or (3) breeding dispersal distances. Generalizing from these findings requires that there is no systematic variation with distance from the study area. Similarly, the findings that females were more likely to breed in their second calendar year, and that natal dispersal was longer than breeding dispersal, also rely on this assumption.

Regardless of the uncertainties outlined above, this study shows that a considerable proportion of Northern Lapwings return to breed close to their natal area. This conclusion is most notably supported by the analysis of regular ring recoveries which provides a more realistic estimate of dispersal distances than the colour-ringing study does. The levels of natal dispersal in our study are partly comparable with findings in British Lapwings reported by Thompson *et al*. (1994). We restricted our search for colour-ringed birds to a much smaller area; the radius of the British study area was 5 km as compared with the maximum of 1.5 km in our study. The small radius most likely explains why the return rate of chicks at Gimramyra (21%) was lower than that of the two British study sites (22.2% and 43.2%). However, the proportion of regular ring recoveries reported within 10-km distance from ringing localities was even higher in Norway (72% vs. 61% in Britain) and similar to Europe in general (about 70%; Glutz von Blotzheim 2001). Thus, in contrast to Grimeland (1966), we suggest that Norwegian Northern Lapwings do not disperse farther than Lapwings from other European populations.

Also, the lack of sex differences in returning rates and dispersal distances agrees with the findings in British Lapwings (Thompson *et al*. 1994). Hence, Northern Lapwings differ from the most common avian pattern, in which dispersal is less extensive in males than in females (Greenwood 1980, Gauthreaux 1982, Greenwood & Harvey 1983, Lindberg *et al*. 1998). Greenwood (1980) proposed that dispersal strategies in animals are influenced by their breeding system and territorial behaviour. For example, assuming that familiarity with the breeding area is advantageous in intra-sexual competition (prior residency effect) the competing sex should benefit most from being site-faithful. In the Northern Lapwing, males are territorial and frequently polygynous (e.g., Berg 1993, Byrkjedal *et al*. 1997, Parish *et al*. 1997, Liker & Székely 1999). However, intra-sexual competition for mates, including fierce fights, is also frequent among females in this species (Liker & Zékely 1997, Grønstøl 2001, Grønstøl *et al*. 2003). Therefore, it might be beneficial for both sexes to return and breed in an area they know well. The idea that intra-sexual selection modifies dispersal behaviour in both sexes may deserve more attention especially in species where no sexual differences are evident in this respect (e.g., Oring & Lank 1984, Thompson *et al*. 1994).

As in the majority of bird species (Greenwood & Harvey 1982), we found the range of natal dispersal to be longer than that of breeding dispersal. Based on Norwegian ringing recoveries, and in contrast to Thompson *et al.* (1994), we also found that Lapwings recovered in their second calendar year were located farther away from their natal sites than were older birds. It is possible that a larger proportion of Norwegian birds recovered in their second calendar year were not breeding and that, therefore, they were found outside the natal areas more often than older birds.

Our observation that females started breeding at an earlier age than males agrees with the report of Parish *et al*. (2001), but differs from that of Thompson *et al*. (1994) where no sex differences were found. A possible reason for this inconsistency is that males in different studies have been exposed to unequal environmental conditions during their first year of life and that these conditions have differentially influenced their abilities to compete for territories and mates in their first year (Parish *et al*. 2001). In addition, breeding opportunities for younger males probably depend on the availability of vacant territories (e.g., Summers & Nicoll 2004) which may vary both among Lapwing populations and years. Annual fluctuations

in mortality rates (Peach *et al*. 1994, Catchpole *et al*. 1999) and decreased accessibility of suitable habitat caused by changing agricultural practices (Berg *et al*. 2002) could also influence whether younger males breed or not.

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Levittäytyminen ja ensipesintäikä norjalaisilla töyhtöhyypillä (*Vanellus vanellus*)

Töyhtöhyypän levittäytymistä ja ensipesintäikää tutkittiin eteläisessä Norjassa. Kaikkiaan 40 aikuista (kaksi koirasta) ja 114 pesäpoikasta värirengastettiin. Syntymäpaikalleen kevätmuutolla palaavien osuus oli samanlainen koirailla ja naarailla (n = 10 koirasta ja 14 naarasta). Myöskään syntymä- ja pesimäpaikan välisissä etäisyyksissä ei ollut sukupuolieroa. Sukupuolet yhdistettynä syntymäpisteestä levittäytymisen matka oli pidempi kuin eri pesimäyrityksien välinen (keskietäisyydet vastaavasti 160 m ja 62 m). Värirengastetut naaraat yrittivät koiraita todennäköisemmin pesiä jo toisena kalenterivuonnaan. Tavanomaisista rengaslöydöistä koostuvan aineiston analyysi osoitti, että levittäytymismatkat syntymäpisteestä seuraaviin vuosiin olivat yleisesti lyhyitä. Kaikkiaan 72 % sellaisista yksilöistä, jotka havaittiin pesimäaikana (n = 104), löydettiin 10 km säteellä syntymäpisteestään. Levittäytymismatkat Norjassa ovat samankaltaisia kuin laajassa brittiläisessä tutkimuksessa ja yleisesti Euroopassa.

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