

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

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8

9 **Abstract**

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

27

28 Introduction

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

40 We employed GLS (Global Location Sensing, also called ‘light-level geolocation’ or just
41 ‘geolocation’) technique based on the analysis of diurnal changes in light levels to track annual
42 movements of northern lapwings (*Vanellus vanellus*; here synonymously termed ‘lapwing(s)’).
43 Archival tags (‘geolocators’) record light intensities to determine dusk and dawn times from which
44 geographical positions (two fixes daily) are calculated; day (night) length determines the latitude and
45 time of local midday (midnight) the longitude (Hill 1994).

46 Lapwings have been intensively ringed in many European countries for many years. Imboden
47 (1974) undertook an extensive analysis (nicely summarized in Alerstam 1990) of ring recoveries
48 collected during 1900 to 1969 from birds ringed as unfledged young and recovered within their first
49 year of life or later. Albeit relying mainly on dead recoveries of hunted individuals, this analysis
50 enabled the reconstruction of average seasonal movement patterns at population(s) level. It also
51 revealed a large overlap in non-breeding locations used by lapwings originating from widely
52 separated breeding colonies. Here, we present results from a first-time tracking study on this species
53 by charting the year-round whereabouts of adult lapwings from a Dutch breeding colony. Some

54 individuals were tracked for multiple years thereby providing first insights into individual consistency
55 of migratory timing and choice of non-breeding locations. Finally, we investigate if spatial variation
56 in non-breeding location relates to temporal variation of events at breeding area.

57

58 Methods

59 **Field work**

60 Lapwings were monitored in their breeding colony near the village Nij Beets in the Dutch province of
61 Friesland (53.03°N, 6.01°E). The core study area was formed by the nature reserve “De Dulf”
62 (135 ha) and adjacent farmland (13 ha, consisting of grassland and maize fields). Deployment of GLS
63 loggers and recapture attempts occurred during 2007-2010. An extended study area of approximately
64 15 km² was intensively searched for returning colour-ringed individuals (tagged or untagged) during
65 2008-2011. Each season, searching efforts commenced mid-February and lasted, with decreasing
66 intensity, into June. Active lapwing nests were found and revisited throughout March to June, and
67 individual females laid up to three full (and possibly more partial) clutches during repeated breeding
68 attempts within a season as a consequence of a high rate of nest and chick predation in our study area.

69 Lapwings were caught on their nest during incubation with a self-operating trap (Koopman
70 and Hulscher 1976) and were fitted with a metal ring below the tibiotarsal joint and a combination of
71 two colour rings above the tibiotarsal joint. The GLS logger (weight 1.5 g, model Mk14, British
72 Antarctic Survey) was attached to an additional plastic ring fitted above the tibiotarsal joint. Total
73 attachment mass was 1.9 g, equating to 0.86% of average body mass of lapwings caught during
74 incubation (222 g, n=86, own data). Logger deployment this way allowed easy and quick attachment
75 minimising handling time of incubating birds. Moreover, following earlier approaches of GLS studies
76 with leg-mounted tags in other open-ground nesting species (Eichhorn et al. 2006, Eichhorn et al.
77 2009) the diurnal shading pattern permitted the detection of the start of incubation in females in the
78 year(s) after logger deployment. From this we could estimate the date of laying the first egg by
79 assuming that incubation commences at full clutch and an average laying duration of 5 days (Cramp
80 and Simmons 1983). For (incomplete) clutches found during laying we back-calculated to first-egg

81 stage by assuming 1.5 days egg-laying interval. Due to their smaller share in bi-parental incubation
82 (Cramp and Simmons 1983) male incubation pattern was not reliably discernible from light data. All
83 birds returned to incubating their nest after capture. Loggers were attached to 22 females and 4 males
84 in 2007 and (re-)attached to 3 females in 2008. Loggers were retrieved from 5 females and 1 male in
85 2008, from 2 females and 1 male in 2009, from 2 females in 2010, and from 1 male in 2011. Loggers
86 failed downloading data either completely (1 male in 2011) or partly in two instances. Overall, we
87 were able to track the full year-round movements of 8 different individuals (6 females, 2 males); of
88 those, 2 females were tracked over 3 consecutive years and a further female over 2 consecutive years,
89 yielding a total of 13 return migration journeys.

90 In the end of breeding season 2007 we observed 52 individually marked lapwings in the study
91 area (mainly marked in that season plus few previously marked individuals), of which 27 carried a
92 GLS logger and 25 individually coded rings only. In 2008 (the year with most data) we resighted 13
93 (48%) tagged birds (for 12 of them we could confirm breeding) and 12 (48%) birds fitted with rings
94 only (for 8 of them we could confirm breeding) in our study area. Average start of egg-laying (into
95 first clutches) in 2008 was 6 April (± 9 days SD, $n=9$) for tagged birds and 5 April (± 7 days, $n=17$) for
96 untagged birds (ringed or un-ringed). Mean clutch size (maximum number of eggs observed in any of
97 the nests produced by individual couples throughout 2008) was 3.8 (± 0.4 SD, $n=9$) and 3.9 (± 0.3 ,
98 $n=19$) in nests of, respectively, tagged and untagged birds. Eggs were not measured but appeared of
99 normal size. Based on these observations carrying a logger or not caused no apparent difference in
100 return rate, lay date and clutch size. Body mass of tracked lapwings remained generally at similar
101 levels in subsequent breeding season(s) as compared to mass at tagging (see Supplementary material
102 Appendix 1, Table A1). Noteworthy, however, in 2008 we observed 4 tagged lapwings limping. All
103 of these limping birds belonged to a subsample of 13 birds that had received an adjusted type of leg
104 ring carrying the logger: a plastic ring was lined with a thin layer of soft cellular rubber (Zotefoams
105 Plc) on the inside with the aim to reduce ring rotation and pressure on the leg. Recapture of two
106 limping birds revealed the problem: dead skin cells sloughing off the bird's leg accumulated in the
107 space between leg and ring causing swelling and inflammation. Therefore, we stopped using this
108 adjusted type of leg ring. Limping was not observed in birds where the logger was attached to a

109 simple plastic leg ring that was not extra lined with soft material. The experimental protocol was
110 approved by the animal experimentation committee of the University of Groningen, license DEC
111 4728A.

112 **Data analysis**

113 Light data were analysed using MultiTrace Software (Jensen Software Systems). Sun elevation angles
114 and corresponding thresholds for dusk and dawn events were estimated from calibration periods for
115 each bird–logger combination individually, when birds carrying a logger were observed at known
116 location (i.e. in the breeding area). Used Sun elevation angles ranged from -3.7° to -4.7° . The loggers
117 measured light intensity every 1 min, but recorded only the maximum value of 10 successive readings
118 (i.e. within each 10 min interval) together with the corresponding time at the *end* of that 10 min
119 interval. This can lead to a potential mismatch of time and light value by up to 9 min during the dusk
120 period, because then the maximum light value is more likely to be measured at the *beginning* of a 10
121 min interval. MultiTrace had been adjusted by the developer to shift the dusk times accordingly. The
122 raw light data together with determined dusk and dawn events were inspected manually to identify
123 and annotate sections of obvious light level interference (e.g. caused by shading of logger when bird
124 sat down or tucked the tagged leg into the plumage, or artificial light at night) with subsequent
125 removal of corresponding position estimates. An inherent limitation of GLS is that around equinoxes
126 only longitude can be measured, because similar day and night length prevents reliable estimates of
127 latitude. This limitation posed almost no problem in the current study since most non-breeding
128 movements occurred well between autumn and spring equinoxes, except in one case for the last leg of
129 spring migration (Fig. 1). In this case positions were reconstructed from measured longitude fixes
130 with the assumption that the corresponding latitude crosses the shortest line connecting previous and
131 subsequent higher confidence locations. Longitude and latitude estimates from which we inferred
132 migration and wintering patterns are plotted in Supplementary material Appendix 1, Fig. A1.

133 Position estimates were used to calculate distance to the breeding site as the average of ortho-
134 and loxodromes. We used averages, because we have no prior assumptions about lapwings' ability to
135 potentially perform the one or other route navigation. Mean accuracy of GLS technique normally

136 ranges between approximately 100 and 300 km (Catry et al. 2011, Lisovski et al. 2012 and references
137 therein). We treated locations within a radius of 300 km around the nesting site as being part of the
138 wider breeding (home) area. Movements away from and back to breeding site are illustrated only
139 when position estimates indicated that the bird left this home area for more than three consecutive
140 days. Individual movement trajectories are illustrated in step-line charts as change in distance to
141 breeding colony over time (Figs. 1 and 2). Each distance level (step) represents the mean of all single
142 distances to breeding colony calculated over the given time period. A new subsequent step was
143 introduced when single distances over at least three consecutive days were all off by more than
144 200 km relative to the preceding period's (cumulative) mean distance to colony. We calculated 75%
145 Kernel densities using the Animal Movement Extension 2.0 in ArcView GIS 3.2 (ESRI), selecting
146 least squares cross validation (LSCV) and ad hoc calculation of a smoothing parameter, to outline
147 individual overwintering areas (Figs. 1 and 2). Kernel densities were based on all available
148 locations >300 km away from nesting site, except for bird "WIBL" that spent mid-winter within a
149 radius of 300 km around the breeding colony; in this case winter kernel density was based on
150 locations measured from 10 December 2007 to 10 February 2008. All maps are projected as Lambert
151 equal-area azimuthal centred on the breeding site location. Temperature data were obtained from the
152 Royal Netherlands Meteorological Institute for the weather station at Leeuwarden (53.2N, 5.8E) 24
153 km away from the breeding colony.

154 We calculated Pearson's product-moment correlation coefficients (r) and their 95%
155 confidence intervals (-95%CI, +95%CI) to describe the strength of association between (average)
156 distance to the wintering area and timing of events in the breeding area. Inspection of scatterplots and
157 distributions suggested linear monotonic relationships, no obvious deviation from normality and no
158 outliers, except for arrival date due to the late arrival of one bird (WIOR) in 2008. However, when
159 compared to alternative correlation measures, Pearson's r and associated standard t test is expected to
160 perform reasonably well with regard to both type I error and power even when the underlying
161 distribution departs substantially from bivariate normality as one of the assumptions (Puth et al.
162 2014). For the construction of CIs we used Fisher's z transformation as described in Puth et al.
163 (2014). We performed correlation analysis on sets of data including a) 1 male plus 6 females tracked

164 2007-2008 (n=7), b) 6 females only tracked 2007-2008 (n=6), c) 6 females tracked 2007-2010 (n=11).
165 The latter makes use of a larger data set but violates assumption of independent data points. We argue
166 that, given all data at hand, the best estimate is most likely found somewhere in between such a
167 conservative approach (b) and overconfident approach (c). Unfortunately, sample size did not allow
168 for a mixed effect modelling approach.

169

170 Results

171 **Individually diverse overwintering strategies**

172 Lapwings tracked during the same season (2007-2008) showed pronounced variation in migration and
173 overwintering strategies in terms of travel schedules and destinations: one male stayed virtually all
174 year round within 300 km of the colony and overwintered close to the North Sea mainland coast; two
175 (one male, one female) birds migrated west and northwest to spend the winter in the UK and Ireland;
176 five females travelled southwest for sites in western France and western Iberia, with one of them
177 paying a visit to northwest Morocco for 11 days (Fig. 1). In addition, one colour-ringed but untagged
178 adult male from our breeding colony was re-sighted directly in Burry Inlet, Wales (51.39°N, 4.08°W)
179 on 27 January 2008 (Barry Stewart pers. comm.).

180 During 2007-2008, the tracked birds that wintered outside the wider breeding area (n=7)
181 departed during 23 October to 16 December 2007 (mean 28 November) and returned to the breeding
182 area during 12 February to 26 March 2008 (mean 27 February; Table 1). Accordingly, they had been
183 away from the breeding area for 60 to 128 days (mean 91 days). Outward and homeward migration
184 was mostly direct and fast; some birds covered distances of approximately 2000 km within 2 to 4 days
185 of travel (see birds GROR and ZWGE in Fig. 1). Further displacements occurred within the wintering
186 area, especially by those birds going into France and Iberia, but apparently less so in birds wintering
187 in Ireland or the UK. Such midwinter movements occurred over shorter distances as compared to
188 outward and homeward migratory leaps, and there was no discernible common direction. Homeward
189 migration appeared not markedly more synchronized than outward migration (Fig. 1).

190 **Individual consistency**

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

198 **Overwintering strategy and timing of breeding**

199 Birds that overwintered at greater average distance from the colony commenced outward migration
200 earlier and, additionally, tended to return to colony later. However, the association with arrival date
201 was relatively weak and statistically non-significant and may have suffered from one extreme value
202 among arrival dates (see methods). Looking at the combined effect of these events revealed that the
203 period of time birds were absent from the breeding area increased with remoteness of wintering area
204 (Supplementary material Appendix 1, Table A2, Fig. 3a). The 6 female lapwings tracked back to their
205 nesting site in 2008 started laying their first clutch during 26 March to 19 April (mean 6 April) after
206 spending a pre-laying period of 19 to 54 days (mean 36 days) in the wider breeding area (Table 1).
207 Start of egg laying appeared unrelated to arrival date ($r=0.42$, 95% CI [-0.59, 0.92], $n=6$). Length of
208 pre-laying period was unrelated to overwintering distance (Table A2). However, egg laying started
209 earlier in females that overwintered closer to colony (Table A2, Fig. 3b).

210

211 Discussion

212 A low level of migratory connectivity between breeding and wintering populations of lapwing within
213 Europe has been revealed previously by large-scale ring-recovery analyses (Imboden 1974, Alerstam
214 1990, Leitão and Peris 2004). The present study confirms this pattern and shows that even at the level
215 of a local breeding colony individuals may spread out over almost the entire wintering region known
216 to be used by West and Northwest European breeding populations.

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

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

239 Female lapwings may also be pressed for timely arrival because of intra-sexual competition
240 for males holding high quality territories (Grønstøl et al. 2014), which may explain the generally early
241 arrival of females and, as consequence, long pre-laying period. Our study found females that
242 overwintered closer to colony managed to breed earlier. The mechanism behind this association
243 remains elusive, because data at hand do not suggest a substantial link via arrival time, which could
244 have explained this pattern. Other factors besides arrival time may determine start of breeding.

245 Högstedt (1974) found a strong negative correlation between length of the pre-laying period in female
246 lapwings and food availability (earthworms) in the territory, pointing at the reliance on local food
247 resources for attaining the ‘nutritional plane’ required for clutch formation. Overwintering closer to
248 colony may result in earlier breeding through two additive processes: first, it favours earlier arrival at
249 the breeding site, and second, the lower energetic costs for the shorter migratory journey may leave a
250 higher residue of body stores upon arrival thereby reducing the pre-laying period. The positive
251 correlation coefficients found in this study (Table A2) between overwintering distance and arrival
252 time at breeding site and pre-laying period, respectively, are in line with these ideas, although no
253 statistically quantitative conclusions can be derived at this stage. Whatever the mechanism, an earlier
254 breeding date may rise reproductive prospects of birds overwintering closer to colony due to a general
255 seasonal decline in reproductive output that has been observed in northern lapwing (Hegyí and
256 Sasvári 1998, Bil and Schuurs 2001). It should be realised, however, that the observed correlation
257 does not necessarily imply a direct and causal link between migration distance and timing of
258 reproduction. The observed pattern may also emerge, for instance, if both timing of reproduction and
259 migration distance are each strongly determined by individual quality.

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

273 distribution and advancing reproduction. The present study supports the idea of a direct link between
274 migration distance and timing of reproduction, although more research is needed to elucidate the
275 underlying mechanisms.

276

277

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285

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342

343

344 Supplementary material (Appendix JXXXXXX at <www.oikosoffice.lu.se/appendix>). Appendix 1.

345

346 Table 1. Summary of spatiotemporal data retrieved from 13 GLS-tracked return migrations of 2 male
 347 (M) and 6 female (F) adult northern lapwings. Lay date refers to the first egg of the first clutch laid
 348 within a season, and pre-laying refers to the number of days passed between arrival in the wider
 349 breeding area (within 300 km of nest site) and start of laying. The number of days away and average
 350 distance while outside the breeding area refers to the complete period and related distances the bird
 351 was >300 km away from nesting site. Distance to and coordinates (decimal degrees) of the most
 352 distant wintering site (used for at least three consecutive days) are given in the last two columns
 353 (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

354 * Due to frequent shading around dusk and/or dawn no fixes were available for “GEBL” between 24
 355 November and 3 December 2009; location estimates were at 459 km from colony on 4 December and
 356 this date was taken as departure date.

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Figure Legends:

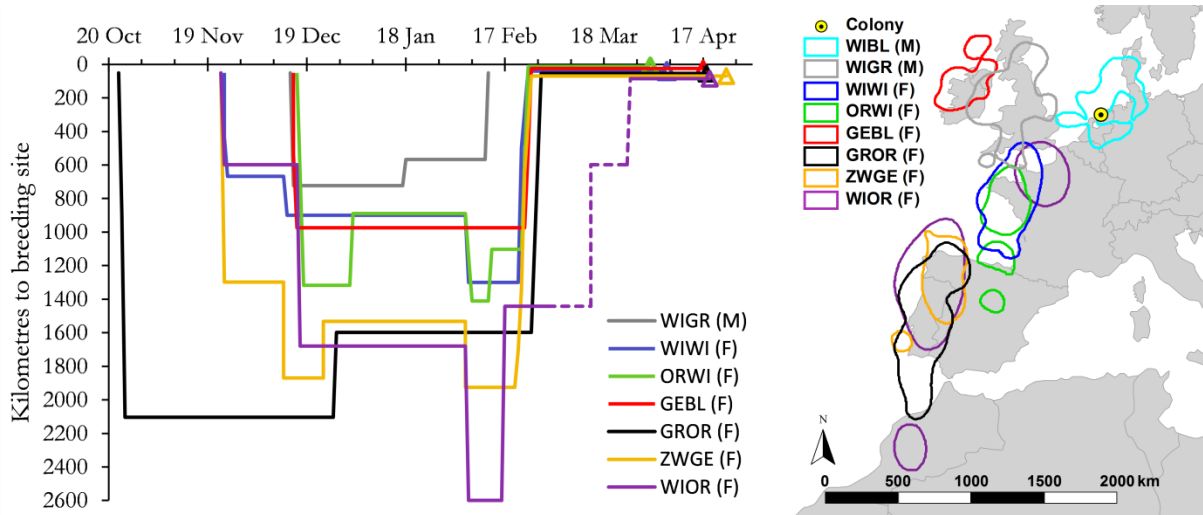
Figure 1. Progress of displacement from and to the breeding site (left panel) of adult northern lapwings tracked from 2007 to 2008 together with their overwintering areas indicated by 75% Kernel contour lines (right panel). Kernel densities were based on all available locations >300 km away from breeding 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 December 2007 to 10 February 2008. For female (F) birds the start of incubating 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.

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 incubating the first clutch for each female and year. For bird “GEBL” no reliable fixes were available between 24 November and 3 December 2009, indicated by a dashed line.

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 Table 2 for correlation coefficients and 95% CIs.

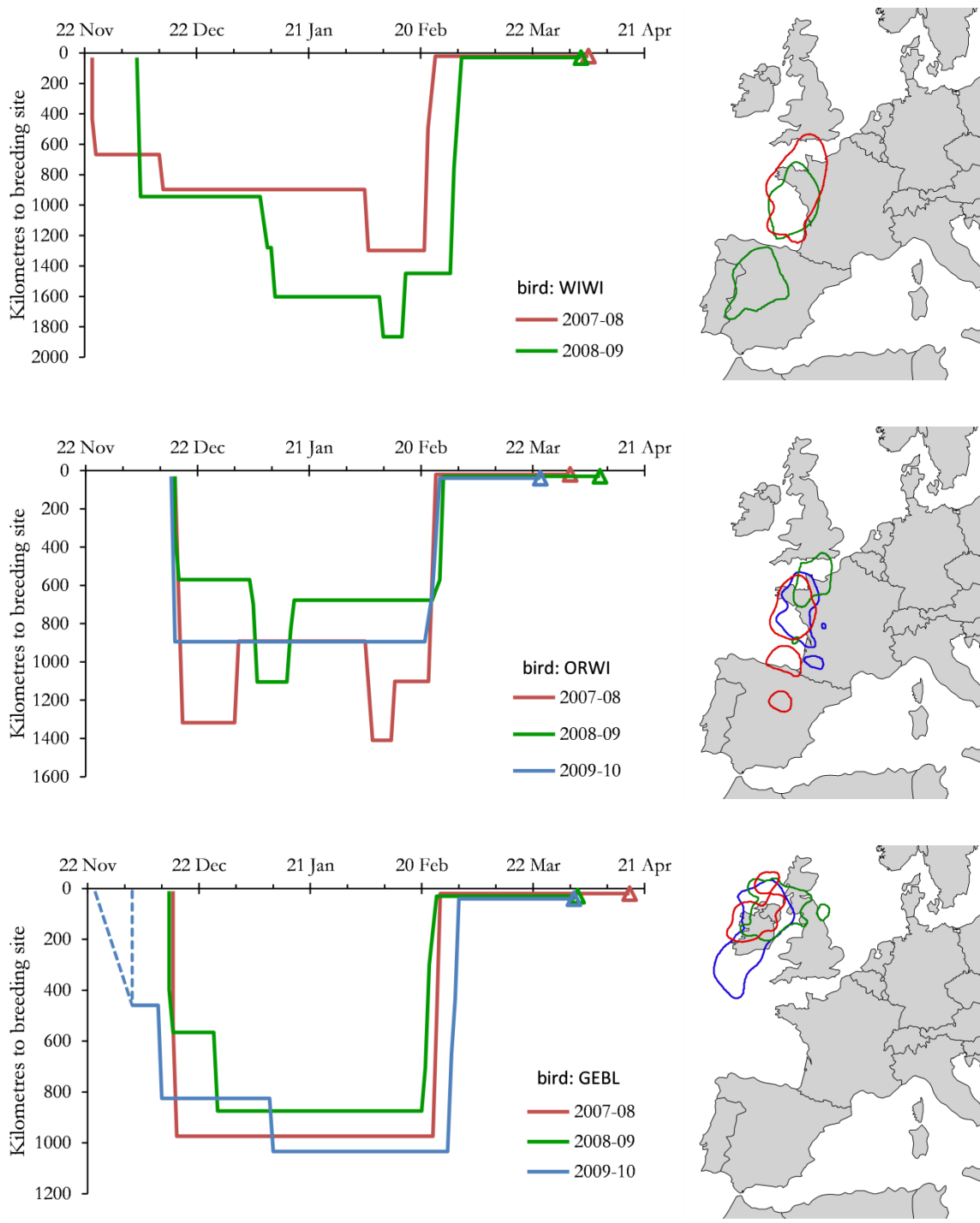
384 **Figures (with panels placed in preferable/final position)**

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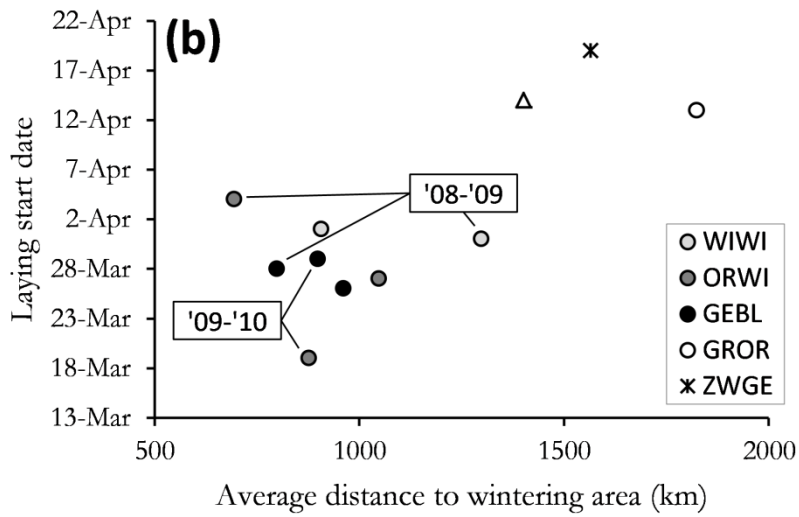
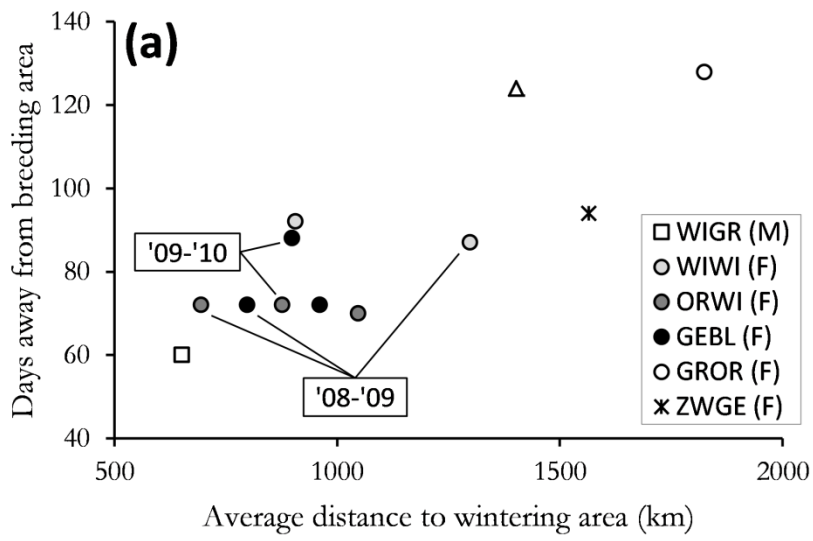


386 Figure 1.

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389 Figure 2.



392 Figure 3.

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