First records of complete annual cycles in water rails *Rallus aquaticus* show evidence of itinerant breeding and a complex migration system

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Abstract

In water rails *Rallus aquaticus*, northern and eastern populations are migratory while southern and western populations are sedentary. Few details are known about the annual cycle of this elusive species. We studied movements and breeding in water rails from southernmost Norway where the species occurs year-round. Colour-ringed wintering birds occurred only occasionally at the study site in summer, and vice versa. Geolocator tracks revealed that wintering birds (n = 10) migrated eastwards in spring to breed on both sides of the Baltic Sea, whereas a single breeding bird from the study site wintered in N Italy. Ambient light records of geolocator birds further indicated that all but one incubated 2–4 clutches per season. By combining information on incubation and movement, we found evidence for itinerant breeding in three individual birds: After a first breeding attempt (one did not incubate), all moved 129–721 km to breed again. This behaviour is rarely recorded in birds and was unexpected because the water rail is described as monogamous with both parents caring for eggs and chicks. The study greatly improves our knowledge about the annual cycle and reproduction in water rails. However, more studies are warranted to evaluate the generality of our findings and causes of breeding itinerancy.

Introduction

Birds are known to show both intra-population differences in migratory propensity (partial migration; Lundberg 1988, Chapman et al. 2011) and inter-population differences which produce leap-frogging, parallel, crosswise or chain migration patterns (Rappole 2013, Chapman et al. 2014). While seasonal migration is common, movements within seasons are rarely documented. Such itinerancy (Moreau 1972) is often explained by seasonally and spatially fluctuating food availability (Thorup et al. 2017, Koleček et al. 2018). During breeding it might also result from mate searching in polygamous birds (Rohwer et al. 2009, Kempenaers & Valcu 2017). Evidence for breeding itinerancy exist in both tropical and temperate birds that move over long (>10 km) distances (Newton 2008, Rohwer et al. 2009, Baldassarre et al. 2019, Cooper & Marra, in press).

The water rail *Rallus aquaticus* is widespread and common in the Palearctic region (Taylor & Christie 2018). Yet, due to the species' secretive behaviour which hamper field studies, many aspects of water rail ecology are poorly known. For instance, even though migration distance of water rails increases towards north and east in Europe (Flegg & Glue 1973, De Kroon 1984, Lugg et al. 2018), the main wintering areas are unknown in most populations and annual schedules are only fragmentarily described. Since the species is regarded as being territorial, monogamous, and bi-parental (Taylor & Christie 2018), we would predict it to show long residency during the breeding season. However, as breeding itinerancy is difficult to observe, and possibly occur in some other rallids (Seifert et al. 2016), it might have been previously overlooked in water rails.

South Norway constitutes the north-western limit of the water rail's breeding distribution (<170 pairs; Shimmings & Øien 2015, Taylor & Christie 2018). The species is also found in

winter along the South-Norwegian coast, although numbers fluctuate with weather conditions (Lislevand & Kjøstvedt 2005). There is no information about migratory habits of water rails from Norway, as only four ring recoveries exist so far (all foreign birds; Stavanger Museum 2020). Some authors have speculated that Norwegian water rails are resident (Bakken et al. 2003) or that the winter population, at least partly, consists of migrants that breed further east (Mork 1994). In any case, this would differ from other Scandinavian water rail populations which migrate towards SW (Fransson et al. 2008, Saurola et al. 2013).

We studied the seasonal occurrence and migration patterns of water rails in southernmost Norway by using observations of individually marked birds and geolocator tracking. From this, we describe detailed and complete annual schedules in this species for the first time. Specifically, we tested the hypotheses that 1) migrants from eastern breeding populations are wintering in Norway, and 2) Norwegian breeding birds are sedentary. Finally, by combining migration tracks and data on incubation behaviour derived from geolocators, we tested if water rails are stationary during breeding, as predicted from current knowledge of their reproductive ecology.

Methods

General field methods

Field work took place at Øreslandskilen near Lillesand, S Norway (58°10' N, 8°14' E), a small wetland (~2 ha) largely covered by reed (*Phragmites australis*). Colour ringing and re-sightings of marked birds were done between 2004 and 2020 (Table 1). We trapped birds by using cage traps baited with oatmeal. To ease the monitoring of birds we cut the reed in five stretches measuring 50–80 cm x 30–50 m. These open areas were distributed in different parts of the reedbed. About 3–4 times per week we here put out oatmeal for the rails (approx. 1 kg

each time) from late September to April. Food was also provided in summer but at a less regular basis. Birds were ringed with a metal ring and a colour ring on one leg, and three colour rings on the other. Sex and age were determined as described by Demongin (2016). Of 262 ringed birds, 226 (excluding three local juveniles) were trapped between 1st September and 31 March, wherein > 70% (n = 162) were captured in November and December (median = 26 November, inter-quartile range = 7 November–17 December; n = 226). The proportions of males and females were similar in the non-breeding period (males, n = 93; females, n = 110). Moreover, 78% (144/185) of birds with known age during winter were ringed as 1y/2y, whereas all but two birds from summer months were local juveniles.

Between October and May each year one observer (SR) checked the area for colour ringed water rails for 1–3 hours c. 3–4 times a week. If birds were present in summer (e.g. as indicated by tracks on the ground) we made 1–2 checks per week lasting c. 30–60 min each. To calculate return rates between winters, we only included birds still present in March of the first year to avoid counting birds that died or only visited the area briefly (Table 1).

Geolocators

Geolocators (Intigeo-C65; Migrate Technology Ltd, UK) were attached to a darvic ring which replaced one of the colour rings. The device weighed about 1.3 g, or approx. 1% of the body mass (males: 158.0 ± 16.2 g, n = 9; females: 135.7 ± 16.1 g, n = 14). We deployed geolocators in January–March 2014 (n = 6) and 2015 (n = 17). In addition, single birds were tagged in September 2015 (a local breeding male) and in April 2016. In the following year, we successfully retrieved geolocators from the September bird and 10 of 23 winter birds (7 females, 3 males). The return rate in winter (43%) is comparable with that of rails which were only colour ringed (Table 1). Two males were aged 3y+, all others were 2y. Except for two on

tibia, all loggers were mounted on the tarsus. In one case the logger apparently caused slight skin abrasion on the leg, but without affecting locomotion. Returning wintering birds did not differ from others in body mass (returning: 138.9 g ± 12.5, n = 10; non-returning: 152.1 g ± 20.4, n = 14; t = 0.81, df = 22, p = 0.08), nor did return rates differ between sexes (n females/males returned: 7/3; not returned: 6/7; Fischer's exact test: p = 0.40).

Data and analyses

Analyses of movements and annual schedules were performed in R (R Core Team 2018). Means are reported ± SD and tests are two-tailed (alpha = 0.05). We used the R-package 'TwGeos' to define sunrise and sunset times from geolocator data and distinguished between movement and stationary periods using the 'invChanges' function from the R package 'GeoLight', version 2.0.1 (Lisovski and Hahn 2012). We then modelled individual migration tracks using the R-package SGAT (Lisovski et al. 2020). To this end, we used the 'group threshold model' and allowed birds to move in any direction, but stationary sites could not be located in the sea. The behavioural model was assumed to follow a gamma distribution (shape = 2.2, scale = 0.08). The twilight model was calibrated by 'in-habitat calibration', using light data recorded while the bird was at the breeding site (Lisovski et al. 2012). The resulting median solar zenith angles ranged between 93.3 and 94.6 for individual birds (mean = 94.2, n = 11). For the initial path, we extrapolated latitudinal positions during the equinox periods by setting the tolerance of solar declination of up to 9°. We initiated the model by drawing 1000 initial samples and then tuned the model a total of five times. When reporting speed we define 'travel' as movement between stationary periods, whereas 'migration' also includes stationary periods. For individual migration data and estimated location coordinates (medians with 95% CI), please see the electronic suppl. material, Appendix S1.

In water rails, both sexes incubate clutches of 6–11 eggs for 19–22 days, and care for the precocial and nidifugous young for 20–30 days (Taylor & Christie 2018). We used light intensity recordings to infer incubation behavior as light levels rapidly shift between darkness and high light intensities when the bird alternates between incubation/brooding (shading the logger) and foraging periods off the nest. We adopted the approach from Gosbell et al. (2012) to derive incubation episodes. First, we quantified darkness as light intensity that did not exceed 5% of maximum light intensity ever recorded by the logger in question. Second, incubation was inferred if there was darkness on the light sensor for > 5% of daylight periods. If such a pattern occurred for several consecutive days, it was interpreted as a breeding attempt. Incubation periods lasting for 21 days or more (Cramp & Simmons 1980) were taken to indicate successful breeding. The migration data set is available upon request from the MoveBank data repository (project id to be entered here).

Results

We confirmed breeding at the study site in 6 of 16 years, but only a single pair each year. The number of wintering birds present at the site varied between 0 and 34 per year (mean = 18.8 ± 10.2, n = 16). Overall, 57% (163/282) were still present in March, and 57% of these (76/134) returned in the following winter (Table 1). Wintering birds were only rarely observed during the breeding season, and vice versa: 1) a wintering male which remained to breed in the study area, 2) a wintering female that after a long period of absence suddenly re-appeared on 23 July (stayed for 3 days), and 3) two young from a local nest that stayed until their first spring. In addition, a male breeding five seasons in a row wintered in the area in the last year.

Geolocator tracks (Figure 1, Table 2, Appendix S1) showed that wintering birds invariably moved eastwards in spring (mean distance = 1153 ± 733 km, n = 10) to breed in S Sweden (n

144 = 4; Figure 1a, c) or in E Baltic (n = 6, Figure 1b, c). Spring migration started 13 March–19
145 April (median = 29 March, n = 10). Birds either moved continuously (n = 6) or stopped 1–3
146 times for 3–19 days (n = 4) and arrived at breeding sites between 15 March and 21 May
147 (median = 14 April, n = 10, Table 2). We recorded at least one full incubation period in all but
148 one of the geolocator birds, starting between 11 April and 2 June (median = 10 May, n = 9;
149 Figure 2). Birds incubated for two (n = 4), three (n = 4) or four (n = 1) periods (Figure 2) and
150 most (7/9) finished egg care by August (median = 14 July; Figure 2). Autumn migration
151 commenced between 8 August and 2 November (median = 9 October, n = 10), and birds
152 either returned directly to Norway (n = 4) or stopped over once (n = 5) or twice (n = 1) for 5–
153 65 days (median = 20 days, n = 7). They arrived 17 September–17 November (median = 24
154 October, n = 10). Birds that stopped over during migration sometimes took considerable
155 detours from a more direct route to/from the breeding area (Figure 1b, c). In contrast to
156 wintering birds, the local breeder from the study area (a 2y male) flew southwards in autumn
157 to winter in N Italy (Figure 1d). It left the breeding area 4 October, stopped over once (15
158 days) and reached the wintering area 2 November. Northbound migration commenced 129
159 days later (10 March) and after a single stop (15 days) it returned to the breeding site 28
160 March.
161
162 We found evidence for breeding itinerancy in three water rails (Figure 1c, Figure 2). First, a
163 2y female which did not seem to incubate at all (D-2014) first settled in W Russia on 19
164 April. On 11 June she moved westwards to Estonia (386 km from previous site) and remained
165 there until autumn. Second, a male (E-2014) first settled at the border between Russia and SE
166 Finland where he incubated for 24 days. He left this area on 3 June and moved 129 km
167 southwards where light patterns showed two brief incubation periods of 4 and 7 days. Finally,
168 a female (H-2015) initially settled in S Sweden (31 March) and incubated for 23 days.

169 Thereafter she travelled 721 km further east to the border between SW Russia and N Belarus
170 (arrived 11 June) where she incubated another clutch for 6 days.
171

172 ## Discussion

173 All 11 geolocator tracks clearly showed that the water rails were seasonal migrants, and this
174 conclusion was largely supported by site occupancy of ringed birds. Water rails wintering in
175 Norway indisputably breed in the Baltic region, as hypothesized by Mork (1994). In contrast,
176 a single Norwegian breeding bird spent the winter in N Italy. These results deviate from ring
177 recoveries of European water rails which primarily show migration along a SW-NE axis
178 (Fransson et al. 2008, Saurola et al. 2013, Lugg et al. 2018). However, since sample sizes are
179 small, especially for locally-breeding individuals, it is uncertain how well the geolocator
180 results reflect the general migratory habits of Norwegian water rails. In fact, our observations
181 of colour ringed birds showed that parts of the breeding population are also sedentary. It is
182 possible that the proportion of non-migratory birds is higher than we recorded, since any
183 individuals wintering on neighbour localities would have gone undetected.
184

185 Contrary to our prediction, we found evidence for breeding itinerancy in three of ten water
186 rails. Due to the restricted sample size one may not easily generalize about how common this
187 behaviour is, but the species is known to often raise several broods per season (Cramp &
188 Simmons 1980) which is a prerequisite for breeding itinerancy. The factors influencing
189 movement decisions within the breeding season are entirely unknown, but itinerancy might be
190 driven by fluctuating habitat suitability (Newton 2008). The advancement of spring along a
191 latitudinal gradient could cause such fluctuations but is unlikely in our case since all tracked
192 birds nested at similar latitudes. However, the wetland habitats where rails are breeding might

193 dry up over the season, perhaps sometimes making it adaptive to pursue better breeding
194 conditions elsewhere (Seifert et al. 2016).
195
196 Incubation periods of first clutches in itinerant water rails were apparently complete (24 and
197 23 days; Figure 2), so movements were not likely triggered by nest failures. Yet, itinerant
198 birds left their broods before the young were independent, i.e. 20–30 days after hatching
199 (Figure 2; Taylor & Christie 2018). Although brood losses could not be entirely excluded,
200 itinerant breeding in this species might perhaps also be explained by brood desertion and
201 polygamy. Detailed studies of breeding behaviour in water rails would be useful to see if key
202 aspects of the species' breeding system, e.g. the duration of pair bonds and parental care, are
203 more flexible than indicated in the general literature (Cramp & Simmons 1980, Taylor &
204 Christie 2018). This may, indeed, be the case as between-individual variation in nest
205 attentiveness was recently shown to affect home range sizes in water rails (Jedlikowski &
206 Brambilla 2017).
207
208 We conclude that Norwegian water rails exhibit a rather complex migration system, including
209 itinerant breeding. Although our results considerably improve the knowledge about the water
210 rail's basic ecology, they also call for further investigation of both migration and breeding
211 behaviour in this elusive bird. Breeding itinerancy might blur population limits, perhaps
212 contributing to the low degree of genetic structuring among European water rail populations
213 (Tavares et al. 2010, Stermin et al. 2014). As their numbers are currently declining globally
214 (BirdLife International 2020), improved information about migration in water rails might
215 have important implications for the species' future conservation.
216

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Conflicts of interests – The authors declare that they have no conflicts of interests.

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348 **Figure legends.**

349

350 **Figure 1.** Migration tracks of water rails from the study site in Norway: (a) birds breeding in
351 Sweden (n = 3), (b) birds breeding in the Eastern Baltic (n = 4), (c) itinerant birds (n = 3; sites
352 are numbered consecutively), and (d) a local breeding bird (n = 1). Stationary sites are shown
353 as medians with their 95% CI.

354

355 **Figure 2.** Incubation in 10 water rails reflected by light traces of geolocators. Curves show
356 the percentage of darkness during daytime recordings (horizontal grey dotted lines designate
357 50%). Patterns outside the breeding sites are shown by black dashed lines, blue lines show
358 patterns at breeding sites. Light traces at second sites are shown in red for breeding itinerant
359 birds. Incubation periods are indicated by a rise in the percentage of darkness/day. Estimated
360 incubation periods are indicated above each curve with triangles showing the date incubation
361 started. The last recorded dates of incubation for incomplete incubation periods (< 21 days of
362 incubation) are indicated by a short vertical line, and circles show estimated hatching dates.

363

364 **Table 1.** The number of colour-ringed water rails present at the study site each winter in the
365 years 2004–2020. Only birds identified by colour rings are included and separate numbers are
366 given during winter months (Dec–Feb) and March. Total return rates exclude bird numbers
367 present in the previous winter for years when return rates are unknown.

Winter	n total	n March	n returning	% Returning
2004–2005	10	10	6	60
2005–2006	20	4	NA	NA
2006–2007	NA	0	0	0
2007–2008	5	5	5	100
2008–2009	22	18	8	44
2009–2010	33	0	0	0
2010–2011	9	0	0	0
2011–2012	0	0	0	0
2012–2013	17	0	0	0
2013–2014	6	6	5	83
2014–2015	24	20	8	40
2015–2016	32	26	17	65
2016–2017	25	16	8	50
2017–2018	34	16	12	75
2018–2019	18	17	7	41
2019–2020	27	25	NA	NA
Total	282	163	76	57

368

Table 2. Migration in water rails wintering along the coast of southernmost Norway and breeding in Sweden (n = 4) or the Baltic and Russia (n = 6). Migration, travel and stopover periods are given in days. A female which did not seem to incubate was excluded from estimates of breeding-related variables. In cases of breeding itinerancy, the time at the breeding site is the sum of two breeding events. Distances (orthodromic) are given in km and speed in km/day. Mean values are given ± SD.

	Females (n = 7)	**Males (n = 3)**	**All (n = 10)**
Spring migration			
Departure date (median)	19 Mar–19 Apr (29 Mar)	13 Mar–19 Apr (29 Mar)	13 Mar–19 Apr (29 Mar)
Travel time	1.4–6.9	1.5–5.6	1.4–6.9
n stopovers	0–2	0–3	0–3
Total stopover time	0–22.4	0–27.5	0–27.5
Total migration time	1.4–27.3	1.5–32.7	1.4–32.7
Migration distance	984 ± 506	1433 ± 1148	1119 ± 715
Travel speed	287 ± 82	322 ± 159	298 ± 102
Migration speed	271 ± 177	129 ± 79	228 ± 164

Breeding			
Arrival date (median)	21 Mar–26 Apr (15 Apr)	15 Mar–21 May (13 Apr)	15 Mar–21 May (14 Apr)
First incubation date (median)	26 Apr – 16 May (11 May)	11 Apr – 2 Jun (2 May)	11 Apr – 2 Jun (10 May)
n days breeding site (median)	115–207 (171)	151–190 (190)	115–207 (171)
Autumn migration			
Departure date (median)	8 Aug–2 Nov (9 Oct)	20 Sept–22 Oct (19 Oct)	8 Aug–2 Nov (9 Oct)
Travel time	1.6–5.2	1.5–4.6	1.5–5.2
n stopovers	0–1	0–2	0–2
Sum stopover time	0–65.1	0–19.4	0–65.1
Total migration time	1.6–68.5	1.5–24.1	1.5–68.5
Migration distance	1059 ± 478	1391 ± 1073	1158 ± 659
Travel speed	306 ± 74	354 ± 165	343 ± 121
Migration speed	149 ± 149	156 ± 59	151 ± 125

Figure 1.

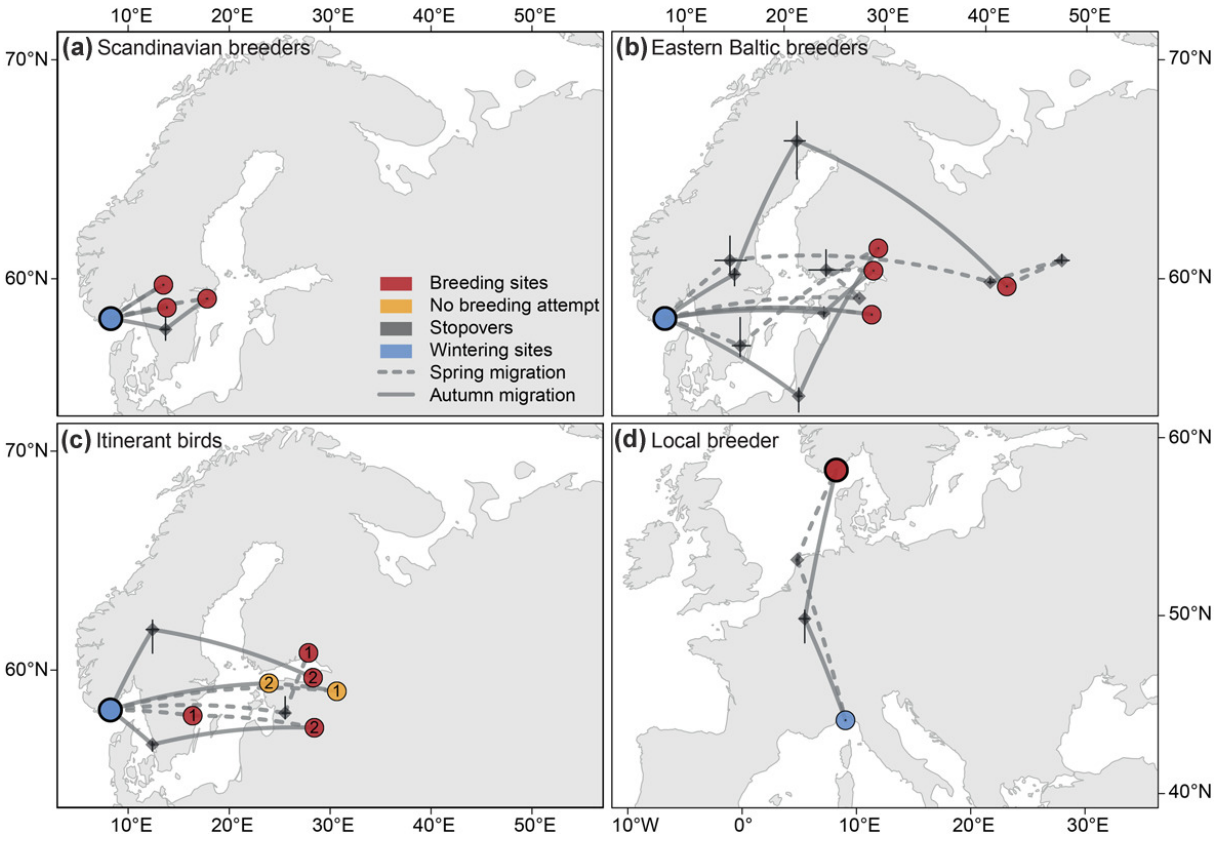
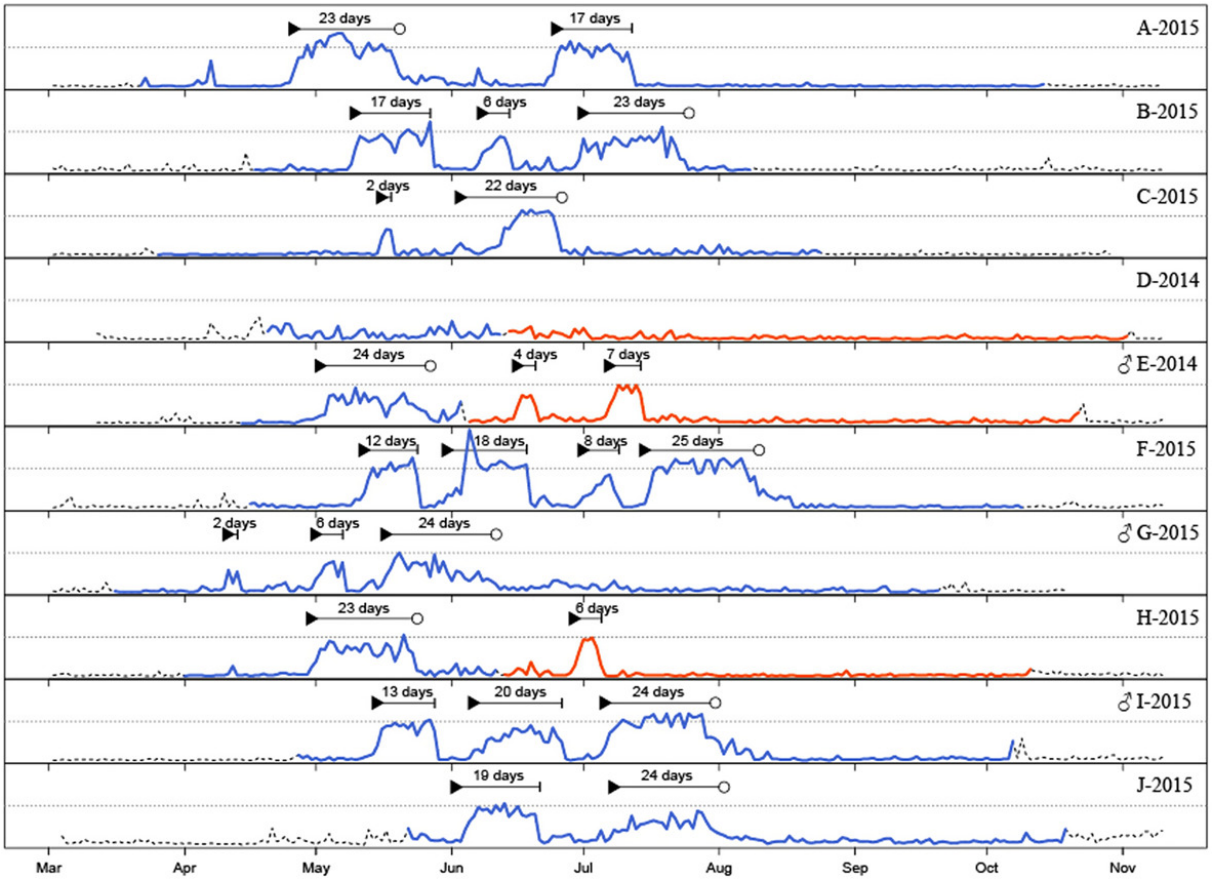

(a) Scandinavian breeders
(b) Eastern Baltic breeders
(c) Itinerant birds
(d) Local breeder
Breeding sites
No breeding attempt
Stopovers
Wintering sites
Spring migration
Autumn migration
10°E
20°E
30°E
40°E
50°E
10°W
0°
70°N
60°N
50°N
40°N

Figure 2.


23 days
17 days
A-2015
17 days
6 days
23 days
B-2015
2 days
22 days
C-2015
D-2014
24 days
4 days
7 days
♂ E-2014
12 days
18 days
8 days
25 days
F-2015
2 days
6 days
24 days
♂ G-2015
23 days
6 days
H-2015
13 days
20 days
24 days
♂ I-2015
19 days
24 days
J-2015
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov