Short communication

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

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

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

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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). Migration timing 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, arrival dates of some bird species to the breeding grounds are advancing in response to climate change, which has been shown to have fitness consequences, with birds failing to raise their offspring at the peak of food abundance (Both *et al.* 2006) or facing increased interspecific competition for nesting sites (Ahola *et al.* 2007). However, estimating the timing and duration of migration is challenging and the impact of choosing alternative methodological approaches 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 (Lukas & Marc 2003, Shamoun-Baranes *et al.*, 2006). In the last few decades, the development and miniaturization of tracking devices has allowed scientists to infer arrival and departure times at the individual level and at greater spatial resolution. GPS devices, in particular, can provide very detailed information on 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), and the relationship between start of migration and migratory route (Hewson *et al.* 2016).

Such detailed movement data also present new analytical challenges. Several methods have been used to determine the timing of migration using GPS data (examples in Table S1 of Appendix S1). To establish the transitions between non-migratory and migratory behaviours, and thus the start, end and duration of migration, researchers use a range of methods of varying complexity. These methods can be broadly classified into five: spatial threshold (S), absolute displacement (AD), spatio-temporal displacement (SD), net squared displacement (NSD) and change point analysis (CPA).

The simplest one is the S method, in which birds reach or leave the breeding or wintering grounds after crossing Y latitude or boundary (López-López *et al.* 2010, Hewson *et al.* 2016, Illan *et al.* 2017, King *et al.* 2017, Monti *et al.* 2018). The AD method, which may incorporate a spatial threshold as well, sets the start of migration as the first day at which daily displacement (i.e. distance between roosting sites) reaches or exceeds

a specific threshold distance, and the end of migration as the last day that daily displacement reaches that distance (Oppel *et al.* 2015, Flack *et al.* 2016, Burnside *et al.* 2017). Rotics *et al.* (2016) combined the AD and S methods by setting the start of autumn migration journeys for White Storks *Ciconia ciconia* breeding in Germany as the bird's first flight day (>100 km displacement) southwards (AD method) and the end of autumn migration as the day birds crossed 17.5°N southwards (S method).

The SD method includes both spatial and displacement thresholds, as well as a temporal threshold. Thus, migration starts on the first day of *T* days where daily displacement is >*X* that leads to the crossing of the *Y* spatial threshold, and finishes on the first day after *T* days where daily displacement is <*X*, after crossing the *Y* spatial threshold (Rodríguez-Ruiz *et al.* 2014, Vansteelant *et al.* 2015, 2017, Rotics *et al.* 2018). For example, Vansteelant *et al.* (2017) studied the migratory journeys of European Honey Buzzards *Pernis apivorus* breeding in the Netherlands and determined that migration started on the first day after the last period of three or more consecutive stationary days in the breeding range (> 51°N) and finished on the first day after the first period of three or more consecutive stationary days in the non-breeding range (<10°N).

The NSD method has been widely used for mammals but also in some bird studies (Singh *et al.* 2016, Buechley *et al.* 2018). To determine the start and end of migration, NSD calculates the square of the straight-line distance between the track starting location and each subsequent point. It estimates the start or end of migration as a function of the distance between seasonal ranges and the proportion of the total movement distance (see Singh *et al.* 2016 and Spitz *et al.* 2017 for a detailed explanation).

Variations of CPA methods have been used to determine migration phenology in MacQueen's Bustards *Chlamydotis macqueenii* and Montagu's Harriers *Circus pygargus* (Limiñana *et al.* 2007, Madon & Hingrat 2014). CPA methods segment the tracks in time series based on abrupt changes in behaviour. These breakpoints can be estimated using regressions or change point algorithms (see Madon & Hingrat 2014 for a detailed explanation and R scripts).

In this study, we use these five techniques to determine the start, end and duration of migration. We compare the results obtained by the five methods and quantify the differences between methods at an individual level. Moreover, we also test whether the method of choice could influence estimates of migratory timing at a population level. To do so, we use a dataset of juvenile and adult White Storks tagged with GPS/GSM transmitters from Portugal to their wintering sites in sub-Saharan Africa and back.

METHODS

Tagging and tracking White Storks

For this study we selected GPS tracks of 18 White Storks (five adults in 2017, eight juveniles in 2017 and five juveniles in 2018) breeding in southern Portugal that performed trans-Saharan migrations. Juveniles were first-year birds tagged before fledging and adults were breeding birds (>3 years old). Birds were tagged with GPS/GSM loggers (Movetech Telemetry and Ornitela, both tag fixes have negligible location error). Adult birds were caught at landfill sites using nylon leg nooses and in nests using a remotely activated clap net. Juvenile birds were taken from the nest for tag deployment and returned afterwards. The devices were back-mounted using a Teflon harness (further details in Gilbert *et al.* 2016). The mass of the tags plus the harness was ~90 g, 1.8–3.7% of the birds' body mass. The tags collected GPS positions every ~20 min.

Spatial threshold method (S)

Sub-Saharan migratory White Storks breeding in Portugal cross three main geographical barriers to reach their wintering grounds: the Mediterranean Sea, the Atlas mountains and the Sahara desert. We therefore established the start of autumn migration as the first day the birds crossed the first barrier, the Mediterranean Sea at the Strait of Gibraltar at 36°N, southwards, and the end of migration was defined as the first day birds crossed the south of the Sahara desert at 18°N, southwards. The start of spring migration was established as the first day birds crossed 18°N northwards and the end was the first day birds crossed 36°N northwards (R code provided in Appendix S2).

Absolute displacement method (AD)

The start of autumn migration was the first day a bird moved >60 km between consecutive roosting sites that led to the crossing of 36°N southwards. The 60-km threshold was defined as a conservative estimate of daily distance travelled during migration, based on the White Stork dataset. The end of autumn migration was the last day the bird moved >60 km between consecutive roosting sites after crossing 18°N southwards. The start 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 18°N and 36°N northwards, respectively (R code provided in Appendix S3).

Spatio-temporal displacement method (SD)

The start 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). The 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). The start and end of migration was calculated as the date at which the top model predictions (depending on the individual migrant, mix-migrant or disperser) reached $p \times \delta$ and $(1 - p) \times \delta$, respectively, where δ represents the distance separating seasonal ranges and p (0.05) is the threshold fraction of total distance moved (Spitz *et al.* 2017) (R code provided in Appendix S5).

Change point analysis method (CPA)

We followed Madon and Hingrat (2014) to perform a change point analysis. To determine the transitions between non-migratory and migratory states, we used the Pruned Exact Linear Time algorithm. Next, we manually classified 30% of the track segments into migratory or non-migratory and used a supervised classification tree to classify the remaining 70% (R code provided in Appendix S6).

Statistical analyses

To quantify the degree to which the methods were consistent when estimating migration phenology for each individual, we calculated the intraclass correlation coefficient (ICC) for the start and end of autumn and spring migration. The ICC varies from 0 to 1, for low to high correlation within each individual. To calculate the ICC, we used the R package 'ICC' (Wolak 2015).

To assess population-level differences among methods, we performed generalized linear mixed models (GLMMs), with start, end and duration of migration as response variables (log-transformed), method as an explanatory variable and individual as a random factor. The date of start and end of migration were included in the models as calendar date (1 January = 1). Next, we performed multiple comparisons using Tukey contrasts to determine which methods provided different estimates of migration phenology.

RESULTS

Spatial range of migration

The start and end of the migratory period varied depending on the threshold method. Using the S method, the location of the migration start and end was delimited by 36°N and 18°N (Fig. 1a and Appendix S2). Using the AD method, departure and arrival locations ranged from the breeding grounds in Portugal to the Strait of Gibraltar (Fig. 1b and Appendix S3). The SD method set the arrival and departure of the breeding grounds in the south of Portugal, and movements between the breeding site and the Gibraltar Strait were classified as migratory (Fig. 1c and Appendix S4). The NSD and CPA methods had the highest spatial variability between individuals in departure and arrival locations from and to the breeding grounds, ranging from the south of Portugal to the south of Morocco (Fig. 1d,e and Appendixes S5 and S6). The location of the start and end of migration in the wintering grounds showed great variability amongst individuals, ranging from 12°N to 18°N when using the AD, SD, NSD or CPA methods (Fig. 1).

Timing and duration of migration

The median start of autumn migration ranged from 3 August with the AD method to 10 August with the NSD method (Fig. 2a). Although it showed high consistency among methods (ICC = 0.89), the model estimates differed significantly ($P = 0.011$) due to differences between the SD and NSD methods ($P = 0.003$). The end of autumn migration ranged from 22 August with the S method to 4 September with the CPA method (Fig. 2c), and it showed a low consistency (ICC = 0.56) and significant differences among multiple methods ($P < 0.001$, see Appendix 7 for Tukey contrasts). Spring migration had a similar pattern. The start of the migration ranged from 12 January with the NSD method to 25 January with the S method (Fig. 2b) and it showed high consistency (ICC = 0.92), but still with significant differences ($P = 0.019$), due to different estimates between the S and NSD methods ($P = 0.004$). The end of spring migration ranged from 7 February (NSD) to 17 April (SD) (Fig. 2d) and showed low consistency (ICC = 0.55) and significant differences among multiple methods ($P < 0.001$, see Appendix 7 for Tukey contrasts).

Overall, the S, AD and SD methods yielded similar results (Fig. 3), except for estimates of the duration of autumn migration under the S and SD methods ($P < 0.001$). The NSD and CPA methods also produced similar estimates (Fig. 3) except, similarly, for the duration of autumn migration ($P = 0.03$). Nevertheless, these two groups of methods predicted different migratory timings; the estimates of S, AD and SD differed from the estimates of NSD and CPA in most cases (Fig. 3, see Appendix 7 for further details).

DISCUSSION

We found substantial differences between methods in the estimation of the start, end and duration of
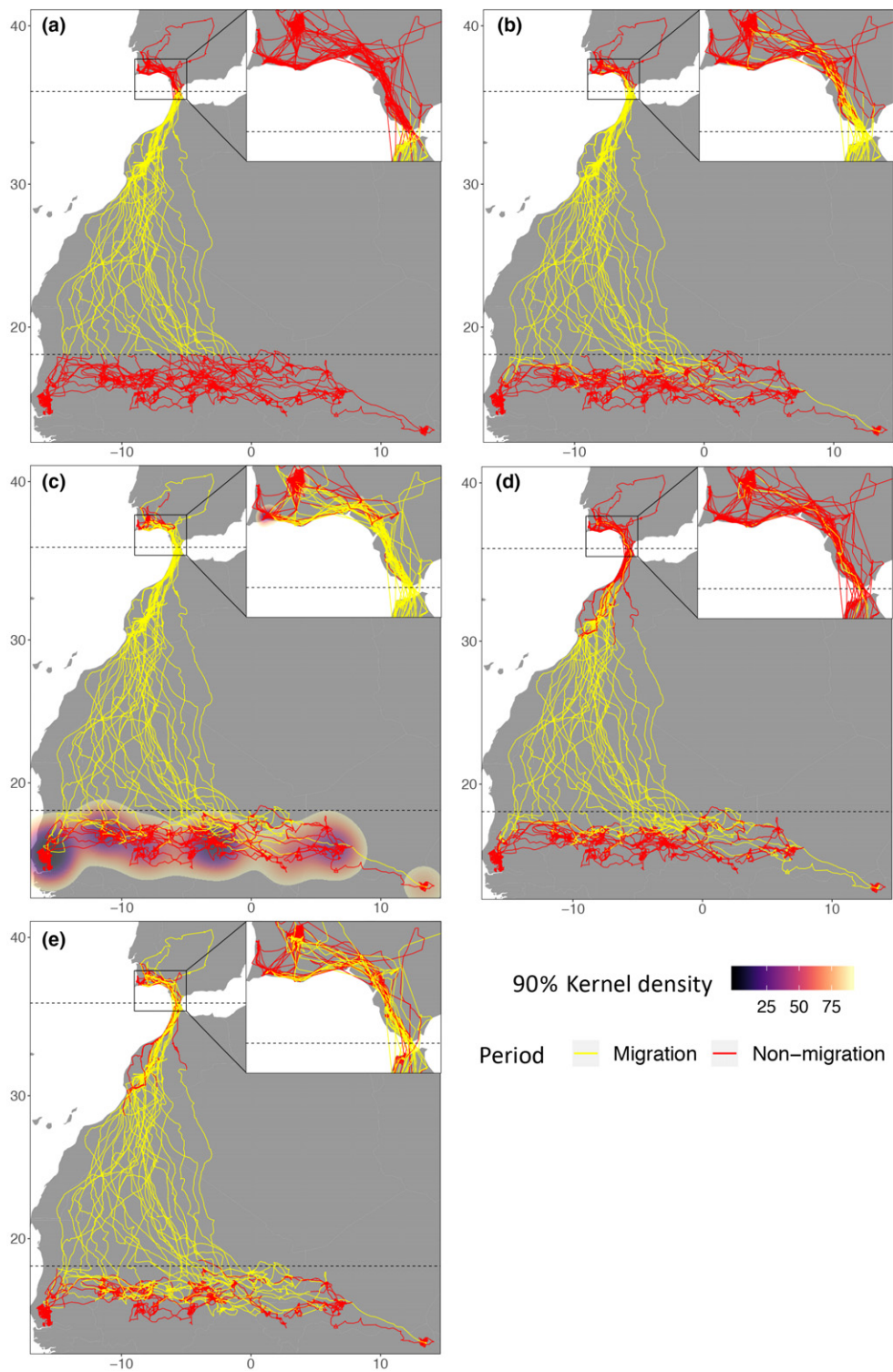
Figure 1. Annual movements of 18 White Storks classified as migratory or non-migratory according to the (a) spatial threshold (S), (b) absolute displacement (AD), (c) spatio-temporal displacement (SD), (d) net squared displacement (NSD) and (e) change point analysis (CPA) methods. Dashed lines represent spatial thresholds (36°N and 18°N) used in the S and AD methods. [Colour figure can be viewed at wileyonlinelibrary.com]
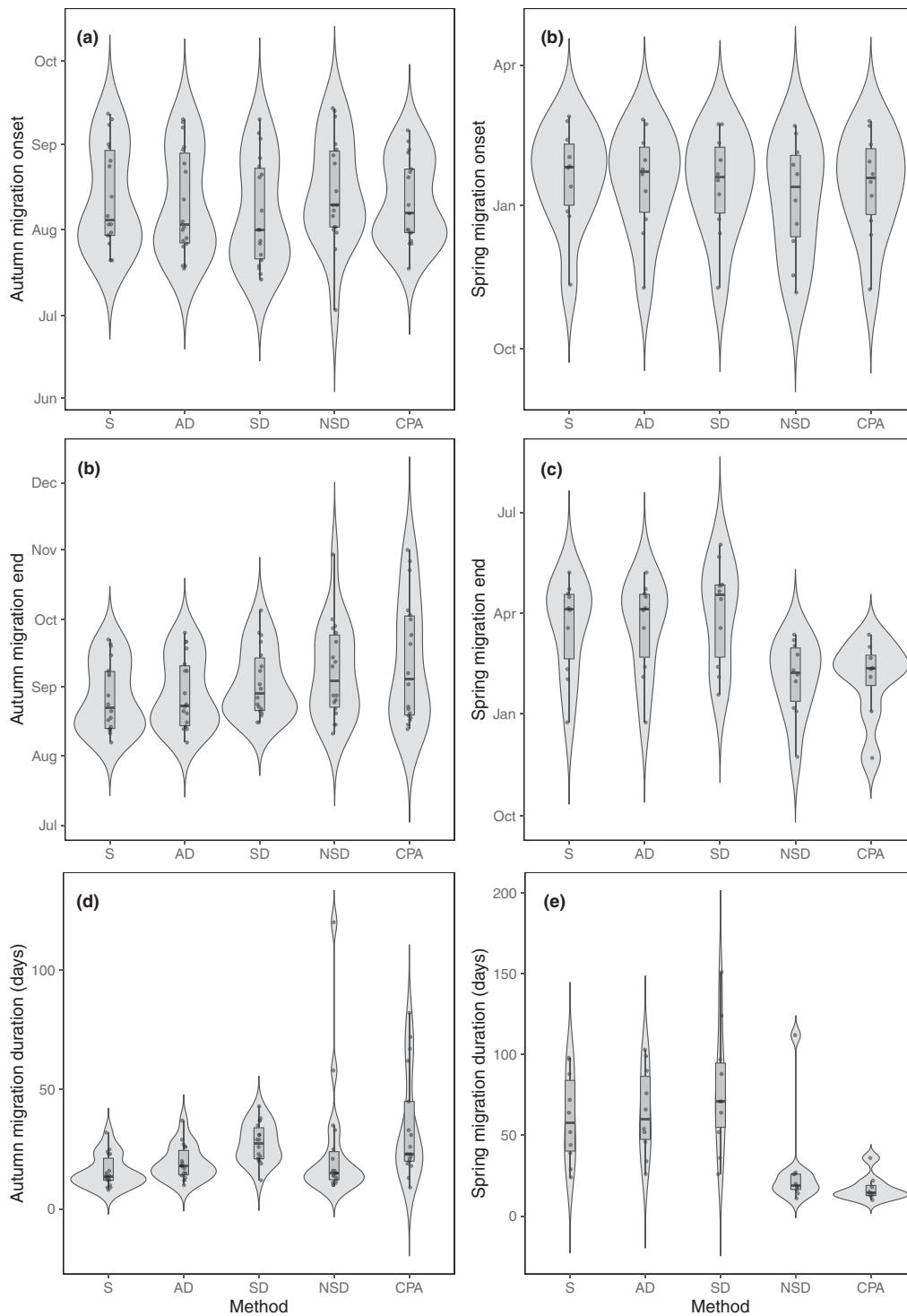
Figure 2. Violin plots of the distribution density of the start of (a) autumn and (b) spring migration; end of (c) autumn and (d) spring migration; and duration in days of (e) autumn and (f) spring migration obtained using different methods. Middle, lower and upper hinges of the boxplot correspond to the median, 25th and 75th percentiles, respectively. Whiskers correspond to the 95% confidence intervals. S, spatial threshold method; AD, absolute displacement method; SD, spatio-temporal displacement method; NSD, net squared displacement method; CPA, change point analysis.
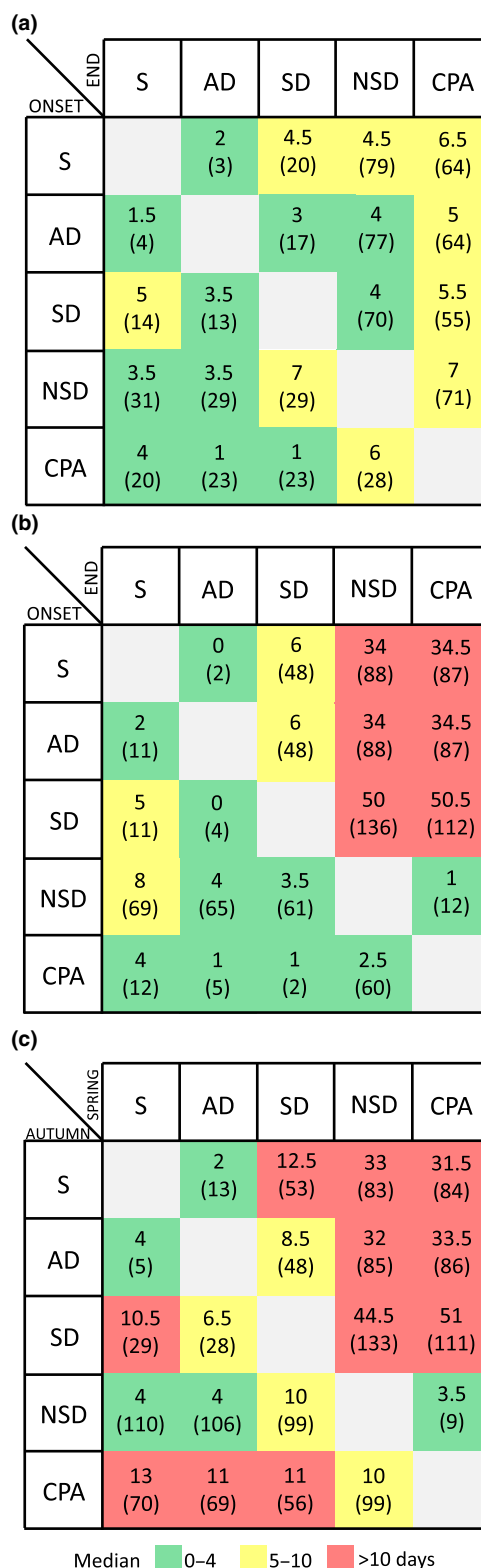
migration of juvenile and adult White Storks tracked from their breeding areas in Portugal to their wintering areas in sub-Saharan Africa and back. Both autumn and spring migration are vulnerable to these differences (Figs 2f and 3b), with up to a 12-fold difference in autumn migration duration depending on the method used, from 10 days using the S method to 120 days using the NSD method (Table S3 of Appendix S7). Our study highlights the need to consider carefully the method used to determine migration phenology based on GPS tracking devices and to assess the sensitivity of the data to the method used.

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

Although we do not advocate a one-size-fits-all approach, our results suggest that the low level of ecological knowledge required by the 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 crossing of the Strait of Gibraltar or spring migrations ending before crossing of the Strait.

The results also show that the S method produced similar estimates 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 in the southernmost areas of their ranges could have their estimated migration period cut short by multiple days.

Figure 3. Median (maximum) difference in number of days of the estimated start and end of (a) autumn and (b) spring migration between methods; and (c) median (maximum) difference in the duration of autumn and spring migrations. S, spatial threshold method; AD, absolute displacement method; SD, spatio-temporal displacement method; NSD, net squared displacement method; CPA, change point analysis. [Colour figure can be viewed at wileyonlinelibrary.com]

(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

Although the AD and SD methods yielded similar results, SD performed better for individuals that had short stops within the breeding or wintering range before the end of migration. Both methods require the establishment of arbitrary thresholds: spatial, displacement and temporal (SD only). Therefore, we suggest (1) a preliminary exploration of the movement data, to estimate the displacement and temporal thresholds during migration; and (2) to use GPS locations obtained during the breeding and wintering periods to perform kernel density estimates that will identify the breeding and wintering area boundaries and reduce the arbitrariness of spatial thresholds adopted.

We recommend that similar studies, comparing the efficacy of these methods in determining the phenology of migration, should be conducted for other bird species. Our results suggest that expert knowledge is needed to determine appropriate spatial, displacement and temporal thresholds. The choice of method used to determine migration phenology can influence the conclusions, especially if parts of the migratory journey are excluded. This is particularly important for studies that examine the start or end of migration at the individual level, or the importance of weather conditions during migration. In this study, some methods would not enable us to account for the crossing of the Mediterranean Sea at the Strait of Gibraltar, an important geographical barrier for White Storks.

In light of the increasing number of species and individuals that have their migratory journeys recorded using GPS data (see Table S1 of Appendix S1 for examples), a certain degree of standardization of the definition of migration, and the method used to estimate it, is required to obtain consistent estimates across studies. To facilitate comparisons between studies, we think that errors associated with estimates of migration phenology should be considered, particularly in interspecific studies that use tracking data from multiple sources. More importantly, we encourage researchers to make data available in data repositories and to report accurately the methods used. We hope this contribution will raise awareness of the challenges associated with the study of migration phenology using GPS tracking data and help researchers find appropriate methods to analyse their data.

DISCLOSURE OF INTERESTS

The authors declare no competing interests.

Data availability statement

Tracking data are stored in Movebank. R code is available in the Supporting information.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. List of methodologies used to estimate migration phenology.

Appendix S2. Spatial threshold method.

Appendix S3. Absolute displacement method.

Appendix S4. Spatio-temporal displacement method.

Appendix S5. Net squared displacement method.

Appendix S6. Change point analysis method.

Appendix S7. Comparison among methods.