



Individuality in northern lapwing migration and its link to timing of breeding

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We tracked eight adult northern lapwings *Vanellus vanellus* (six females and two males) from a Dutch breeding colony by light-level geolocation year-round, three of them for multiple years. We show that birds breeding virtually next to each other may choose widely separated wintering grounds, stretching from nearby the colony west towards the UK and Ireland, and southwest through France into Iberia and Morocco. However, individual lapwings appeared relatively faithful to a chosen wintering area, and timing of outward and homeward migration can be highly consistent between years. Movements of migratory individuals were usually direct and fast, with some birds covering distances of approximately 2000 km within 2 to 4 days of travel. The two males wintered closest and returned earliest to the breeding colony. The female lapwings returned well before the onset of breeding, spending a pre-laying period of 19 to 54 days in the wider breeding area. Despite the potential for high migration speeds, the duration that birds were absent from the breeding area increased with distance to wintering areas, a pattern which was mainly driven by an earlier outward migration of birds heading for more distant wintering grounds. Moreover, females that overwintered closer to colony bred earlier. A large variation in migration strategies found even within a single breeding colony has likely supported the species' responsiveness to recent climate change as evidenced by a shortened migration distance and an advanced timing of reproduction in Dutch lapwings since the middle of the 20th century.

Migration strategies may vary between species, populations, individuals and between years within an individual. Individuals from a particular breeding population may migrate to the same wintering area or they may spread out over much of the non-breeding range. These connections between breeding and non-breeding areas of a migratory species are called 'migratory connectivity', and the strength of migratory connectivity has implications for the species ecology, evolution and conservation (Webster et al. 2002). Furthermore, the choice of a certain wintering area and migratory strategy may affect annual schedules including timing of events at breeding area (Marra et al. 1998), which demonstrates the importance to follow individuals throughout the annual cycle. Knowledge of variation in migratory routines within and between individuals of a population is also important to understanding and predicting the ability of species responses to environmental change, including climate change (Conklin et al. 2013).

We employed GLS (Global Location Sensing, also called 'light-level geolocation' or just 'geolocation') technique based on the analysis of diurnal changes in light levels to

track annual movements of northern lapwings (*Vanellus vanellus*; here synonymously termed 'lapwing(s)'). Archival tags ('geolocators') record light intensities to determine dusk and dawn times from which geographical positions (two fixes daily) are calculated; day (night) length determines the latitude and time of local midday (midnight) the longitude (Hill 1994).

Lapwings have been intensively ringed in many European countries for many years. Imboden (1974) undertook an extensive analysis (nicely summarized in Alerstam 1990) of ring recoveries collected during 1900 to 1969 from birds ringed as unfledged young and recovered within their first year of life or later. Albeit relying mainly on dead recoveries of hunted individuals, this analysis enabled the reconstruction of average seasonal movement patterns at population(s) level. It also revealed a large overlap in non-breeding locations used by lapwings originating from widely separated breeding colonies. Here, we present results from a first-time tracking study on this species by charting the year-round whereabouts of adult lapwings from a Dutch breeding colony. Some individuals were tracked for multiple years thereby providing first insights into individual consistency of migratory timing and choice of non-breeding locations. Finally, we investigate if spatial variation in non-breeding location relates to temporal variation of events at breeding area.

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Material and methods

Field work

Lapwings were monitored in their breeding colony near the village Nij Beets in the Dutch province of Friesland (53.03°N, 6.01°E). The core study area was formed by the nature reserve 'De Dulf' (135 ha) and adjacent farmland (13 ha, consisting of grassland and maize fields). Deployment of GLS loggers and recapture attempts occurred during 2007–2010. An extended study area of approximately 15 km² was intensively searched for returning colour-ringed individuals (tagged or untagged) during 2008–2011. Each season, searching efforts commenced mid-February and lasted, with decreasing intensity, into June. Active lapwing nests were found and revisited throughout March to June, and individual females laid up to three full (and possibly more partial) clutches during repeated breeding attempts within a season as a consequence of a high rate of nest and chick predation in our study area.

Lapwings were caught on their nest during incubation with a self-operating trap (Koopman and Hulscher 1976) and were fitted with a metal ring below the tibiotarsal joint and a combination of two colour rings above the tibiotarsal joint. The GLS logger (weight 1.5 g, model Mk14, British Antarctic Survey) was attached to an additional plastic ring fitted above the tibiotarsal joint. Total attachment mass was 1.9 g, equating to 0.86% of average body mass of lapwings caught during incubation (222 g, $n = 86$, own data). Logger deployment this way allowed easy and quick attachment minimising handling time of incubating birds. Moreover, following earlier approaches of GLS studies with leg-mounted tags in other open-ground nesting species (Eichhorn et al. 2006, Eichhorn et al. 2009) the diurnal shading pattern permitted the detection of the start of incubation in females in the year(s) after logger deployment. From this we could estimate the date of laying the first egg by assuming that incubation commences at full clutch and an average laying duration of 5 d (Cramp and Simmons 1983). For (incomplete) clutches found during laying we back-calculated to first-egg stage by assuming 1.5 d egg-laying interval. Due to their smaller share in bi-parental incubation (Cramp and Simmons 1983) male incubation pattern was not reliably discernible from light data. All birds returned to incubating their nest after capture. Loggers were attached to 22 females and 4 males in 2007 and (re-)attached to 3 females in 2008. Loggers were retrieved from 5 females and 1 male in 2008, from 2 females and 1 male in 2009, from 2 females in 2010, and from 1 male in 2011. Loggers failed downloading data either completely (1 male in 2011) or partly in two instances. Overall, we were able to track the full year-round movements of 8 different individuals (6 females, 2 males); of those, 2 females were tracked over 3 consecutive years and a further female over 2 consecutive years, yielding a total of 13 return migration journeys.

In the end of breeding season 2007 we observed 52 individually marked lapwings in the study area (mainly marked in that season plus few previously marked individuals), of which 27 carried a GLS logger and 25 individually coded rings only. In 2008 (the year with most data) we sighted

13 (48%) tagged birds (for 12 of them we could confirm breeding) and 12 (48%) birds fitted with rings only (for 8 of them we could confirm breeding) in our study area. Average start of egg-laying (into first clutches) in 2008 was 6 Apr (± 9 d SD, $n = 9$) for tagged birds and 5 Apr (± 7 d, $n = 17$) for untagged birds (ringed or un-ringed). Mean clutch size (maximum number of eggs observed in any of the nests produced by individual couples throughout 2008) was 3.8 (± 0.4 SD, $n = 9$) and 3.9 (± 0.3 , $n = 19$) in nests of, respectively, tagged and untagged birds. Eggs were not measured but appeared of normal size. Based on these observations carrying a logger or not caused no apparent difference in return rate, lay date and clutch size. Body mass of tracked lapwings remained generally at similar levels in subsequent breeding season(s) as compared to mass at tagging (Supplementary material Appendix 1 Table A1). Noteworthy, however, in 2008 we observed 4 tagged lapwings limping. All of these limping birds belonged to a subsample of 13 birds that had received an adjusted type of leg ring carrying the logger: a plastic ring was lined with a thin layer of soft cellular rubber (Zotefoams Plc) on the inside with the aim to reduce ring rotation and pressure on the leg. Recapture of two limping birds revealed the problem: dead skin cells sloughing off the bird's leg accumulated in the space between leg and ring causing swelling and inflammation. Therefore, we stopped using this adjusted type of leg ring. Limping was not observed in birds where the logger was attached to a simple plastic leg ring that was not extra lined with soft material.

Data analysis

Light data were analysed using MultiTrace Software (Jensen Software Systems). Sun elevation angles and corresponding thresholds for dusk and dawn events were estimated from calibration periods for each bird–logger combination individually, when birds carrying a logger were observed at known location (i.e. in the breeding area). Used Sun elevation angles ranged from -3.7° to -4.7° . The loggers measured light intensity every 1 min, but recorded only the maximum value of 10 successive readings (i.e. within each 10 min interval) together with the corresponding time at the end of that 10 min interval. This can lead to a potential mismatch of time and light value by up to 9 min during the dusk period, because then the maximum light value is more likely to be measured at the beginning of a 10 min interval. MultiTrace had been adjusted by the developer to shift the dusk times accordingly. The raw light data together with determined dusk and dawn events were inspected manually to identify and annotate sections of obvious light level interference (e.g. caused by shading of logger when bird sat down or tucked the tagged leg into the plumage, or artificial light at night) with subsequent removal of corresponding position estimates. An inherent limitation of GLS is that around equinoxes only longitude can be measured, because similar day and night length prevents reliable estimates of latitude. This limitation posed almost no problem in the current study since most non-breeding movements occurred well between autumn and spring equinoxes, except in one case for the last leg of spring migration (Fig. 1). In this case positions were reconstructed from measured

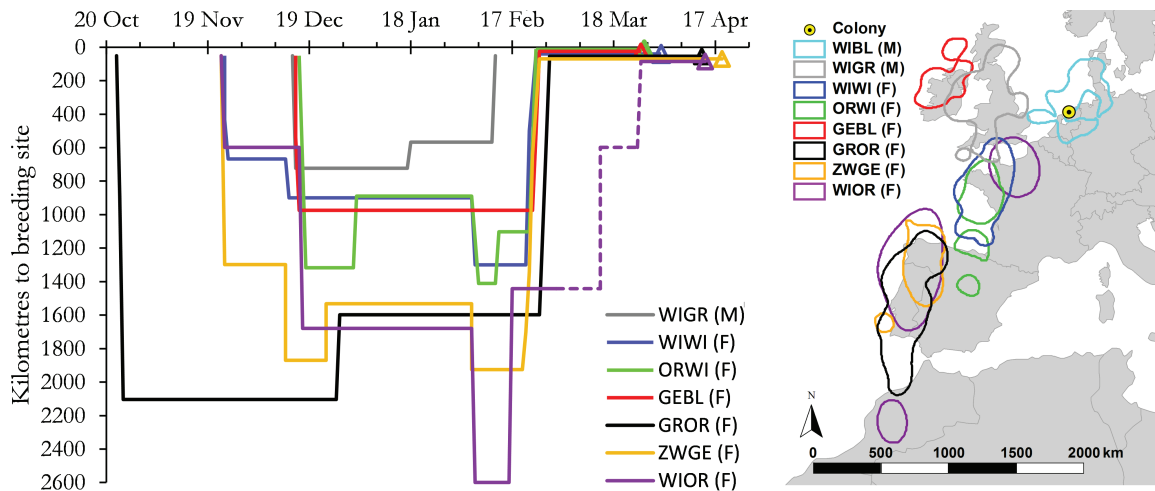


Figure 1. Progress of displacement from and to the breeding site (left panel) of adult northern lapwings tracked from 2007 to 2008 together with their overwintering areas indicated by 75% Kernel contour lines (right panel). Kernel densities were based on all available locations > 300 km away from breeding site for each bird, except for male bird 'WIBL' that overwintered closer to breeding colony; in this case winter kernel density was based on locations measured from 10 Dec 2007 to 10 Feb 2008. For female (F) birds the start of laying the first clutch is marked by triangular symbols. Movements of bird 'WIOR' partly coincided with spring equinox preventing reliable latitude measurements and were, therefore, reconstructed from longitude fixes only (indicated by a dashed line). For further details see methods.

longitude fixes with the assumption that the corresponding latitude crosses the shortest line connecting previous and subsequent higher confidence locations. Longitude and latitude estimates from which we inferred migration and wintering patterns are plotted in Supplementary material Appendix 1 Fig. A1.

Position estimates were used to calculate distance to the breeding site as the average of ortho- and loxodromes. We used averages, because we have no prior assumptions about lapwings' ability to potentially perform the one or other route navigation. Mean accuracy of GLS technique normally ranges between approximately 100 and 300 km (Cstry et al. 2011, Lisovski et al. 2012 and references therein). We treated locations within a radius of 300 km around the nesting site as being part of the wider breeding (home) area. Movements away from and back to breeding site are illustrated only when position estimates indicated that the bird left this home area for more than three consecutive days. Individual movement trajectories are illustrated in step-line charts as change in distance to breeding colony over time (Fig. 1, 2). Each distance level (step) represents the mean of all single distances to breeding colony calculated over the given time period. A new subsequent step was introduced when single distances over at least three consecutive days were all off by more than 200 km relative to the preceding period's (cumulative) mean distance to colony. We calculated 75% Kernel densities using the Animal Movement Extension 2.0 in ArcView GIS 3.2 (ESRI), selecting least squares cross validation (LSCV) and ad hoc calculation of a smoothing parameter, to outline individual overwintering areas (Fig. 1, 2). Kernel densities were based on all available locations > 300 km away from nesting site, except for bird 'WIBL' that spent mid-winter within a radius of 300 km around the breeding colony; in this case winter kernel density was based on locations measured from 10 Dec 2007 to 10 Feb 2008. All maps

are projected as Lambert equal-area azimuthal centred on the breeding site location. Temperature data were obtained from the Royal Netherlands Meteorological Institute for the weather station at Leeuwarden (53.2N, 5.8E) 24 km away from the breeding colony.

We calculated Pearson's product-moment correlation coefficients (r) and their 95% confidence intervals ($-95\%CI$, $+95\%CI$) to describe the strength of association between (average) distance to the wintering area and timing of events in the breeding area. Inspection of scatterplots and distributions suggested linear monotonic relationships, no obvious deviation from normality and no outliers, except for arrival date due to the late arrival of one bird (WIOR) in 2008. However, when compared to alternative correlation measures, Pearson's r and associated standard t test is expected to perform reasonably well with regard to both type I error and power even when the underlying distribution departs substantially from bivariate normality as one of the assumptions (Puth et al. 2014). For the construction of CIs we used Fisher's z transformation as described in Puth et al. (2014). We performed correlation analysis on sets of data including 1) 1 male plus 6 females tracked 2007–2008 ($n = 7$), 2) 6 females only tracked 2007–2008 ($n = 6$), 3) 6 females tracked 2007–2010 ($n = 11$). The latter makes use of a larger data set but violates assumption of independent data points. We argue that, given all data at hand, the best estimate is most likely found somewhere in between such a conservative approach (2) and overconfident approach (3). Unfortunately, sample size did not allow for a mixed effect modelling approach.

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.qf20f>> (Eichhorn et al. 2017).

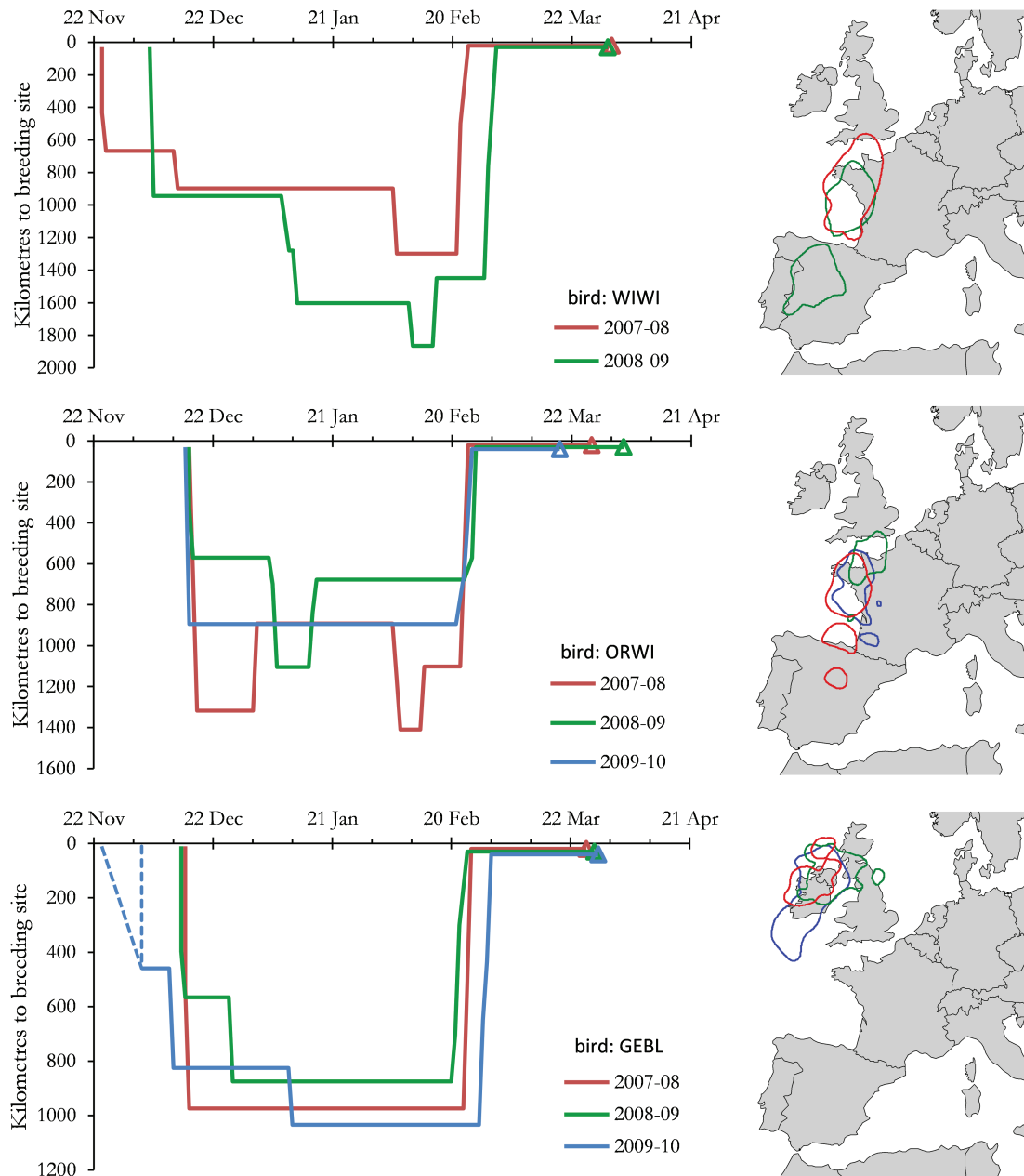


Figure 2. Progress of displacement from and to the breeding site (left panels) of all three female northern lapwings tracked consecutively for up to three years (2007–2010) together with their overwintering areas indicated by 75% Kernel contour lines (right panels). Kernel densities were based on all available locations > 300 km away from breeding site. Triangular symbols mark the start of laying the first clutch for each female and year. For bird ‘GEBL’ no reliable fixes were available between 24 Nov and 3 Dec 2009, indicated by a dashed line.

Results

Individually diverse overwintering strategies

Lapwings tracked during the same season (2007–2008) showed pronounced variation in migration and overwintering strategies in terms of travel schedules and destinations: one male stayed virtually all year round within 300 km of the colony and overwintered close to the North Sea mainland coast; two (one male, one female) birds migrated west and northwest to spend the winter in the UK and Ireland; five females travelled southwest for sites in western France and

western Iberia, with one of them paying a visit to northwest Morocco for 11 d (Fig. 1). In addition, one colour-ringed but untagged adult male from our breeding colony was re-sighted directly in Burry Inlet, Wales (51.39°N, 4.08°W) on 27 Jan 2008 (Barry Stewart pers. comm.).

During 2007–2008, the tracked birds that wintered outside the wider breeding area ($n = 7$) departed during 23 Oct to 16 Dec 2007 (mean 28 Nov) and returned to the breeding area during 12 Feb to 26 Mar 2008 (mean 27 Feb; Table 1). Accordingly, they had been away from the breeding area for 60 to 128 d (mean 91 d). Outward and homeward migration was mostly direct and fast; some birds covered distances

Table 1. Summary of spatiotemporal data retrieved from 13 GLS-tracked return migrations of 2 male (M) and 6 female (F) adult northern lapwings. Lay date refers to the first egg of the first clutch laid within a season, and pre-laying refers to the number of days passed between arrival in the wider breeding area (within 300 km of nest site) and start of laying. The number of days away and average distance while outside the breeding area refers to the complete period and related distances the bird was >300 km away from nesting site. Distance to and coordinates (decimal degrees) of the most distant wintering site (used for at least three consecutive days) are given in the last two columns (mean values).

Bird	Sex	Breeding area					Outside breeding area		
		Departure date	Arrival date	Days away	Days pre-laying	Lay date	Average distance (km)	Most distant site (km)	Most distant site (lat/lon)
WIBL	M	–	–	0	n/a	n/a	< 300	< 300	
WIGR	M	14-Dec-07	12-Feb-08	60	n/a	n/a	652	723	53.1N, 4.4W
WIWI	F	24-Nov-07	24-Feb-08	92	37	1-Apr-08	907	1299	42.8N, 2.2W
		6-Dec-08	3-Mar-09	87	28	31-Mar-09	1299	1865	37.5N, 2.8W
ORWI	F	16-Dec-07	24-Feb-08	70	32	27-Mar-08	1048	1410	41.8N, 2.5W
		16-Dec-08	26-Feb-09	72	37	4-Apr-09	695	1104	44.7N, 2.1W
		15-Dec-09	25-Feb-10	72	22	19-Mar-10	877	895	46.9N, 1.8W
GEBL	F	15-Dec-07	25-Feb-08	72	30	26-Mar-08	962	974	54.5N, 8.3W
		14-Dec-08	24-Feb-09	72	32	28-Mar-09	799	875	54.8N, 6.7W
		*4-Dec-09	2-Mar-10	88	27	29-Mar-10	899	1034	52.3N, 8.9W
GROR	F	23-Oct-07	28-Feb-08	128	45	13-Apr-08	1824	2104	36.9N, 8.0W
ZWGE	F	23-Nov-07	25-Feb-08	94	54	19-Apr-08	1565	1926	38.1N, 6.3W
WIOR	F	23-Nov-07	26-Mar-08	124	19	14-Apr-08	1402	2600	31.9N, 7.6W

*Due to frequent shading around dusk and/or dawn no fixes were available for 'GEBL' between 24 Nov and 3 Dec 2009; location estimates were at 459 km from colony on 4 Dec and this date was taken as departure date.

of approximately 2000 km within 2 to 4 d of travel (see birds GROR and ZWGE in Fig. 1). Further displacements occurred within the wintering area, especially by those birds going into France and Iberia, but apparently less so in birds wintering in Ireland or the UK. Such midwinter movements occurred over shorter distances as compared to outward and homeward migratory leaps, and there was no discernible common direction. Homeward migration appeared not markedly more synchronized than outward migration (Fig. 1).

Individual consistency

In contrast to the diverse overwintering strategies found among different individuals from the same breeding colony, individual lapwings tracked consecutively for several years showed considerably consistent overwintering strategies. They appeared largely faithful to their chosen wintering areas, as can be seen from the largely overlapping seasonal Kernel plots (Fig. 2). Moreover, migratory schedules were often (but not always) followed consistently too. Timing of both departure from and arrival to the breeding area occurred each within ± 1 d over 3 years of tracking in bird ORWI and over 2 consecutive years in bird GEBL (Fig. 2, Table 1).

Overwintering strategy and timing of breeding

Birds that overwintered at greater average distance from the colony commenced outward migration earlier and, additionally, tended to return to colony later. However, the association with arrival date was relatively weak and statistically non-significant and may have suffered from one extreme value among arrival dates (see methods). Looking at the combined effect of these events revealed that the period of time birds were absent from the breeding area increased with remoteness of wintering area (Supplementary material Appendix 1 Table A2, Fig. 3a). The 6 female lapwings tracked back to

their nesting site in 2008 started laying their first clutch during 26 Mar to 19 Apr (mean 6 Apr) after spending a pre-laying period of 19 to 54 d (mean 36 d) in the wider

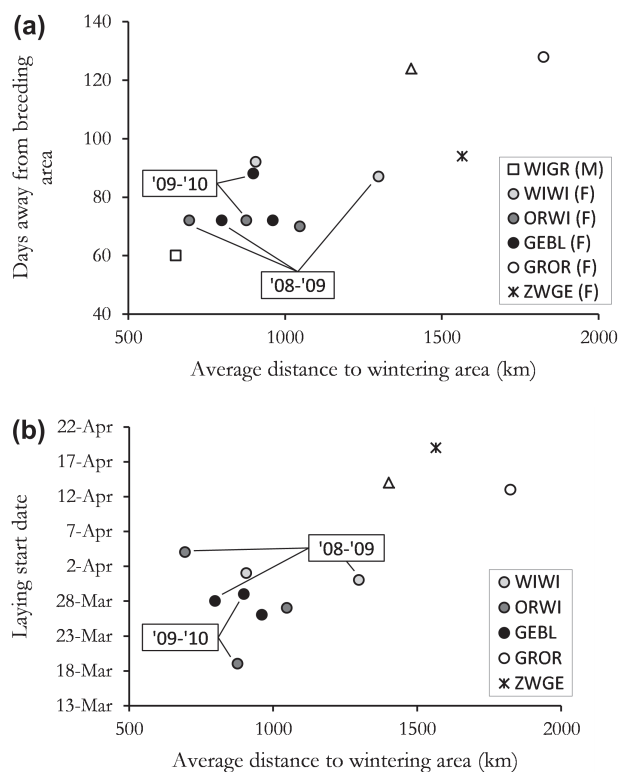


Figure 3. Distance to wintering areas of individually tracked lapwings in relation to time spent outside the breeding area (a) and in relation to start of laying the first clutch (b). Filled circles mark three females tracked repeatedly over more than one season with labels referring to data from 2008–2009 and 2009–2010 seasons; all other data are from 2007–2008 season. See Supplementary material Appendix 1 Table A2 for correlation coefficients and 95% CIs.

breeding area (Table 1). Start of egg laying appeared unrelated to arrival date ($r = 0.42$, 95% CI [-0.59, 0.92], $n = 6$). Length of pre-laying period was unrelated to overwintering distance (Supplementary material Appendix 1 Table A2). However, egg laying started earlier in females that overwintered closer to colony (Supplementary material Appendix 1 Table A2, Fig. 3b).

Discussion

A low level of migratory connectivity between breeding and wintering populations of lapwing within Europe has been revealed previously by large-scale ring-recovery analyses (Imboden 1974, Alerstam 1990, Leitão and Peris 2004). The present study confirms this pattern and shows that even at the level of a local breeding colony individuals may spread out over almost the entire wintering region known to be used by western and northwestern European breeding populations.

From such pattern of diffuse migratory connectivity and observations of 'rush migration' in response to cold winter spells (Imboden 1974, Shrubbs 2007) one may get the impression of the lapwing as an erratic migrant. However, as the present study also indicates, individual lapwings (at least those that returned to breeding colony) appeared relatively faithful to a chosen wintering area, and timing of outward and homeward migration can be highly consistent between years, despite considerable yearly variation in ambient temperature (Fig. 2, Supplementary material Appendix 1 Fig. A2). Furthermore, individuals heading (apparently faithfully) for more remote wintering sites (which they can reach quickly) left the breeding site earlier than their colony members aiming for wintering sites closer to colony. Altogether this suggests that migratory timing in lapwing is not merely driven by immediate external weather circumstances but, to some extent, under endogenous control.

Another, not mutually exclusive, explanation for the observed relationship between migratory timing and wintering distance (Fig. 3a) could be that individuals respond to external factors differently. When the first individuals left the breeding area mean daily temperature was still at 5°C or above; at departure of the last individuals several weeks later temperatures dropped to zero or below (Supplementary material Appendix 1 Fig. A2). Some individual intrinsic 'quality' related to, for instance, thermal tolerance, body size and competitive ability may allow some individuals to remain longer in and stay closer to the breeding area during winter (Gauthreaux 1982). Noteworthy in this context, the two males from this study wintered the closest and returned the earliest to breeding area. Lapwing males are, on average, slightly larger and heavier (during autumn and winter) than females (Cramp and Simmons 1983). However, lapwing males are also the territory establishing sex, and competition over territories may additionally select for early arrival of males.

Female lapwings may also be pressed for timely arrival because of intra-sexual competition for males holding high quality territories (Grønseth et al. 2014), which may explain the generally early arrival of females and, as consequence, long pre-laying period. Our study found females

that overwintered closer to colony managed to breed earlier. The mechanism behind this association remains elusive, because data at hand do not suggest a substantial link via arrival time, which could have explained this pattern. Other factors besides arrival time may determine start of breeding. Högstedt (1974) found a strong negative correlation between length of the pre-laying period in female lapwings and food availability (earthworms) in the territory, pointing at the reliance on local food resources for attaining the 'nutritional plane' required for clutch formation. Overwintering closer to colony may result in earlier breeding through two additive processes: first, it favours earlier arrival at the breeding site, and second, the lower energetic costs for the shorter migratory journey may leave a higher residue of body stores upon arrival thereby reducing the pre-laying period. The positive correlation coefficients found in this study (Supplementary material Appendix 1 Table A2) between overwintering distance and arrival time at breeding site and pre-laying period, respectively, are in line with these ideas, although no statistically quantitative conclusions can be derived at this stage. Whatever the mechanism, an earlier breeding date may rise reproductive prospects of birds overwintering closer to colony due to a general seasonal decline in reproductive output that has been observed in northern lapwing (Hegyí and Sasvári 1998, Bil and Schuurs 2001). It should be realised, however, that the observed correlation does not necessarily imply a direct and causal link between migration distance and timing of reproduction. The observed pattern may also emerge, for instance, if both timing of reproduction and migration distance are each strongly determined by individual quality.

A large variation in migration strategies is suggestive of ample genetic variation for migratory behaviour in populations of northern lapwing. This should be advantageous when coping with rapidly changing selective pressures including those that result from climate change (Webster et al. 2002, Parmesan 2006). An analysis of winter recovery distances of birds ringed during the breeding season (mostly as unfledged young, occasionally as breeding adult) in the Netherlands between 1932 and 2004 revealed a shortening of migration distance in Dutch lapwings, a trend that could be associated with increasing winter temperatures in the Netherlands (Visser et al. 2009). Also, since the middle of the 20th century an advancement in both first egg laying date and ringing date of nestlings (proxy for hatch date) have been observed in Dutch lapwings, which could be associated with increasing spring temperatures in the Netherlands (Both et al. 2005, Musters et al. 2010). Although in all these analyses year remained a significant variable in the statistical models beside temperature, indicating year-related effects not accounted for by (local) temperature, these studies suggest that lapwings have been responding to climate change by shifting their non-breeding distribution and advancing reproduction. The present study supports the idea of a direct link between migration distance and timing of reproduction, although more research is needed to elucidate the underlying mechanisms.

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References

- Alerstam, T. 1990. Bird migration. Cambridge Univ. Press.
- Bil, W. and Schuurs, J. 2001. Nadere analyse overlevingskansen kieviten pulli op intensief gebruikt grasland 1992–1997. – *Vogeljaar* 49: 61–64.
- Both, C., Piersma, T. and Roodbergen, S. P. 2005. Climatic change explains much of the 20th century advance in laying date of northern lapwing *Vanellus vanellus* in The Netherlands. – *Ardea* 93: 79–88.
- Catry, I., Dias, M. P., Catry, T., Afanasyev, V., Fox, J., Franco, A. M. A. and Sutherland, W. J. 2011. Individual variation in migratory movements and winter behaviour of Iberian lesser kestrels *Falco naumanni* revealed by geolocators. – *Ibis* 153: 154–164.
- Conklin, J. R., Battley, P. F. and Potter, M. A. 2013. Absolute consistency: individual versus population variation in annual-cycle schedules of a long-distance migrant bird. – *PLoS One* 8: e54535.
- Cramp, S. and Simmons, K. E. L. (eds) 1983. The birds of the Western Palearctic. Oxford Univ. Press.
- Eichhorn, G., Afanasyev, V., Drent, R. H. and Van Der Jeugd, H. P. 2006. Spring stopover routines in Russian barnacle geese *Branta leucopsis* tracked by resightings and geolocation. – *Ardea* 94: 667–678.
- Eichhorn, G., Drent, R. H., Stahl, J., Leito, A. and Alerstam, T. 2009. Skipping the Baltic: the emergence of a dichotomy of alternative spring migration strategies in Russian barnacle geese. – *J. Anim. Ecol.* 78: 63–72.
- Eichhorn, G., Bil, W. and Fox, J. W. 2017. Data from: Individuality in northern lapwing migration and its link to timing of breeding. – Dryad Digital Repository, <<http://dx.doi.org/10.5061/dryad.qf20f>>.
- Gauthreaux, S. A., Jr. 1982. The ecology and evolution of avian migration systems. In: Farner, D. S. and King, J. R. (eds), *Avian biology*. Vol. VI. Academic Press, pp. 93–168.
- Grønstøl, G., Lislevand, T. and Byrkjedal, I. 2014. Resident female northern lapwings *Vanellus vanellus* fight to exclude settlement by secondary females. – *Ibis* 156: 461–465.
- Hegyí, Z. and Sasvári, L. 1998. Components of fitness in lapwings *Vanellus vanellus* and black-tailed godwits *Limosa limosa* during the breeding season: Do female body mass and egg size matter? – *Ardea* 86: 43–50.
- Hill, R. D. 1994. Theory of geolocation by light levels. In: Le Boeuf, B. J. and Laws, R. M. (eds), *Elephant seals: population ecology, behaviour and physiology*. Univ. of California Press, pp. 227–236.
- Högstedt, G. 1974. Length of the pre-laying period in the lapwing *Vanellus vanellus* L. in relation to its food resources. – *Ornis Scand.* 5: 1–4.
- Imboden, C. 1974. Zug, Fremdansiedlung und Brutperiode des Kiebitz *Vanellus vanellus* in Europa. – *Orn. Beob.* 71: 5–134.
- Koopman, K. and Hulscher, J. 1976. Catching breeding waders on their nests. – *Wader Study Group Bull.* 19: 17–19.
- Leitão, D. and Peris, S. 2004. The origin of lapwings *Vanellus vanellus* and golden plovers *Pluvialis apricaria* wintering in Portugal. – *Ornis Fennica* 81: 49–64.
- Lisovski, S., Hewson, C. M., Klaassen, R. H. G., Korner-Nievergelt, F., Kristensen, M. W. and Hahn, S. 2012. Geolocation by light: accuracy and precision affected by environmental factors. – *Methods Ecol. Evol.* 3: 603–612.
- Marra, P. P., Hobson, K. A. and Holmes, R. T. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. – *Science* 282: 1884–1886.
- Musters, C. J. M., Ter Keurs, W. J. and De Snoo, G. R. 2010. Timing of the breeding season of black-tailed godwit *Limosa limosa* and northern lapwing *Vanellus vanellus* in The Netherlands. – *Ardea* 98: 195–202.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. – *Annu. Rev. Ecol. Evol. Syst.* 37: 637–669.
- Puth, M. T., Neuhäuser, M. and Ruxton, G. D. 2014. Effective use of Pearson’s product-moment correlation coefficient. – *Anim. Behav.* 93: 183–189.
- Shrubb, M. 2007. The lapwing. T. and A. D. Poyser.
- Visser, M. E., Perdeck, A. C., Van Balen, J. H. and Both, C. 2009. Climate change leads to decreasing bird migration distances. – *Global Change Biol.* 15: 1859–1865.
- Webster, M. S., Marra, P. P., Haig, S. M., Bensch, S. and Holmes, R. T. 2002. Links between worlds: unraveling migratory connectivity. – *Trends Ecol. Evol.* 17: 76–83.

Supplementary material (Appendix JAV-01374 at <www.avianbiology.org/appendix/jav-01374>). Appendix 1.