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Simpler methods can outperform more sophisticated ones when assessing bird migration starting date

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1 **Simpler methods can outperform more sophisticated ones when assessing bird** 2 **migration starting date**

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9

10 **Abstract**

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20 **Key words**

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22

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33 **Introduction**

34 Understanding the phenology of migration is important for outlining bird movement strategies and for
35 planning effective management and/or conservation actions (Arzel et al. 2006; Runge et al. 2014). The
36 correct identification of the migration starting date (MSD) is crucial, especially to assess the species
37 migratory time budget (Hedenström and Alerstam 1997), to investigate the environmental factors affecting
38 the start of migratory movements (Bauer et al. 2008; Kölzsch et al. 2015; Kelly et al. 2016; Thorup et al.
39 2017), and to make inferences on the response of migrating animals to the changing environment, for
40 instance to assess if they are able to adjust their migratory strategy to the environmental conditions
41 experienced (e.g. Clausen and Clausen 2013; Clausen et al. 2018). Thus, an incorrect evaluation of the
42 seasonal onset of migration could invalidate the successive analyses of migratory phenology leading to a
43 biased estimate of the intra-individual variability in migratory behaviour (Schmaljohann et al. 2018).

44 A proper evaluation of the start of migration coupled with a more in-depth knowledge of bird migratory
45 strategy is also necessary to develop sustainable management of migrants. In particular, hunting regulations
46 of quarry species must be based on accurate scientific data regarding the migratory ecology of the species
47 considered, including the timing of their breeding migration (Arzel et al. 2006; Madsen et al. 2015). This
48 information should be derived not only through bird ringing and counts, as it has been done so far, but also
49 with the help of the more precise information gained from bird tracking.

50 However, estimating the MSD can pose several methodological problems, mostly related to the tracking
51 devices. For instance, small tags often have to be programmed with duty cycles with long off-periods to
52 preserve their battery life (e.g. Chan et al. 2019; Ruthrauff et al. 2019). The discontinuous tracking records
53 obtained in this way only permit an estimation of the MSD, given that the exact departure date is usually not
54 observed. A similar limitation applies to birds using dense vegetation cover during the day (Tedeschi et al.
55 2019) or with a strictly nocturnal activity (English et al. 2017; Norevik et al. 2017), that may prevent the use
56 of rechargeable tags. In addition, the spatial behaviour of tracked birds can affect the identification of MSD,
57 as some species can visit several areas in sequence during the wintering period (Bächler et al. 2010; Lemke
58 et al. 2013); in these cases, distinguishing wintering movements from actual migration may be quite
59 challenging.

60 Previous studies have often relied on subjective criteria to identify MSD. For example, distance thresholds
61 are frequently used to identify the migration starting date (e.g. Arizaga et al. 2014; Giunchi et al. 2019;
62 Tedeschi et al. 2019), assuming that migration starts when a bird moves more than a given distance. Even if
63 this approach is adapted to the studied system, a comparison among studies can be difficult, as threshold
64 choice is somewhat subjective. This limitation leads to several theoretical and practical consequences: for
65 instance, performing meta analytical studies becomes challenging, as well as developing management
66 strategies at continental scales by integrating the results of studies performed on different populations. These
67 problems can be partially overcome by estimating the start of migration using a modelling approach, like
68 fitting models to the Net Square Displacement (e.g. Bunnefeld et al. 2011, see below), but to our knowledge
69 this technique has been rarely adopted in bird migration studies (Orgeret et al. 2019; Soriano-Redondo et al.
70 2020). Another possible way to identify MSD is by segmenting the observed track using methods
71 distinguishing different behavioural states basing on changes in turning angles and speeds (e.g. Gurarie et al.
72 2016; Garriga et al. 2016; Michelot et al. 2016). These techniques however do not apply well to data sets
73 with highly irregular sampling, such as those typically obtained with small tags and/or with Argos telemetry
74 systems.

75 In this paper, we compared four methods to identify the MSD, two based on thresholds and two based on
76 modelling Net Square Displacement (NSD, the straight-line distance between the first location and the
77 subsequent locations of an animal, Turchin 1998). The methods were tested on two species which adopt a

78 completely different migratory strategy: the Eurasian Teal (*Anas crecca*, hereafter teal) that migrates for
79 thousands of kilometers stopping several times along the journey (Giunchi et al. 2019) and the Eurasian
80 Stone-curlew (*Burhinus oedicnemus*, hereafter stone-curlew) that conversely performs a rapid and direct
81 migration towards the final goal rarely stopping along their route (Giunchi et al. 2015). Our aim was to
82 assess whether methods based on modelling NSD provide a significant improvement with respect to
83 threshold methods when applied to different migratory strategies and tracking systems. The outcomes of the
84 present work will be especially beneficial for studies on species difficult to be tracked, such as small
85 passerines or strictly nocturnal birds, that have major tracking problems with low temporal resolution.

86 **Methods**

87 We considered the pre-breeding migration of thirty teal, captured at their wintering sites and tracked using
88 duty-cycled Argos transmitters (model PTT-100, 9.5 g, Microwave Telemetry Inc., Columbia, MD, USA),
89 that produced an irregular tracking record, and of eight stone-curlews, captured at their breeding sites and
90 tracked with GPS loggers (Harrier GPS logger, 16 g, Ecotone, Poland) providing 1 location/hour (Table S1
91 and Fig. S1). Given the different temporal accuracy of the two systems, stone-curlew data were randomly
92 resampled to obtain one location every 12-36 hours on average (median = 26.4; IQR = 24.9 – 28.4; n = 8), so
93 to have a dataset more comparable to the teal, for which a median of 1 location every 32.9 hours (IQR 23.1–
94 53.6, n = 30), was available. Stone-curlew data were not resampled at an even lower rate because we wanted
95 to keep some fixes along the migratory route of each bird, that was completed in a few days. The tracking
96 instruments had a different accuracy in localizing the birds. For Argos transmitters, the location error was
97 higher than 150 m (CLS 2016), while the GPS error was around 25 m as reported by the manufacturers.

98 *Distance threshold method*

99 We used a distance threshold (DT) to distinguish between short movements performed in the wintering area
100 and the actual migratory movements, and this threshold was objectively defined for each species by using a
101 finite mixture modelling approach (McLachlan and Peel 2000). We hypothesized that the distribution of
102 distances between successive fixes collected during the tracking period (see Table S2) was actually a mixture
103 of two distributions, one related to area-restricted movements during the wintering or stopover phases and
104 one deriving from the longer movements during migration.

105 We estimated the density of component distributions by assuming that each component has a completely
106 unspecified density except that it is symmetric around zero. We then used the semiparametric Expectation-
107 Maximization (EM) algorithm for location mixtures of univariate data and symmetric component density
108 (Bordes et al. 2007; Benaglia et al. 2009) using the package “mixtools” (v. 1.1.0; Benaglia et al. 2009) to
109 obtain the maximum likelihood estimation of model parameters. The density distribution of each component
110 was estimated using the Kernel approach setting the bandwidth according to the “Silverman’s rule of thumb”
111 (Silverman 1986). For both species the DT was then identified as the distance (rounded to the nearest
112 kilometer) where the density component related to long-range migratory movements exceeds the density
113 component related to area restricted movements. The resulting DT were 24 km for teal and 23 km for stone-
114 curlews (see Figure S2). Considering the sampling rate of the transmitters, the migration was considered
115 started when birds moved more than the DT in any direction without returning to the wintering site within 2
116 days. Following Arizaga et al. (2014), the MSD was defined as the mean date between the last location in the
117 wintering area and the first location during migration.

118 In teal, we also compared the MSD estimated through the finite mixture model with those obtained using a
119 more subjective method (Giunchi et al. 2019) that returned a threshold of 30 km deriving from the maximum
120 distances travelled between successive locations by the individuals while staying in the wintering site (which
121 in this case corresponded to the capture area).

122 *Distance and heading threshold method*

123 The distance method was implemented by adding a criterion based on the direction followed by the animal
124 (Distance and Heading Threshold method, DHT; Fig. S3).

125 We estimated individual headings as the beeline between two consecutive locations, which for teal were the
126 centroids of the areas where the bird was stationary, for stone-curlews the daily resampled locations. Each
127 heading was compared to the mean direction of the breeding grounds (BGD), estimated for teals as the mean
128 beeline between capture and breeding sites of all tracked individuals (Giunchi et al. 2019) and for stone-
129 curlew as the mean beeline between each fix and the breeding grounds.

130 When the distance between successive locations was $>DT$, we checked if the heading was included in the
131 sector $BGD \pm 60^\circ$. If both filters were passed, we considered the migration started otherwise we iterated the
132 same procedure with the next pair of consecutive areas.

133 We tested both $BGD \pm 45^\circ$ and $BGD \pm 60^\circ$ sector as DHT thresholds but no differences were recorded in the
134 SDM estimated for both species, so we only report the results obtained with $BGD \pm 60^\circ$.

135 *Fitting logistic models to net square displacement*

136 To assess the movement strategy adopted by a given animal, Bunnefeld and colleagues (2011) proposed to fit
137 different models, corresponding to idealized movement strategies, to NSD. Following this approach, we used
138 the R-package “migrateR” (v. 1.0.7; Spitz et al. 2017) to fit a sigmoid function to the NSD data of each
139 tracked bird and we estimated the migration starting date as the time of the first inflection point of the
140 function (Bunnefeld et al. 2011) (NSDlogi method; Fig. S4).

141 *Fitting mixture models to net square displacement*

142 Bastille-Rosseau et al. (2016) used a latent discrete-state model fitted to NSD to identify the type of
143 movement performed. We use the R-package “lsmnsd” (v. 0.0.0.9000; Bastille-Rosseau et al. 2019) to model
144 the NSD data of each individual and estimated the start of migration as the time of the switch between an
145 encamped movement mode and a transitional movement mode (migration; NSDmix method; Fig. S4). The
146 model was run using 3 chains and 250,000 iterations and the Gelman and Rubin criterion was used to assess
147 the convergence of the MCMC output (Gelman et al. 2003). In the 19 cases where convergence was not
148 achieved, we increased the iterations to 500,000, but in six teal and three stone-curlews the model failed to
149 converge.

150 *Comparison among methods*

151 Estimated MSD were compared by fitting Linear Mixed Models (LMM) for each species separately, with
152 MSD as dependent variable and the method used to estimate it as independent variable. The animal ID was
153 included in the model as random factor. Fixed factor significance was tested using the Likelihood Ratio (LR)
154 test. LMM were run using package “lme” (v. 4 1.1-21; Bates et al. 2015). We used the package “multicomp”
155 (v. 1.4-10; Hothorn et al. 2008) to test the pairwise comparisons between the two general approaches
156 (threshold methods vs NSD methods) and within them (DT vs. DHT and NSDlogi vs. NSDmix). Marginal
157 means and 95% confidence intervals (95% CI) were calculated and plotted using the package “ggeffects” (v.
158 0.10.0; Lüdtke 2018).

159 In teal we evaluated the reliability of estimated MSD by calculating the ratio between the time spent in
160 stopover areas and the time spent travelling (St/Tr ratio; Hedenström and Alerstam 1997). We assumed that a
161 correctly estimated MSD would lead to: 1) a relatively homogeneous St/Tr ratios among individuals, given
162 that birds of the same species wintering in the same geographic area are supposed to follow a similar
163 migratory strategy; 2) a St/Tr ratio close to 7:1 or even larger than that, considering that this ratio has been

164 derived for small time-minimizing migrants (Hedenström and Ålerstam 1997; Pennycuik 2008). The St/Tr
165 ratios estimated by the different methods for birds completing spring migration were compared using the
166 overdispersed binomial logit model (Williams 1982) implemented in the package “dispmod” (v 1.2; Scrucca
167 2018). A two-vector response variable (the number of days spent in stopover areas and the number of days
168 spent flying) was used as dependent variable and method as independent variable. The significance of the
169 predictor was tested using the LR test, performing the same comparisons reported above for LMM. Pairwise
170 comparisons of the coefficients of variation of the St/Tr ratios obtained from the four methods were
171 performed by means of the modified signed-likelihood ratio test (Krishnamoorthy and Lee 2014) with 10,000
172 simulations, implemented in the package “cvequality” (v. 0.1.3; Marwick and Krishnamoorthy 2018). To
173 avoid pseudoreplication, we used only one randomly selected datum per individual, and we adjusted the p-
174 values obtained in these comparisons by using the false discovery rate technique (Benjamini and Hochberg
175 1995).

176 All statistical analyses were performed in R 3.5.3 (R Core Team 2019).

177

178 **Results and Discussion**

179 *Comparison between different methods for estimating distance threshold in teal*

180 Migration starting date identified by the finite mixture modelling approach was not significantly different
181 from that obtained with the subjective approach (Giunchi et al. 2019), both considering DT ($\chi^2 = 0.0$, $df = 1$,
182 $p > 0.5$, $SD_{\text{individual}} = 22.2$, $n = 30$) and DHT ($\chi^2 = 0.0$, $df = 1$, $p > 0.5$, $SD_{\text{individual}} = 20.8$, $n = 30$) methods. In
183 the following analyses, we therefore only considered MSD estimated using DT and DHT with thresholds
184 deriving from the more objective and replicable finite mixture modelling approach.

185 *Comparison between distance threshold and net square displacement methods*

186 The MSD estimated from the four methods on teal dataset were significantly different (Fig. 1; Table S2).
187 NSD methods identified significantly later MSD compared to threshold methods ($z = -13.6$, $p < 0.001$), while
188 no significant differences were recorded in the comparisons made within the two groups (NSD methods: $z =$
189 3.7 , $p = 0.3$; DT methods: $z = -2.8$, $p = 0.5$; Table S4, e.g. in Fig. S5). The MSD estimated for stone-curlews
190 were comparable among methods (Fig.1; Table S2). The maximum difference between methods was 12
191 days, but in most cases the differences were equal or less than 1 day. As the stone-curlew data were
192 resampled to make them comparable with teal dataset, it is likely that the contrasting outcomes recorded in
193 the two species were due to the different migratory strategies rather than to differences in temporal accuracy
194 of the tracking methods. Stone-curlew made short (distance travelled: median = 889.8; IQR = 739.4 –
195 1218.9) and fast migratory movements with few stopovers, while teal migrated over relatively long distances
196 (distance travelled: median = 2781.4; IQR: 1791.9 – 3280.2) and showed a large variability in stopover
197 duration, with very long stopovers often occurring at the very beginning of the migratory journey (Giunchi et
198 al. 2019).

199 NSD methods significantly postponed teal MSD, often extending the wintering period till the first long
200 stopover. This estimate seems however unreliable when looking at the time budget of migration, expressed
201 as St/Tr ratio. The coefficient of variation of the St/Tr ratio of threshold methods was significantly lower
202 than that of NSD methods [0.77 ($n = 42$) vs. 1.72 ($n = 37$), MSLRT = 6.73, $p = 0.03$], while we did not
203 record any difference in the comparisons within the two approaches [DT vs. DHT: 0.74 ($n = 21$) vs. 0.82 ($n =$
204 21), MSLRT = 0.09, $p = 0.8$; NSDlogi vs. NSDmix: 1.22 ($n = 21$) vs. 2.00 ($n = 16$), MSLRT = 0.71, $p = 0.6$].
205 This indicates that threshold methods estimate more homogeneous St/Tr ratios among individuals. Moreover,
206 DT and DHT methods estimated significantly higher St/Tr ratios than NSD ones, with the former being

207 closer to the 7:1 ratio expected for a time-minimizing migrant (Hedenström and Alerstam 1997) (Fig. 2). Our
208 data suggest that modelling NSD, while useful for identifying movement strategies on animals belonging to
209 different taxa (e.g. Allen et al. 2016; van Eeden et al. 2017; Orgeret et al. 2019; Stears et al. 2019), can not
210 be reliably used to estimate the timing of migration, especially when dealing with datasets characterized by
211 irregular sampling and high variability of stopover length at the very beginning of the migratory journey. It is
212 worth considering that difference in NSD and DT methods in assessing the migration starting date were
213 sometimes very high (in some cases more than one month), leading to important consequences not only on
214 the evaluation of the bird migratory phenology but also for the sustainable management of species
215 significantly affected by human activities (e.g. quarry species Arzel et al. 2006; Madsen et al. 2015).

216 The use of a distance threshold still represents the best approach for estimating MSD. This approach not only
217 provides more reliable estimates but can also be used when the modelling approach (e.g. NSDmix) fails in
218 providing results (Fig. S5). The method used to determine DT does not have a significant effect on the
219 estimation of migration starting date. Thus, the finite mixture modelling approach proposed in the present
220 study could represent a viable solution to reliably estimate DT while mitigating the subjectivity usually
221 implicitly linked to standard threshold estimations (e.g. Arizaga et al. 2015; Giunchi et al. 2019; Tedeschi et
222 al. 2019). We therefore suggest authors to estimate DT following this objective method which provides
223 repeatable results. In case a subjective method is still preferred, we recommend to describe in detail their
224 selection criteria, possibly including a sensitivity analysis of the effects of using different, threshold values.
225 Among threshold methods, even if we have not observed any significant difference between DT and DHT in
226 MSD estimations and in the St/Tr ratios evaluated in teal, DHT method seems more robust in avoiding some
227 inconsistencies in the determination of the MSD, as it was observed for some teal in our dataset (see
228 examples in Fig. S6).

229 Threshold methods can be used to estimate the MSD for birds with incomplete tracks, e.g. in the teal for
230 which the tracking stopped abruptly before they completed the migration, since the estimate of a threshold is
231 done by considering data belonging to all individuals. This is in contrast with more complex and possibly
232 more accurate approaches (e.g. Gurarie et al. 2016; Michelot et al. 2016) which analyse individual tracks
233 and, thus, are less reliable when tracks are incomplete and/or highly irregular. Furthermore, these methods
234 usually identify the moment when some kind of behavioural change takes place, which may not be
235 necessarily indicative of the start of migration and be rather due to other changes in behaviour (e.g. from
236 roosting to foraging while still in the wintering site). In these cases, the use of a DT method, that is
237 straightforward to adopt, may provide an independent check of the individual modelling approach, even
238 when accurate tracking data are available such as high frequency GPS data (see also Soriano-Redondo et al.
239 2020).

240 In conclusion, our results indicate that relatively simple methods can provide reliable estimates of migration
241 starting dates. Further investigation with different tracking systems, including conventional radiotracking
242 (Taylor et al. 2017), and for more irregular duty-cycle schedules, are needed to assess the possible
243 generalization of our results.

244

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370 <https://doi.org/10.2307/2347977>Figure legends

371 **Figure legends**

372 Fig. 1 Marginal means \pm 95% CI estimated from the model $MSD \sim method + (1/individual)$ (teal: $\chi^2 = 81.36$,
373 $df = 3$, $p < 0.001$, $SD_{individual} = 18.0$, $n = 30$; stone-curlews: $\chi^2 = 0.51$, $df = 3$, $p = 0.9$, $SD_{individual} = 10.6$, $n = 8$).
374 The MSD are expressed as day from 1 January.

375 Fig. 2 Marginal means \pm 95% CI estimated from the model *stopover permanence/total duration of migration*
376 $\sim method$ (Overdispersed binomial logit models: $\chi^2 = 7.94$, $df = 3$, $p = 0.04$, $n = 24$; threshold methods vs.
377 NSD methods: $z = 0.22$, $p = 0.006$; DT vs. DHT: $z = 0.07$, $p = 0.56$; NSDlogi vs. NSDmix: $z = 0.01$, $p =$
378 0.94). The horizontal dashed line corresponds to the St/Tr ratio of 7:1 expected for a time-minimizing
379 migrant, according to (Hedenström and Ålerstam 1997).

Figure 1

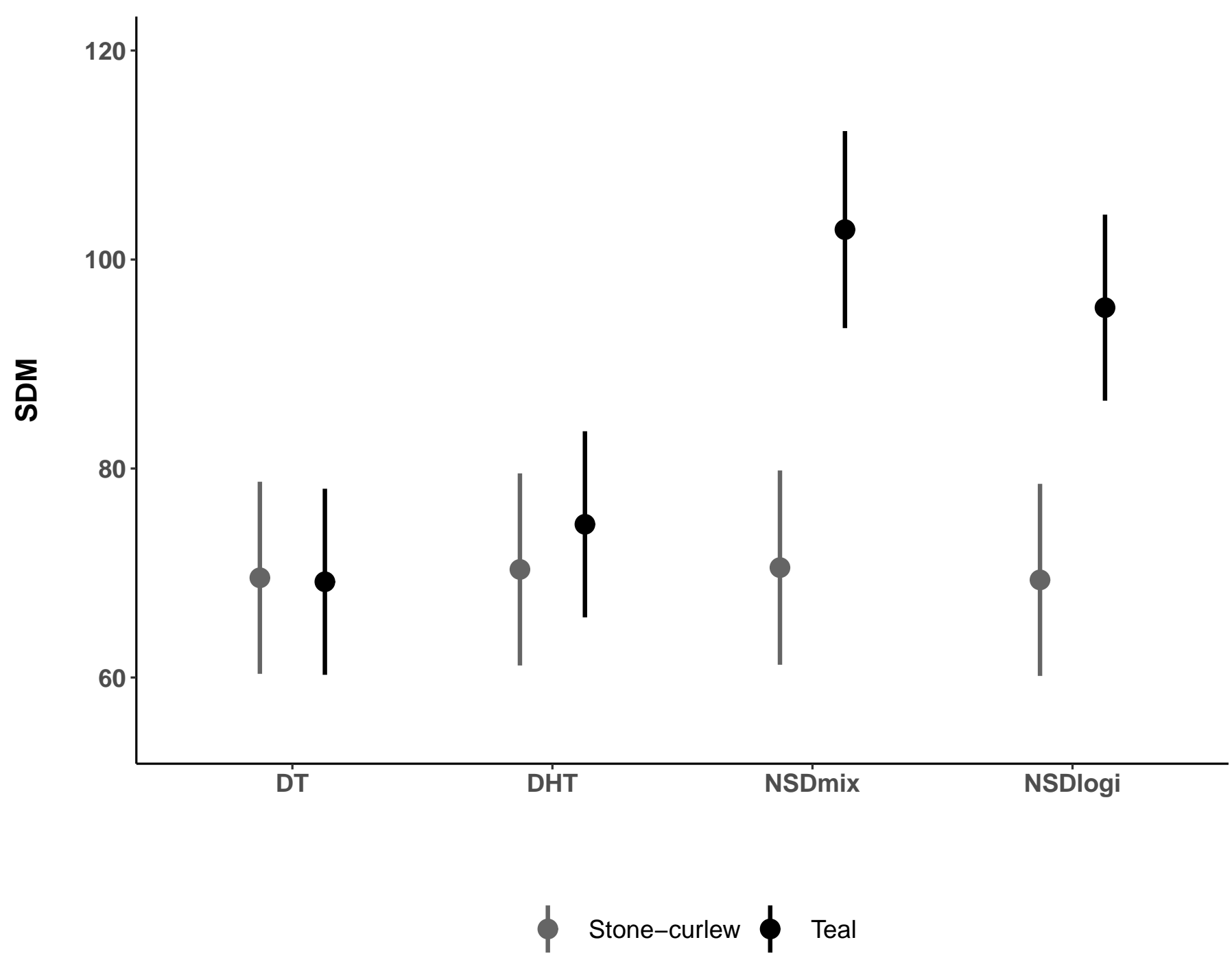


Figure 2

