Testing alternative methods for estimation of bird migration phenology from GPS tracking data

Andrea Soriano-Redondo[1,2], Marta Acácio[3], Aldina M.A. Franco[3], Bruno Herlander Martins[1,2], Francisco Moreira[1,4], Katharine Rogerson[3], Inês Catry[1,2,3]

[1] CIBIO/InBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Laboratório Associado, Universidade do Porto, 4485-661 Vairão, Portugal

[2] CIBIO/InBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Laboratório Associado, Instituto Superior de Agronomia, Universidade de Lisboa, 1349-017 Lisbon, Portugal

[3] School of Environmental Sciences, University of East Anglia, NR4 7TJ Norwich, UK

[4] REN Biodiversity Chair, CIBIO/InBIO-UP, Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto, Campus Agrário de Vairão, Rua Padre Armando Quintas, 4485–601 Vairão, Portugal

Abstract

The development and miniaturization of GPS tracking devices has enabled a better understanding of migration phenology, but identifying where and when migration starts and ends can be challenging, and researchers rely on multiple methods to estimate it. Here, we use GPS tracks of 18 trans-Saharan migrant white storks (*Ciconia ciconia*) to determine how the choice of approach influences the estimation of migratory timing, and discuss its implications. We evaluate and provide R code for the implementation of five different methods: spatial threshold, absolute displacement, spatio-temporal displacement, net squared displacement and change point analysis. Our results show that spatial threshold, absolute displacement and spatio-temporal displacement methods produce, in most cases, significantly different estimates of migration timing and duration compared to net squared displacement and change point analysis.

Keywords: biologging, birds, GPS/GSM loggers, migratory timing, migration phenology

28

Introduction

Migration phenology, the timing of seasonal movements between breeding and non-breeding

areas, is of paramount importance for many biological processes and has been linked to bird

population declines (Møller et al. 2008, Both et al. 2010, Newson et al. 2016). The timing of

migration has been used to assess the impacts of weather conditions, climate change or

anthropogenic food subsidies on individuals and populations (Vansteelant et al. 2015, Flack et

al. 2016, Usui et al. 2017). For example, for some bird species arrival dates to the breeding

grounds are advancing in response to climate change, which has been shown to have

downstream effects with birds failing to raise their offspring at the peak of food abundance

(Both et al. 2006) or facing an increased interspecific competition for nesting sites (Ahola et al.

2007). However, estimating the timing and duration of migration is challenging and how the

choice of approach influences the estimation of migratory timing remains largely unknown.

The study of migration phenology has long relied on the observation or capture of the

first arriving or last departing birds from the breeding or wintering grounds to determine the

timing of migration (Lukas & Marc 2003, Shamoun-Baranes *et al.* 2006). In the last decades,

the development and miniaturization of tracking devices has allowed scientists to infer arrival

and departure times at individual level and at greater spatial detail. GPS devices, in particular,

can provide extraordinarily detailed information of movement and behaviour during

individuals' annual cycles. GPS data have revealed fitness advantages of earlier migration onset

(Rotics et al. 2016); costs of early departure from the wintering grounds (Rotics et al. 2018);

effects of weather conditions on migration timing (Vansteelant et al. 2015, 2017, Illan et al.

2017); or the relationship between onset of migration and migratory route (Hewson et al. 2016).

This detailed movement data also presents new analytical challenges. Various methods

have been used to determine timing of migration using GPS data (examples in Table S1). To

establish the transitions between non-migratory and migratory behaviours, and thus the onset,

end and duration of migration, researchers use a range of methods of varying complexity. These

55 methods can be broadly classified into five: spatial threshold (S), absolute displacement (AD),

56 spatio-temporal displacement (SD), net squared displacement (NSD) and change point analysis

57 (CPA).

58   The simplest one is the S method where birds reach or leave the breeding or wintering

59 grounds after crossing Y latitude or boundary (López-López et al. 2010, Hewson et al. 2016,

60 Illan et al. 2017, King et al. 2017, Monti et al. 2018). The AD method, which can incorporate a

61 spatial threshold as well, sets the start of migration as the first day where daily displacement

62 (i.e. distance between roosting sites) reaches X distance and the end of migration as the last day

63 daily displacement reaches X distance (Oppel et al. 2015, Flack et al. 2016, Burnside et al.

64 2017). For example, Rotics et al. 2016 set the onset of autumn migrations for white storks

65 (*Ciconia ciconia*) breeding in Germany, as the birds first flight day (> 100 km displacement)

66 southwards (AD method) and the end of autumn migration as the day birds crossed 17.5°N

67 southwards (S method).

68   The SD method includes both spatial and displacement thresholds, plus a temporal

69 threshold. In the SD method, migration starts the first day of T days where daily displacement

70 is $>X$ that leads to the crossing of the Y spatial threshold, and finishes the first day after T days

71 where daily displacement is $<X$, after crossing the Y spatial threshold (Rodríguez-Ruiz et al.

72 2014, Vansteelant et al. 2015, 2017, Rotics et al. 2018). For example, Vansteelant et al. 2017

73 studied the migratory journeys of European honey buzzards (*Pernis apivorus*) breeding in the

74 Netherlands and determined that migration started the first day after the last >= 3 consecutive

75 stationary days in the breeding range (> 51°N) and finished the first day after >= 3 consecutive

76 stationary days in the non-breeding range (< 10°N).

77   The NSD method has been widely used for mammals, but also in some bird studies

78 (Singh et al. 2016, Buechley et al. 2018). To determine onset and end of migration, NSD

79 calculates the square of the straight-line distance between the track starting location and each

80 subsequent point. It estimates the onset or end of migration as a function of the distance

81   between seasonal ranges and the proportion of the total movement distance (see Singh et al.

82   2016 and Spitz et al. 2017 for a detailed explanation).

83   Variations of CPA methods have been used to determine migration phenology in

84   Macqueen's bustards (*Chlamydotis macqueenii*) and Montagu's harriers (*Circus pygargus*)

85   (Limiñana et al. 2007, Madon & Hingrat 2014). CPA methods segment the tracks in time series

86   based on abrupt changes in behaviour. These breakpoint can be estimated using regressions or

87   change point algorithms (see Madon & Hingrat 2014 for a detailed explanation and R scripts).

88   In this study, we use these five techniques to determine the onset, end and duration of

89   migration. We compare the results obtained by the five methods and quantify the differences

90   between methods at an individual level. Moreover, we also test if the method of choice could

91   influence estimates of migratory timing at a population level. To do so, we use a dataset of

92   juveniles and adult white storks tagged with GPS/GSM transmitters from Portugal to their

93   wintering sites in sub-Saharan Africa and back.

94   **Material and Methods**

95   *Tagging and tracking white storks*

96   For this study we selected GPS tracks of 18 white storks (5 adults in 2017, 8 juveniles in 2017

97   and 5 juveniles in 2018) breeding in southern Portugal that performed trans-Saharan migrations.

98   Juveniles were 1st year birds tagged before fledging and adults were breeding birds (> 3 years

99   old). Birds were tagged with GPS/GSM loggers (Movetech Telemetry and Ornitela, both tags

100   fixes have negligible location error). Adult birds were caught at landfill sites using nylon leg

101   nooses and, in the nests, using a remotely activated clap net. Juvenile birds were taken from the

102   nests for tag deployment and returned back to the nests after the procedure. The devices were

103   back-mounted using a Teflon harness (further details in Gilbert et al. 2016). The mass of the

104   tags plus the harness was ~90g, 1.8-3.7% of the birds' body mass. The tags collected GPS

105   positions every ~20 minutes.

106   *Spatial threshold method (S)*

Sub-Saharan migratory white storks breeding in Portugal cross three main geographic barriers to reach their wintering grounds: the Mediterranean Sea, the Atlas mountains and the Sahara desert. Therefore, we established the onset of autumn migration as the first day the birds crossed the first barrier, the Mediterranean Sea at the Strait of Gibraltar, 36ºN southwards, while the end of migration was defined as the first day birds crossed the south of the Sahara desert, 18ºN southwards. The onset of spring migration was established as the first day birds crossed 18ºN northwards and the end was the first day birds crossed 36ºN northwards (R code provided in Appendix S2).

Absolute displacement method (AD)

Onset of autumn migration was the first day a bird moved > 60 km between consecutive roosting sites that led to the crossing of 36ºN southwards. The 60 km threshold was defined as a conservative estimate of daily distance travelled during migration, based on the white stork dataset. End of autumn migration was the last day the bird moved > 60 km between consecutive roosting sites after crossing 18ºN southwards. The onset and end of spring migration was set as the first day a bird moved > 60 km between roosting sites that led to the crossing of 18ºN and 36ºN northwards, respectively (R code provided in Appendix S3).

Spatio-temporal displacement method (SD)

Onset of autumn (and spring) migration was the first day a bird moved during three consecutive days > 60 km between consecutive roosting sites that led to the crossing of the breeding (or wintering) range boundary (90% Kernel probability density). End of autumn (and spring) migration was the last day the bird moved during three consecutive days > 60 km between consecutive roosting sites after crossing the wintering (or breeding) range boundary.

Net squared displacement method (NSD)

To determine migratory timing, we first fit several movement models to our tracks using the R package 'MigrateR' (Spitz et al. 2017). Onset and end of migration was calculated as the date at which the top model predictions (depending on the individual migrant, mix-migrant or

133   disperser) reached $p \times \delta$ and $(1 - p) \times \delta$, respectively. Where δ represents the distance

134   separating seasonal ranges and p (0.05), the threshold fraction of total distance moved (Spitz et

135   al. 2017) (R code provided in Appendix S5).

136   *Change point analysis method (CPA)*

137   We followed Madon & Hingrat (2014) to perform a change point analysis. To determine the

138   transitions between non-migratory and migratory states, we used the Pruned Exact Linear Time

139   algorithm. Next, we manually classified 30% of the track segments into migratory or non-

140   migratory and used a supervised classification tree to classify the remaining 70% (R code

141   provided in Appendix S6).

142   *Statistical analyses*

143   To quantify the degree to which the methods were consistent when estimating migration

144   phenology for each individual, we calculated the intraclass correlation coefficient (ICC) for the

145   onset and end of the autumn and spring migration. The ICC varies from 0 to 1, for low to high

146   correlation within each individual. To calculate the ICC we used the R package 'ICC' (Wolak

147   2015).

148   To assess population level differences among methods we performed GLMMs, with

149   onset, end and duration of migration as response variables (log-transformed), method as an

150   explanatory variable and individual as a random factor. Date of onset and end of migration were

151   included in the models, as day of year. Next, we performed multiple comparisons by Tukey

152   contrasts to determine which methods provided different estimates of migration phenology.

153   **Results**

154   *Spatial range of migration*

155   The start and end of the migratory period varied depending on the threshold method. Using the

156   S method, the location of the migration start and end was delimited by 36ºN and 18ºN (Fig. 1a

157   and Appendix S2). Using the AD method departure and arrival locations ranged from the

158   breeding grounds in Portugal to the Strait of Gibraltar (Fig. 1b and Appendix S3). The SD

159 method set the arrival and departure of the breeding grounds in the south of Portugal;

160 movements between the breeding site and the Gibraltar Strait were classified as migratory (Fig.

161 1c and Appendix S4). The NSD and CPA methods had the highest spatial variability between

162 individuals, for the departure and arrival locations from and to the breeding grounds, ranging

163 from the south of Portugal to the south of Morocco (Fig. 1d-e and Appendix S5-6). The location

164 of onset and end of migration in the wintering grounds showed great variability amongst

165 individuals, ranging from 12°N to 18°N when using the AD, SD, NSD or CPA methods (Fig. 1).

166 *Timing and duration of migration*

167 The median start of the autumn migration ranged from the 3rd of August with the AD method to

168 the 10th of August with the NSD (Fig. 2a). Although it showed high consistency among methods

169 (ICC = 0.89), the models estimates significantly differed (p = 0.011) due to differences between

170 the SD and NSD methods (p = 0.003). The end of the autumn migration ranged from the 22nd of

171 August with the S method to the 4th of September with the CPA (Fig. 2c), and it showed a low

172 consistency (ICC = 0.56) and significant differences among multiple methods (p < 0.001, see

173 Appendix 7 for Tukey contrasts).The spring migration had a similar pattern. The start of the

174 migration ranged from the 12th of January with the NSD method to the 25th of January with the

175 S method (Fig. 2b); and it show high consistency (ICC = 0.92), but still presented significant

176 differences (p = 0.019), due to different estimates between S and NSD (p = 0.004). The end of

177 spring migration ranged from the 7th of February (NSD) to the 17th of April (SD) (Fig. 2d) and

178 showed low consistency (ICC = 0.55) and significant differences among multiple methods (p <

179 0.001, see Appendix 7 for Tukey contrasts).

180 Overall, the S, AD and SD method yielded similar results (Fig. 3), except for the

181 estimates of duration of autumn migration of the S and SD methods (p < 0.001). On the other

182 hand, the NSD and CPA approaches produced similar estimates (Fig. 3), except, as well, for the

183 duration of autumn migration (p = 0.03). Nevertheless, these two groups of methods predicted

184 different migratory timings; the estimates of S, AD and SD were different to the estimates of

185 NSD and CPA in most cases (Fig. 3, see Appendix 7 for further details).

Discussion

We found substantial differences between methodologies in the estimation of the onset, end and duration of migration of juvenile and adult white storks tracked from their breeding areas in Portugal to their wintering areas in sub-Saharan Africa and back. Both autumn and spring migration are vulnerable to these biases (Fig. 2f and 3b), with up to a twelvefold difference in autumn migration duration depending on the method used, from 10 days using the S method to 120 days using the NSD method (Table S3). Our study highlights the need to carefully consider the methodology used to determine migration phenology based on GPS tracking devices and to assess the sensitivity of the data to methodology used.

The sensitivity to the approach varied depending on the phenological metric estimated; the onset of the autumn and spring migrations was more consistent among methods (ICC = 0.89 and 0.92) than the end (ICC = 0.56 and 0.55). Importantly, we found that NSD and CPA were significantly different from S, AD and SD in most estimates. This could be explained by several differences between these two groups of methods: (1) NSD and CPA make minimum a priory assumptions, while the AD and SD require prior assumptions about daily displacement during migration; (2) NSD and CPA are only based on animal movement, while the S, AD and SD require ecological knowledge to broadly determine breeding and wintering areas.

Although we do not advocate for a one-size-fits-all approach, our results suggest that the low level of ecological knowledge required by NDS and CPA methods is detrimental to the estimation of the migration phenology of white storks. The NDS and CPA methods fail to distinguish a realistic threshold in the breeding range, which, in this case, leads to autumn migrations only starting after the crossing of the Strait of Gibraltar or spring migrations ending before the crossing of the Strait.

The results also show that the S method produced similar results to the AD and SD methods, but it does not capture the spatial variability of individual breeding and wintering sites within the species' breeding and wintering ranges. Thus, in the Northern hemisphere for species with large wintering or breeding ranges, individuals breeding in the northernmost and wintering

213 in the southernmost areas of their ranges, could have their migration period cut short by

214 multiple days.

215   Although, the AD and SD methods yielded similar results, the SD performed better for

216 individuals that had short stops within the breeding or wintering range before the end of

217 migration. Both methods require the establishment of arbitrary thresholds: spatial, displacement

218 and temporal (SD only). We suggest (1) a preliminary exploration of the movement data, to

219 estimate the displacement and temporal thresholds during migration; and (2) to use GPS

220 locations obtained during the breeding and wintering period to perform Kernel density estimates

221 that will inform the breeding and wintering area boundaries and reduce the arbitrariness of

222 spatial thresholds adopted.

223   We recommend that similar studies, comparing the efficacy of these methods at

224 determining the phenology of migration, should be conducted on other bird species. Our results

225 suggest that expert knowledge is needed to set up appropriate spatial, displacement and

226 temporal thresholds. The choice of method used to determine migration phenology can

227 influence the conclusions especially if parts of the migratory journey are excluded. This is

228 particularly important on studies that examine the onset or end of the migration at the individual

229 level, or the importance of meteorological phenomenon during migration. In this study, some

230 methods would not enable us to capture, the crossing of the Mediterranean Sea at the Strait of

231 Gibraltar, an important geographic barrier for white storks.

232   In light of the increasing number of species and individuals that have their migratory

233 journeys recorded using GPS data (see Table S1 for examples) a certain degree of

234 standardisation on the definition of migration and the approach is required to obtain consistent

235 estimates across studies. To facilitate comparisons between studies, we recommend that errors

236 associated to estimates of migration phenology should be considered, particularly in

237 interspecific studies that use tracking data from multiple sources. More importantly, we

238 encourage researchers to make data available in data repositories and to accurately report the

239 methods used. We hope this contribution will raise awareness to the challenges associated with

240 the study of migration phenology using GPS tracking data and help researchers find appropriate

241 methodologies to analyse their data.

242 **Declarations.** The authors declare no competing interests.

243 **Data.** Tracking data are stored in Movebank. R code is available in supplementary material.

244 **References**

245 Ahola, M. P., Laaksonen, T., Eeva, T. and Lehikoinen, E. 2007. Climate change can alter

246   competitive relationships between resident and migratory birds. - J. Animal Ecol. 76:

247   1045–1052.

248 Both, C., Bouwhuis, S., Lessells, C. M. and Visser, M. E. 2006. Climate change and population

249   declines in a long-distance migratory bird. - Nature 441: 81.

250 Both, C., Van Turnhout, C. A. M., Bijlsma, R. G., Siepel, H., Van Strien, A. J. and Foppen, R.

251   P. B. 2010. Avian population consequences of climate change are most severe for long-

252   distance migrants in seasonal habitats. - Proc. Royal Soc. B 277: 1259–1266.

253 Buechley, E. R., Oppel, S., Beatty, W. S., Nikolov, S. C., Dobrev, V., Arkumarev, V., Saravia,

254   V., Bougain, C., Bounas, A., Kret, E., Skartsi, T., Aktay, L., Aghababyan, K., Frehner,

255   E. and Şekercioğlu, Ç. H. 2018. Identifying critical migratory bottlenecks and high-use

256   areas for an endangered migratory soaring bird across three continents. – J. Avian Biol.

257   49: e01629.

258 Burnside, R. J., Collar, N. J. and Dolman, P. M. 2017. Comparative migration strategies of wild

259   and captive-bred Asian Houbara Chlamydotis macqueenii. - Ibis 159: 374–389.

260 Flack, A., Fiedler, W., Blas, J., Pokrovsky, I., Kaatz, M., Mitropolsky, M., Aghababyan, K.,

261   Fakriadis, I., Makrigianni, E., Jerzak, L., Azafzaf, H., Feltrup-Azafzaf, C., Rotics, S.,

262   Mokotjomela, T. M., Nathan, R. and Wikelski, M. 2016. Costs of migratory decisions:

263   A comparison across eight white stork populations. - Sci. Adv. 2: e1500931.

264 Gilbert, N. I., Correia, R. A., Silva, J. P., Pacheco, C., Catry, I., Atkinson, P. W., Gill, J. A. and

265   Franco, A. M. A. 2016. Are white storks addicted to junk food? Impacts of landfill use

266   on the movement and behaviour of resident white storks (Ciconia ciconia) from a

267   partially migratory population. – Mov. Ecol. 4: 7.

268 Hewson, C. M., Thorup, K., Pearce-Higgins, J. W. and Atkinson, P. W. 2016. Population

269   decline is linked to migration route in the Common Cuckoo. – Nat. Commun. 7: 12296.

270 Illan, J. G., Wang, G., Cunningham, F. L. and King, D. T. 2017. Seasonal effects of wind

271   conditions on migration patterns of soaring American white pelican. - PLOS One 12:

272   e0186948.

273 King, D. T., Wang, G., Yang, Z. and Fischer, J. W. 2017. Advances and Environmental

274   Conditions of Spring Migration Phenology of American White Pelicans. - Sci. Rep. 7:

275   40339.

276 Limiñana, R., Soutullo, A. and Urios, V. 2007. Autumn migration of Montagu's harriers *Circus*

277   *pygargus* tracked by satellite telemetry. J. Ornithol. 148: 517-523.

278 López-López, P., Limiñana, R., Mellone, U. and Urios, V. 2010. From the Mediterranean Sea to

279   Madagascar: Are there ecological barriers for the long-distance migrant Eleonora's

280   falcon? - Landscape Ecol. 25: 803–813.

281 Lukas, J. and Marc, K. 2003. Timing of autumn bird migration under climate change: advances

282   in long–distance migrants, delays in short–distance migrants. - Proc. Royal Soc. B 270:

283   1467–1471.

284 Madon, B. and Hingrat, Y. 2014. Deciphering behavioral changes in animal movement with a

285   'multiple change point algorithm-classification tree' framework. Front. Ecol. Evol. 2:

286   30.

287 Møller, A. P., Rubolini, D. and Lehikoinen, E. 2008. Populations of migratory bird species that
288   did not show a phenological response to climate change are declining. - PNAS 105:
289   16195–16200.

290 Monti, F., Grémillet, D., Sforzi, A., Sammuri, G., Dominici, J. M., Bagur, R. T., Navarro, A.
291   M., Fusani, L. and Duriez, O. 2018. Migration and wintering strategies in vulnerable
292   Mediterranean Osprey populations. - Ibis 160: 554–567.

293 Newson, S. E., Moran, N. J., Musgrove, A. J., Pearce-Higgins, J. W., Gillings, S., Atkinson, P.
294   W., Miller, R., Grantham, M. J. and Baillie, S. R. 2016. Long-term changes in the
295   migration phenology of UK breeding birds detected by large-scale citizen science
296   recording schemes. - Ibis 158: 481–495.

297 Oppel, S., Dobrev, V., Arkumarev, V., Saravia, V., Bounas, A., Kret, E., Velevski, M.,
298   Stoychev, S. and Nikolov, S. C. 2015. High juvenile mortality during migration in a
299   declining population of a long-distance migratory raptor. - Ibis 157: 545–557.

300 Rodríguez-Ruiz, J., Puente, J. de la, Parejo, D., Valera, F., Calero-Torralbo, M. A., Reyes-
301   González, J. M., Zajková, Z., Bermejo, A. and Avilés, J. M. 2014. Disentangling
302   Migratory Routes and Wintering Grounds of Iberian Near-Threatened European Rollers
303   Coracias garrulus. - PLOS One 9: e115615.

304 Rotics, S., Kaatz, M., Resheff, Y. S., Turjeman, S. F., Zurell, D., Sapir, N., Eggers, U., Flack,
305   A., Fiedler, W., Jeltsch, F., Wikelski, M. and Nathan, R. 2016. The challenges of the
306   first migration: movement and behaviour of juvenile vs. adult white storks with insights
307   regarding juvenile mortality (C Both, Ed.). – J. Anim. Ecol. 85: 938–947.

308 Rotics, S., Kaatz, M., Turjeman, S., Zurell, D., Wikelski, M., Sapir, N., Eggers, U., Fiedler, W.,
309   Jeltsch, F. and Nathan, R. 2018. Early arrival at breeding grounds: Causes, costs and a
310   trade-off with overwintering latitude. - J. Anim. Ecol. 87: 1627–1638.

311 Shamoun-Baranes, J., Loon, E. V., Alon, D., Alpert, P., Yom-Tov, Y. and Leshem, Y. 2006. Is
312   there a connection between weather at departure sites, onset of migration and timing of
313   soaring-bird autumn migration in Israel? - Glob. Ecol. Biogeogr. 15: 541–552.

314 Singh, N. J., Allen, A. M. and Ericsson, G. 2016. Quantifying Migration Behaviour Using Net
315   Squared Displacement Approach: Clarifications and Caveats. - PLOS One 11:
316   e0149594.

317 Spitz, D. B., Hebblewhite, M. and Stephenson, T. R. 2017. 'MigrateR': extending model-driven
318   methods for classifying and quantifying animal movement behavior. - Ecography 40:
319   788–799.

320 Usui, T., Butchart, S. H. M. and Phillimore, A. B. 2017. Temporal shifts and temperature
321   sensitivity of avian spring migratory phenology: a phylogenetic meta-analysis (B
322   Sheldon, Ed.). – J. Anim. Ecol. 86: 250–261.

323 Vansteelant, W. M. G., Bouten, W., Klaassen, R. H. G., Koks, B. J., Schlaich, A. E., Diermen,
324   J. van, Loon, E. E. van and Shamoun-Baranes, J. 2015. Regional and seasonal flight
325   speeds of soaring migrants and the role of weather conditions at hourly and daily scales.
326   – J. Avian Biol. 46: 25–39.

327 Vansteelant, W. M. G., Shamoun-Baranes, J., van Manen, W., van Diermen, J. and Bouten, W.
328   2017. Seasonal detours by soaring migrants shaped by wind regimes along the East
329   Atlantic Flyway. – J. Anim. Ecol. 86: 179–191.

330 Wolak, M. 2015. Package 'ICC'. Facilitating estimation of the Intraclass Correlation
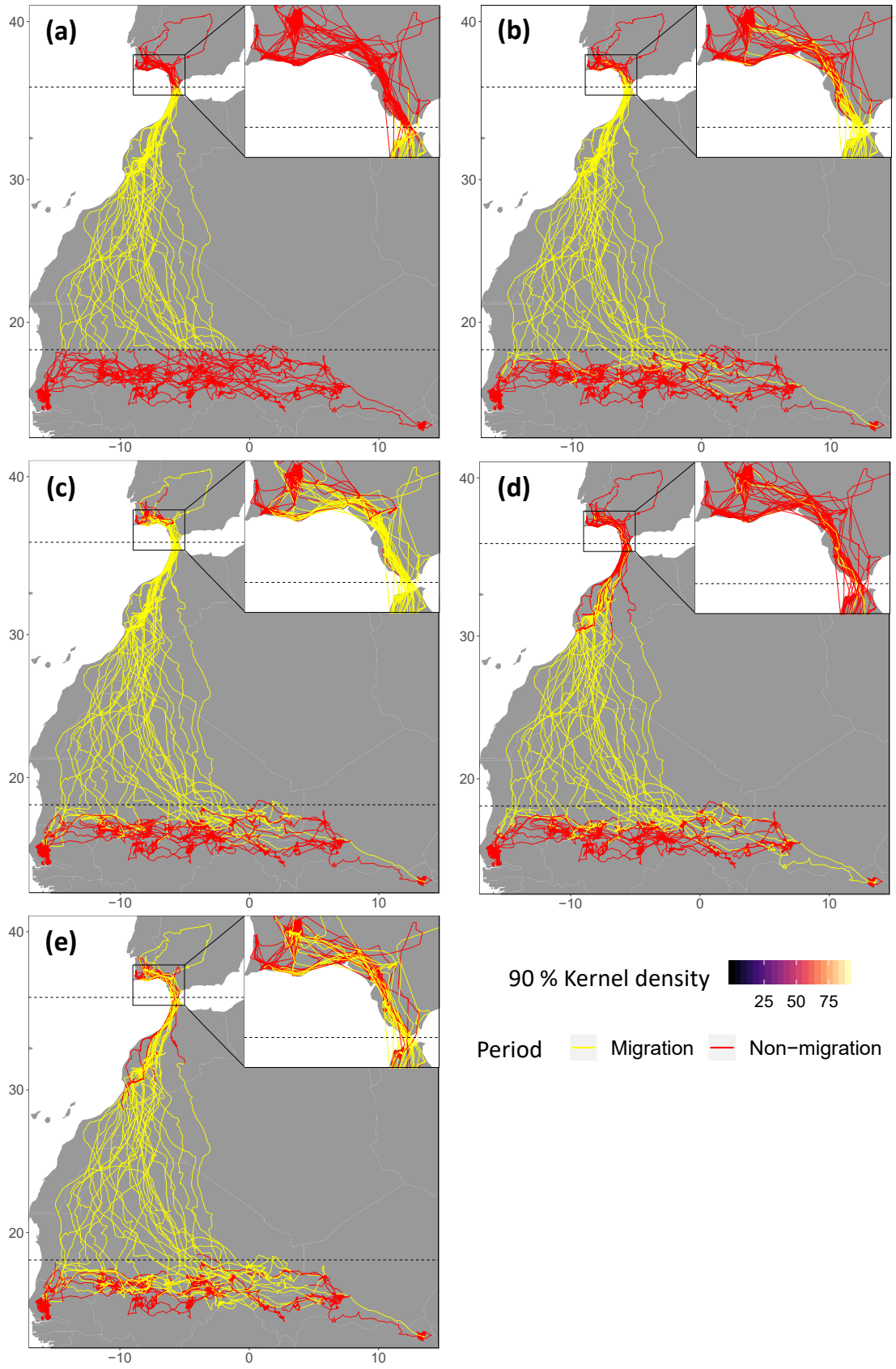331   Coefficient.

332

333

334

335

336

90 % Kernel density

25 50 75

Period   Migration   Non−migration

337

338

339   Figure 1: Annual movements of eighteen white storks classified as migratory or non-migratory

340   according to (a) spatial threshold (S), (b) absolute displacement (AD), (c) spatio-temporal

341   displacement (SD), (d) net squared displacement (NSD) and (e) change point analysis (CPA)

342   methods. Dashed lines represent spatial thresholds (36ºN and 18ºN) used in the S and AD

343   methods.
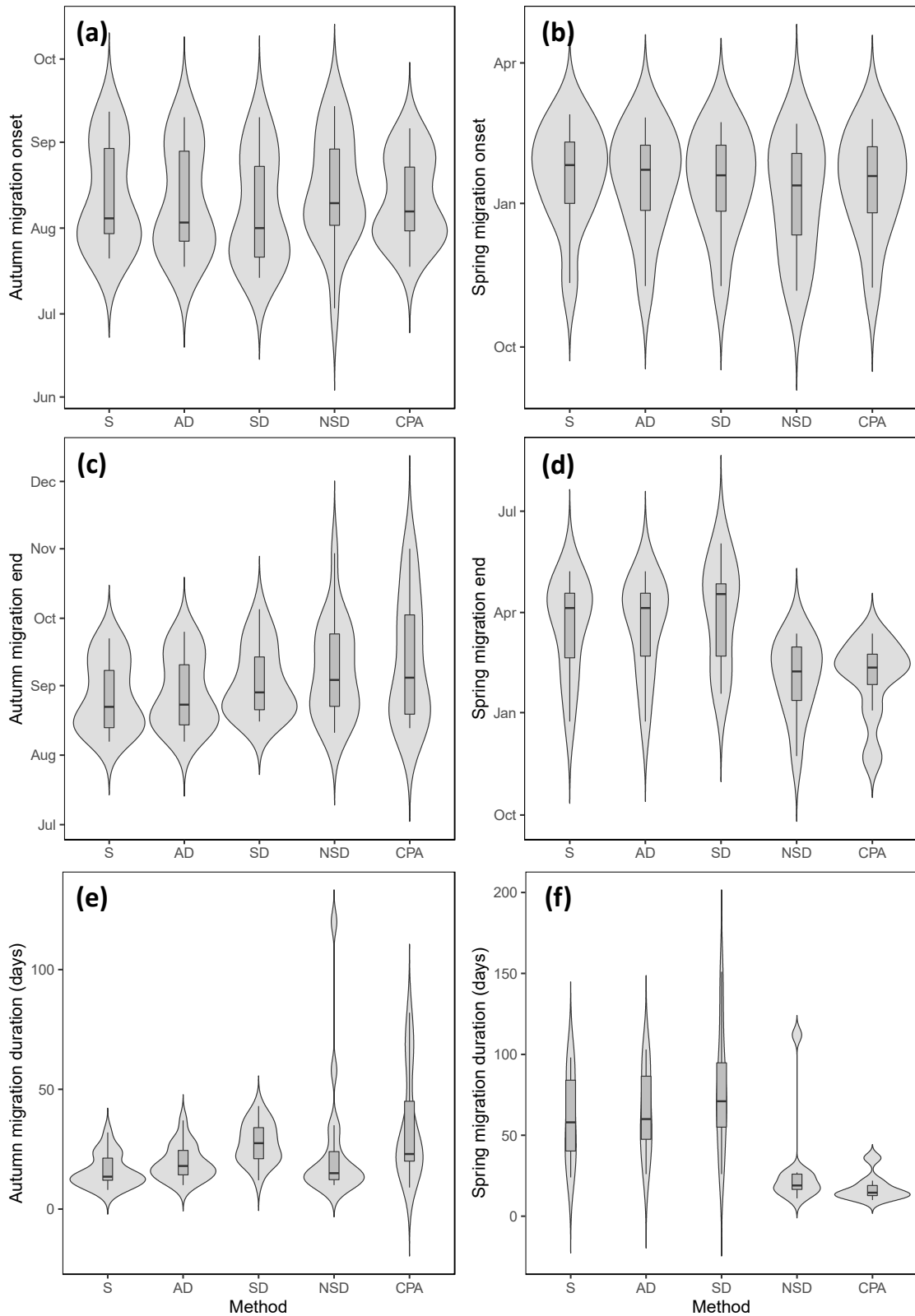
Figure 2: Violin plots of the density of the distribution of the onset of (a) autumn and (b) spring migration; end of (c) autumn and (d) spring migration; and duration in days of (e) autumn and

348 (f) spring migration obtained using different methods. Medium, lower and upper hinges of the

349 boxplot correspond to the median, 25th and 75th percentiles, respectively. Whiskers correspond

350 to the 95% confidence intervals. S = spatial threshold method; AD = absolute displacement

351 method; SD = spatio-temporal displacement method; NSD = net squared displacement method;

352 CPA = change point analysis.

353

(a)

ONSET \ END	S	AD	SD	NSD	CPA
S		2 (3)	4.5 (20)	4.5 (79)	6.5 (64)
AD	1.5 (4)		3 (17)	4 (77)	5 (64)
SD	5 (14)	3.5 (13)		4 (70)	5.5 (55)
NSD	3.5 (31)	3.5 (29)	7 (29)		7 (71)
CPA	4 (20)	1 (23)	1 (23)	6 (28)	

(b)

ONSET \ END	S	AD	SD	NSD	CPA
S		0 (2)	6 (48)	34 (88)	34.5 (87)
AD	2 (11)		6 (48)	34 (88)	34.5 (87)
SD	5 (11)	0 (4)		50 (136)	50.5 (112)
NSD	8 (69)	4 (65)	3.5 (61)		1 (12)
CPA	4 (12)	1 (5)	1 (2)	2.5 (60)	

(c)

AUTUMN \ SPRING	S	AD	SD	NSD	CPA
S		2 (13)	12.5 (53)	33 (83)	31.5 (84)
AD	4 (5)		8.5 (48)	32 (85)	33.5 (86)
SD	10.5 (29)	6.5 (28)		44.5 (133)	51 (111)
NSD	4 (110)	4 (106)	10 (99)		3.5 (9)
CPA	13 (70)	11 (69)	11 (56)	10 (99)	

Median   0-4   5-10   >10 days

354

355

356 Figure 3: Median (maximum) difference in number of days of the estimated onset and end of (a)

357 autumn and (b) spring migration between methods; and (c) median (maximum) difference in the

358 duration of the autumn and spring migrations . S = spatial threshold method; AD = absolute

359 displacement method; SD = spatio-temporal displacement method; NSD = net squared

360 displacement method; CPA = change point analysis.

361

362

363