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5 1 **Emergence of the wrapped Cauchy distribution in**  
6 2 **mixed directional data**

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9 3 **Joseph D. Bailey · Edward A. Codling**

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19 6 **Abstract** Inferring the most appropriate distribution (or distributions) to  
20 7 describe observed directional data is important in many applications of cir-  
21 8 cular statistics. In particular, animal movement paths are typically analysed  
22 9 and modelled by considering the distribution of step lengths and turning (or  
23 10 absolute) angles. Here we demonstrate that a single wrapped Cauchy distri-  
24 11 bution can appear to fit directional data mixed from two different underlying  
25 12 wrapped normal distributions. We derive mathematical expressions to calcu-  
26 13 late the parameter space for which this occurs and illustrate the result by  
27 14 analysing an example data set of the movements of African bull elephants  
28 15 (*Loxodonta Africana*). We conclude that the presence of a wrapped Cauchy  
29 16 distribution in observed directional data can, in certain cases, be explained by  
30 17 data coming from two distinct underlying distributions. We discuss how this  
31 18 may relate to the presence of multiple movement modes within an observed  
32 19 path when analysing animal movement data.  
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37 21 animal movement · directional data

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## 1 Introduction

The analysis and applications of circular statistics to directional data plays a significant role in the study of many environmental processes from plant phenology (Morellato et al (2010)) and tree growth (Aradottir et al (1997)) to wind direction (Masseran et al (2013)) and the general movement patterns of animals and cells (Rivest et al (2016); Landler et al (2018)). Ascertaining the distribution which most closely describes circular data is important as characteristics of circular distributions, such as sharper peaks and slow decaying tails, have significant effects on the qualitative and quantitative results of descriptive and predictive models.

The most common distributions used to describe angular data are the wrapped normal (WN), von Mises (vM) (or circular normal) and the wrapped Cauchy (WC) (Jammalamadaka and SenGupta (2001); Mardia and Jupp (2000); McClintock et al (2012); McClintock and Michelot (2018)). These are defined by a probability density function (PDF) on the unit circle, and in the case of the WN and WC distributions, can be formed by ‘wrapping’ the equivalent one dimensional distributions on the real line around the unit circle (Stephens (1963); Jammalamadaka and SenGupta (2001); Mardia and Jupp (2000); Abe and Shimatani (2018)). Although the von Mises and wrapped normal distributions have differing PDFs, the two approximate each other very closely and produce similar qualitative results (Stephens (1963); Collett and Lewis (1981); Jammalamadaka and SenGupta (2001); Mardia and Jupp (2000); Codling et al (2010)). The WC distribution qualitatively differs from the WN and vM as it has a taller peak around the mean value and heavier tails which decay more slowly. Hence, many analyses classify angular data as being either having a sharp peaks with slow decaying tails (and therefore similar to wrapped Cauchy) or near normal (and thus either a von Mises or wrapped normal).

In particular, when modelling movement by random walk (RW) or step-turn processes it is often necessary to understand the distribution of turning angles and movement directions (Kareiva and Shigesada (1983); Bartumeus et al (2008); Codling et al (2008, 2010); Parton and Blackwell (2017)). Methods to determine the distribution which best describes observed directional data typically involves finding MLE parameters for the model distributions and choosing between them by the use of a likelihood or distance measure (Nilsen et al (2013); Li and Bolker (2017)).

Evidence that a WC distribution is the ‘best-fit’ for the distribution of turning angles or global orientations in a movement path has been found across a wide range of animals from insects and beetles, such as pea aphids *Acyrtosiphon pisum* (Nilsen et al (2013)) and the Baltimore checkerspot butterfly *Euphydryas phaeton* (Brown and Crone (2016)) to larger animals such as common brushtail possums *Trichosurus Vulpecula* (Postlethwaite and Dennis (2013)), cow elk, *Cervus elaphus*, (Morales et al (2004)), free-range cattle *Nothofagus Antarctica* (Seoane (2015)), Florida panthers, *Puma concolor coryi*, (van de Kerk et al (2015); Li and Bolker (2017)), California sea lions *Zalophus californianus* (Breed et al (2012)), Giant tortoises *Testudinidae* (Blake

68 et al (2013)), american lobster *Homarus americanus* (Bowlby et al (2007))  
69 and seals *Erignathus barbatus* and *Monachus schauinslandi* (McClintock et al  
70 (2015)). The studies mentioned above range from high frequency data having  
71 locations given every second to large scale movement with data sent every  
72 24hr.

73 In comparison the WN or vM distribution has been reported across a sim-  
74 ilarly wide range of animals, from *E. coli* bacterium (Taylor-King et al, 2015),  
75 Fender’s blue butterfly *Icaricia icarioides* fender (Schultz and Crone (2001))  
76 and bog fritillary butterfly *Proclossiana Eunomia* (Schtickzelle et al (2007)) to  
77 larger animals such as red-cockaded woodpecker *Picooides borealis* (McKellar  
78 et al (2014)), lesser black-backed gull *L. fuscus* (Taylor-King et al (2015)), king  
79 penguin *Aptenodytes patagonicus* (Pistorius et al (2017)), reindeer *Rangifer*  
80 *tarandus* (Langrock et al (2014)) and southern elephant seal *Mirounga leonine*  
81 (Michelot et al (2017)).

82 A basic search on Google Scholar reveals that whilst both types of distribu-  
83 tion have been frequently used and reported in recent animal movement data  
84 analyses, there has been a marked increase in the prevalence of the WC dis-  
85 tribution over the last 10-15 years. A key word search of “animal movement”  
86 and “wrapped Cauchy” returns only 22 articles published before 2008, com-  
87 pared to the equivalent for either “von Mises” or “wrapped normal” returning  
88 81, a four-fold difference. However, since 2008 this ratio has halved with 200  
89 articles mentioning WC and 398 for WN demonstrating a marked increase in  
90 the prevalence of the WC distribution.

91 One biological interpretation of the presence of a WC distribution is that  
92 the individual mainly travels on a near constant bearing, with the majority of  
93 turns occurring within small deviations from 0 whereas medium to large turns  
94 happen only occasionally but with a similar frequency. This would indicate  
95 the animal has a tendency for sudden large changes in direction of movement,  
96 rather than a gradual change in orientation over a course of a series of larger  
97 turns which would be expected from a normal or Gaussian distribution. Var-  
98 ious RW movement models have shown that observably different qualitative  
99 and quantitative results are produced depending upon whether a WC or vM  
100 distribution has been used (Bartumeus et al (2008); Codling et al (2010)),  
101 demonstrating the importance of accurately determining the underlying dis-  
102 tributions.

103 If the way in which data is collected, analysed or processed can affect how  
104 well a candidate distribution fits the observed data then this needs to be well  
105 understood and acknowledged. For example it has been shown that errors in  
106 GPS data locations can give rise to spurious large 180° turns, which would  
107 enhance the slow decaying tailed nature of recorded turning angles (Jerde and  
108 Visscher (2005); Hurford (2009)). Other reported issues with data collection  
109 which artificially increased the number of large turns include the effect of  
110 recording data in a restricted area, where edge effects can cause sudden large  
111 turns as the animal encounters a wall. Young et al (2013) found that flour  
112 beetles, *Tribolium confusum* took smaller steps with larger turn angles closer to  
113 the border of the experimental setup, which resulted in a distribution with slow

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114 decaying tails. Similar results relating the experimental setup to artificially  
115 enhancing the presence of distributions with slower decaying tails (such as  
116 a WC) has been recorded in other species such as parasitic wasps, *Encarsia*  
117 *formosa* (Drost et al (2000)).

118 When considering movement behaviour it is known that animals can ex-  
119 hibit different movement modes when travelling (Schtickzelle et al (2007); Gu-  
120 rarie et al (2016); Cagnacci et al (2016); Nicosia et al (2017)), perhaps due  
121 to switching from a foraging/exploration phase to an encamped/feeding phase  
122 which can lead to periods of small turns followed by periods of larger turns  
123 (McClintock et al (2015); Torres et al (2017); Nicosia et al (2017)). Similarly,  
124 changes in the terrain or climate could alter the movement behaviour (Pat-  
125 terson et al (2009); Dahmen et al (2017); Pérez-Barbería et al (2015)). The  
126 qualitative behaviour of each movement phase will be best described by a  
127 specific model and set of parameters and if these strategies are not known a  
128 priori the movement data could be analysed under the assumption of a single  
129 movement strategy resulting in the mixing of the data from the individual be-  
130 havioural states. The simplest example of such multiple movement behaviour is  
131 a two state movement model where one phase is described by large variability  
132 in turning angles between steps relating to highly tortuous movement perhaps  
133 indicative of foraging or encamped behaviour, and another phase with more  
134 directed, straighter movement where the deviation in turning angles from the  
135 mean is smaller, akin to purposeful goal based movement or flight behaviour  
136 (Patterson et al (2010); Langrock et al (2012); Jonsen et al (2013); Nams  
137 (2014); Parton and Blackwell (2017); Nicosia et al (2017); McClintock and  
138 Michelot (2018)).

139 Here we demonstrate that a single wrapped Cauchy distribution can appear  
140 to fit directional data mixed from two different underlying wrapped normal  
141 distributions. We derive analytical expressions used to calculate the parame-  
142 ter space for which this occurs. Our results show that, in general, when the  
143 two WN distributions forming the mixed distribution have a large difference  
144 in their respective concentration parameters ( $\geq 0.5$ ) a WC is the best fitting  
145 single distribution, indicating that a mixed distribution can enhance the ap-  
146 pearance of a slow decaying tails in the distribution of turning angles when  
147 interpreted as a single distribution.

## 148 2 Background: Circular Statistics and Distributions

149 A symmetric wrapped stable (SWS) distribution has the density function given  
150 by:

$$151 \quad f_{\text{sws}}(\theta; \rho, \mu) = \frac{1}{2\pi} \left( 1 + 2 \sum_{n=1}^{\infty} \rho^{n^a} \cos n(\theta - \mu) \right), \quad n \in \mathbb{N}, \quad (1)$$

152 where  $\rho \in [0, 1)$  is the concentration parameter,  $\mu \in [-\pi, \pi)$  is the location  
153 parameter around which the distribution is symmetric and  $a \in (0, 2]$ , with  
154  $\theta \in [-\pi, \pi)$ .

In the specific case for  $a = 1$  the SWS distribution returns the WC distribution and for  $a = 2$  we get the WN distribution (Jammalamadaka and SenGupta (2001)).

It is well known that for any given WN distribution a vM can be found as an accurate approximation (Stephens (1963); Collett and Lewis (1981); Jammalamadaka and SenGupta (2001)). Hence, both give qualitatively similar results when used in random walk (RW) models (Codling et al (2010)). Therefore, we consider only a WN distribution as it allows for easier algebraic manipulation.

If we let the SWS be centred around 0 or  $\pm\pi$ , ( $\mu = 0, \pm\pi$ ), then  $\rho^{n^\alpha} = \alpha_n$ , where  $\alpha_n$  is the  $n$ th cosine moment of  $f_{\text{sws}}$ . Note that in this case we need only consider the cosine moments as the sine moments are 0 (Mardia and Jupp (2000); Jammalamadaka and SenGupta (2001)).

## 2.1 Mixed wrapped distributions

One can also consider distributions formed by mixing two circular distributions,  $f_{\text{md}}$ , where random variables are drawn from one of the two distributions according to a certain probability,  $\omega$ . Defined as,

$$f_{\text{md}}(\theta; \omega) = \omega f_1(\theta) + (1 - \omega) f_2(\theta),$$

where  $f_1$  and  $f_2$  are SWS distributions and  $\omega \in [0, 1]$  is defined as the mixing parameter of the two initial distributions. Note that the trivial cases for  $\omega = 0, 1$  are equivalent to  $f_{\text{md}} = f_2$  and  $f_{\text{md}} = f_1$  respectively.

**Lemma 1** *Let  $f_{\text{md}}(\theta; \omega)$  be a distribution formed by mixing two SWS distributions centred around zero ( $\mu = 0$ ), then  $f_{\text{md}}$  itself is a wrapped distribution with cosine moments,  $\alpha_n^{\{\text{md}\}}$ , given by*

$$\alpha_n^{\{\text{md}\}} = \omega \alpha_n^{\{1\}} + (1 - \omega) \alpha_n^{\{2\}},$$

where  $\alpha_n^{\{1\}}$ ,  $\alpha_n^{\{2\}}$  are the  $n$ th cosine trigonometric moments of  $f_1$  and  $f_2$  respectively.

*Proof* Lemma 1 follows directly from the definition of  $f_{\text{md}}$  and  $f_{\text{sws}}$ .

As both  $f_1$  and  $f_2$  are SWS distributions with  $\mu = 0$ , we have

$$\begin{aligned} f_{\text{md}}(\theta) &= \omega \frac{1}{2\pi} \left( 1 + 2 \sum_{n=1}^{\infty} \alpha_n^{\{1\}} \cos(n\theta) \right) + (1 - \omega) \frac{1}{2\pi} \left( 1 + 2 \sum_{n=1}^{\infty} \alpha_n^{\{2\}} \cos(n\theta) \right) \\ &= \frac{1}{2\pi} \left( 1 + 2 \sum_{n=1}^{\infty} \left[ \omega \alpha_n^{\{1\}} + (1 - \omega) \alpha_n^{\{2\}} \right] \cos(n\theta) \right). \end{aligned}$$

This is the form of a general SWS given in (1) centred around 0 with trigonometric moments  $\omega \alpha_n^{\{1\}} + (1 - \omega) \alpha_n^{\{2\}}$  as required. Note, as  $f_{\text{md}}$  is a

184 wrapped distribution, symmetric around  $\mu = 0$  the trigonometric sine mo-  
 185 ments are all 0 and hence the trigonometric moments of  $f_{md}$  are purely the  
 186 cosine moments.

## 187 2.2 Determining between best-fit circular distributions

188 When calculating a measure of the distance between two given PDFs, one can  
 189 consider many statistical measures (Gibbs and Su (2002)). However one of  
 190 the simplest is to consider the sum of the squares of the differences between  
 191 the distributions across their domain; equivalent to finding the  $L^2$ -distance.  
 192 Hence, we will consider the distance,  $d(\cdot, \cdot)$  between two continuous probability  
 193 functions,  $f$  and  $g$ , over the finite domain  $X$  as

$$d(f, g) = \int_{x \in X} [f(x) - g(x)]^2 dx .$$

194 We use the  $L^2$  distance throughout this study as it allows for simple alge-  
 195 braic manipulation, however Online Resource 1 (Figs. S1-S4) detail the results  
 196 of using other metrics, found using simulations and show they are qualitatively  
 197 similar to those found using the  $L^2$  distance (Figure 1). Therefore, when com-  
 198 paring between multiple PDFs we infer the closest fitting distribution as the  
 199 one which minimises,  $d$ , the  $L^2$  distance.

## 200 3 Fitting individual wrapped distributions to a mixed distribution

### 201 3.1 Statement of main claim

202 Here we consider a mixed distribution formed from two WN distributions  
 203 and demonstrate the parameter space for which it is best described by either  
 204 a single WN or single WC distribution. By considering the  $L^2$  distance we  
 205 derive expressions for calculating the best-fitting WN and WC distributions  
 206 as functions of the parameters of the mixed distribution. Subsequently we  
 207 determine the parameter space for whether a WN or WC best describes the  
 208 mixed distribution, by selecting the distribution with the smallest  $L^2$  distance.

209 **Proposition 1** *Let  $f_{md}$  be a mixed wrapped distribution formed by mixing two*  
 210 *wrapped normal distributions, defined as*

$$211 \quad f_{md}(\theta; \mu_0, \rho_1, \rho_2, \omega) = \omega f_{wn}(\theta; \mu_0, \rho_1) + (1 - \omega) f_{wn}(\theta; \mu_0, \rho_2), \quad (2)$$

for  $\theta \in [-\pi, \pi)$ , with  $\mu_0 \in [-\pi, \pi)$ ,  $\rho_1, \rho_2 \in [0, 1)$  and  $\omega \in [0, 1]$ . Define

$$212 \quad \Delta_{wn}(\rho, \mu) = d(f_{wn}(\theta; \rho, \mu), f_{md}(\theta; \mu_0, \rho_1, \rho_2, \omega)),$$

$$213 \quad \Delta_{wc}(\rho, \mu) = d(f_{wc}(\theta; \rho, \mu), f_{md}(\theta; \mu_0, \rho_1, \rho_2, \omega)).$$

214 *Let  $\rho_{wn}, \mu_{wn}$  minimise  $\Delta_{wn}$  and  $\rho_{wc}, \mu_{wc}$  minimise  $\Delta_{wc}$ . Then there always*  
 215 *exists  $\rho_1, \rho_2, \omega$ :*

$$216 \quad \Delta_{wc}(\rho_{wc}, \mu_{wc}) < \Delta_{wn}(\rho_{wn}, \mu_{wn}).$$

As  $\Delta_{\text{wn}}$  and  $\Delta_{\text{wc}}$  give the values of the  $L^2$  distance for each distribution compared to  $f_{\text{md}}$ , the smaller value of  $\Delta_{\text{wn}}$  and  $\Delta_{\text{wc}}$  indicates the closer fitting distribution.

Note, as both distributions forming the mixed distribution,  $f_{\text{md}}$ , are from the same family of distributions (2) without loss of generality we can consider the distribution with concentration parameter  $\rho_1$  to be the distribution which has the smaller probability of being chosen and, therefore, by symmetry we need only consider  $\omega \in [0, 1/2]$ .

We only consider the distributions within the mixed distribution  $f_{\text{md}}$  to be WN rather than WC as the latter leads to the mixed distribution always being classified as a single WC and our main concern is determining when a slowly decaying tailed distribution fits data from distributions with normal type tails (see Online Resource 2 for a complete discussion of this along with the results of having a WC and a WN as the initial mixed distributions). More generalised cases, such as when one distribution is centred at  $\pm\pi$  and having a mixed distribution formed of multiple underlying distributions, are commented upon in the Discussion (sect. 6) as well as in Online Resources 4-5.

To demonstrate this proposition we give an analytical method for calculating the specific parameter values which minimise  $\Delta_{\text{wn}}$  and  $\Delta_{\text{wc}}$  for fixed  $\rho_1, \rho_2, \omega$ . By directly comparing these minimised values we show the parameter space for which the WC distribution (or WN) is the closest fitting distribution when the  $L^2$  distance metric is used.

### 3.2 Demonstration of main claim

First we note that if we assume both underlying WN distributions are centred around the same value, here  $\mu = 0$ , then clearly  $f_{\text{md}}$  is centred around the same value also,  $\mu_{\text{md}} = 0$ , and we must have  $\mu_{\text{wn}} = \mu_{\text{wc}} = \mu_{\text{md}} = 0$  (Mardia and Sutton (1975)).

Using Lemma 1 we can write  $f_{\text{md}}$  from Prop. 1 as

$$f_{\text{md}} = \frac{1}{2\pi} \left( 1 + 2 \sum_{n=1}^{\infty} \alpha_n^{\{\text{md}\}} \cos(n\theta) \right),$$

with

$$\alpha_n^{\{\text{md}\}} = \omega \alpha_n^{\{1\}} + (1 - \omega) \alpha_n^{\{2\}},$$

where  $\alpha_n^{\{1\}}$  and  $\alpha_n^{\{2\}}$  are the  $n$ th cosine moments of the WN distributions with concentration parameters  $\rho_1$  and  $\rho_2$  respectively.

Recalling that  $\alpha_n^{\text{wn}} = \rho_{\text{wn}}^{n^2}$ , we have

$$\alpha_n^{\{\text{md}\}} = \omega \rho_1^{n^2} + (1 - \omega) \rho_2^{n^2}.$$

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245 We now show that when considering the  $L^2$  distance between two zero cen-  
246 tred SWS distributions it suffices to calculate the sum of the squares of the  
247 differences between their respective cosine moments.

248 **Lemma 2** Let  $f_1(\theta)$  and  $f_2(\theta)$  be SWS distributions centred around 0 with  
249 cosine moments  $\alpha_n^{\{1\}}$  and  $\alpha_n^{\{2\}}$  respectively, then

$$d(f_1, f_2) = \frac{1}{\pi} \sum_{n=1}^{\infty} \left( \alpha_n^{\{1\}} - \alpha_n^{\{2\}} \right)^2.$$

250 *Proof* As  $f_1(\theta)$  and  $f_2(\theta)$  are zero-centred SWS distributions, the square of  
251 the difference between the distributions at any given value of  $\theta \in [-\pi, \pi)$  is  
252 given by

$$\begin{aligned} [f_1(\theta) - f_2(\theta)]^2 &= \left[ \frac{1}{2\pi} \left( 1 + 2 \sum_{n=1}^{\infty} \alpha_n^{\{1\}} \cos(n\theta) \right) - \frac{1}{2\pi} \left( 1 + 2 \sum_{n=1}^{\infty} \alpha_n^{\{2\}} \cos(n\theta) \right) \right]^2 \\ &= \left[ \frac{1}{\pi} \sum_{n=1}^{\infty} \left( \alpha_n^{\{1\}} - \alpha_n^{\{2\}} \right) \cos(n\theta) \right]^2, \end{aligned}$$

253 integrating over  $[-\pi, \pi)$  with respect to  $\theta$  gives

$$\int_{-\pi}^{\pi} [f_1(\theta) - f_2(\theta)]^2 d\theta = \int_{-\pi}^{\pi} \left[ \frac{1}{\pi} \sum_{n=1}^{\infty} \left( \alpha_n^{\{1\}} - \alpha_n^{\{2\}} \right) \cos(n\theta) \right]^2 d\theta.$$

254 Expanding the right hand side gives

$$\begin{aligned} &= \frac{1}{\pi^2} \int_{-\pi}^{\pi} \left[ \sum_{n=1}^{\infty} \left( \alpha_n^{\{1\}} - \alpha_n^{\{2\}} \right)^2 \cos^2(n\theta) \right. \\ &\quad \left. + 2 \sum_{i=1}^{\infty} \sum_{j=i+1}^{\infty} \left( \alpha_i^{\{1\}} - \alpha_i^{\{2\}} \right) \left( \alpha_j^{\{1\}} - \alpha_j^{\{2\}} \right) \cos(i\theta) \cos(j\theta) \right] d\theta, \\ &= \frac{1}{\pi^2} \left[ \sum_{n=1}^{\infty} \left( \alpha_n^{\{1\}} - \alpha_n^{\{2\}} \right)^2 \int_{-\pi}^{\pi} \cos^2(n\theta) d\theta \right. \\ &\quad \left. + 2 \sum_{i=1}^{\infty} \sum_{j=i+1}^{\infty} \left( \alpha_i^{\{1\}} - \alpha_i^{\{2\}} \right) \left( \alpha_j^{\{1\}} - \alpha_j^{\{2\}} \right) \int_{-\pi}^{\pi} \cos(i\theta) \cos(j\theta) d\theta \right], \end{aligned}$$

255 noting that the integral in the first term yields  $\pi$  and the integral in the second  
256 gives 0, this expression reduces to



$$\frac{1}{\pi} \sum_{n=1}^{\infty} \left( \alpha_n^{\{1\}} - \alpha_n^{\{2\}} \right)^2.$$

257 For a more complete derivation including the intermediary steps see Online  
258 Resource 3

259 Therefore, we can re-write  $\Delta_{wc}$  and  $\Delta_{wn}$  as

$$\Delta_{wc}(\rho, 0) = \frac{1}{\pi} \sum_{n=1}^{\infty} \left( \alpha_n^{\{wc\}} - \alpha_n^{\{md\}} \right)^2 = \frac{1}{\pi} \sum_{n=1}^{\infty} \left[ \rho^n - \left( \omega \rho_1^{n^2} + (1 - \omega) \rho_2^{n^2} \right) \right]^2, \quad (3)$$

$$\Delta_{wn}(\rho, 0) = \frac{1}{\pi} \sum_{n=1}^{\infty} \left( \alpha_n^{\{wn\}} - \alpha_n^{\{md\}} \right)^2 = \frac{1}{\pi} \sum_{n=1}^{\infty} \left[ \rho^{n^2} - \left( \omega \rho_1^{n^2} + (1 - \omega) \rho_2^{n^2} \right) \right]^2. \quad (4)$$

260 As  $\rho_{wc}$  and  $\rho_{wn}$  are the values which minimise  $\Delta_{wc}$  and  $\Delta_{wn}$  respectively, they  
261 can be found by differentiating (3) & (4) with respect to  $\rho$  and equating for 0.

262 Hence, we require

$$0 = \frac{d}{d\rho} \Delta_{wc} = \frac{1}{\pi} \sum_{n=1}^{\infty} 2n \rho^{n-1} \left[ \rho^n - \left( \omega \rho_1^{n^2} + (1 - \omega) \rho_2^{n^2} \right) \right], \quad (5)$$

$$0 = \frac{d}{d\rho} \Delta_{wn} = \frac{1}{\pi} \sum_{n=1}^{\infty} 2n^2 \rho^{n^2-1} \left[ \rho^{n^2} - \left( \omega \rho_1^{n^2} + (1 - \omega) \rho_2^{n^2} \right) \right]. \quad (6)$$

263 The precise values of  $\rho$  which satisfy (5) & (6) will therefore be the values for  
264  $\rho_{wc}$  and  $\rho_{wn}$  respectively, and can be found via numerical methods. Substitut-  
265 ing  $\rho_{wc}$  and  $\rho_{wn}$  back into the expressions for  $\Delta_{wc}$  and  $\Delta_{wn}$  in (3) & (4) yield  
266 the respective minimum values. We can now determine the parameter space  
267 of  $\rho_1, \rho_2, \omega$  for which a WC distribution is favoured over a WN distribution  
268 when compared to  $f_{md}$  by considering when  $\Delta_{wc}(\rho_{wc}, \mu_{wc}) < \Delta_{wn}(\rho_{wn}, \mu_{wn})$ .  
269 Therefore, calculating

$$D_{\Delta} = \Delta_{wc}(\rho_{wc}, 0) - \Delta_{wn}(\rho_{wn}, 0),$$

270 will give us an indication, not only of which distribution is favoured (negative  
271 in the case of a WC and positive for a WN), but also the relative ‘strength’;  
272 that is the larger the absolute value, the larger the difference in the  $L^2$  distance  
273 between the distributions, and thus the closer the preferred distribution is to  
274 the mixed distribution.

275 %%Figure 1 here%%

## 4 Results

Fig. 1 shows the results of plotting  $D_\Delta$  across the parameter space of  $\rho_1, \rho_2, \omega$  with the areas in yellow (areas bounded by the dashed line) representing combinations for which the WN distribution is considered closer to the mixed distribution  $f_{\text{md}}$  and blue areas showing where a WC is considered closer; the darker the colour the stronger the preference.

In the simplest case where the mixed distribution is formed by mixing the two underlying distributions equally ( $\omega = 0.5$ ; Fig 1K) the plot is symmetric about the lead diagonal (corresponding to  $\rho_1 = \rho_2$ ) as expected, with the WN favoured whenever  $|\rho_1 - \rho_2|$  is small. The areas for which the WC is favoured occur predominantly when the difference between  $\rho_1, \rho_2$  is large ( $|\rho_1 - \rho_2| \geq 0.5$ ). However, in the case when both concentration parameters are greater than 0.5, the area for which a WC is favoured is much smaller occurring now only if  $5\rho_1 - \rho_2 \geq 4$  (or  $5\rho_2 - \rho_1 \geq 4$ ).

In general the plots remain almost unchanged across  $0.35 \leq \omega \leq 0.5$  (Figs 1H-J). In particular, the areas of the plots above the lead diagonal (corresponding to  $\rho_1 > \rho_2$ ) remain remarkably unchanged for  $0.1 \leq \omega \leq 0.5$ . However, as  $\omega \rightarrow 0$  the area favouring the WC (blue) begins to vanish (demonstrated in Fig 1B with  $\omega = 0.05$ ) and disappears entirely when  $\omega = 0$  (Fig 1A) due to the definition of the mixed distribution,  $f_{\text{md}}$  (2) ( $\omega = 0$  is equivalent to  $f_{\text{md}} = f_2$  and since  $f_2$  was chosen to be WN it will never be best classified as WC).

Considering now the areas of the plots below the lead diagonal (corresponding to  $\rho_2 > \rho_1$ ), as  $\omega$  decreases below 0.3 (Fig. 1A-G) the area favouring the WC shrinks and only exists for large values of  $\rho_2$  ( $> 0.8$ ). And for  $\omega \leq 0.15$ , corresponding to distributions where the majority of angles are drawn from the distribution with parameter  $\rho_2$ , the plots indicate that there is no combination of parameters for which the WC will be favoured when  $\rho_2 > \rho_1$  (Figs 1A-C).

## 5 Example: analysis of elephant movement

As an example of data which is well-fitted by a single WC and after a simple analysis appears to be better fitted by a mixed distribution, we use tracking data from bull African elephants *Loxodonta africana* previously published in Wall et al (2014b)). Here, location data were recorded for two elephants, we consider the data for the elephant id: *Habiba* which had locations recorded every 15 minutes for a period of over 4 days giving 1522 data points (data from Movebank data repository; Wall et al (2014a)). Turning angles were found by calculating the difference in bearings for subsequent pairs of locations. Visual inspection of the movement path (Fig. 2A) appears to show segments of high tortuosity where the movement path includes large variations in turning angles, along with periods of more straight-line behaviour with mainly small deviations in direction and fewer larger turns. Simply pooling the turning

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318 angles across the entire path gives the distribution shown in Fig. 2B. Using the  
319 standard practice of best fitting a WN and WC distribution using the packages  
320 in *R* (in this case *CircStats*) reveals that a WN (black dotted,  $\rho_{\text{wn}} = 0.3558$ )  
321 is a poor fit, whereas a WC (black dashed,  $\rho_{\text{wc}} = 0.4385$ ) is a close fit (Fig  
322 2C). If instead, we assume turns are drawn from two distinct distributions,  
323 we can consider the observed data to be a mixed distribution (as in (2)).  
324 Further assuming that the underlying distributions are WN, the best fitting  
325 mixed distribution can be found by simply comparing the density distribution  
326 of the observed data (calculated using the circular package in *R* (R Core  
327 Team (2018)) with all possible mixed distributions formed with parameters  
328  $\rho_1, \rho_2, \omega$  at 0.01 intervals, selecting the specific combination of parameters  
329 which minimises the  $L^2$  distance. In this case we find that the best fitting  
330 mixed distribution is one with  $\rho_1 = 0.20, \rho_2 = 0.91, \omega = 0.71$  (Fig 2D). In  
331 calculating the continuous density curve for the discrete observed data, the  
332 bandwidth used was the automatic selection from *R* as would be the case for  
333 a simple initial analysis, however, fixing this width at other values did not  
334 change the qualitative results.

335 When comparing this mixed distribution with the best fitting WC we see  
336 that both are close matches (Fig 2C & 2D), however, as the visual inspection  
337 of the movement path indicated more than one movement behaviour, then  
338 one could conclude the mixed distribution is the better for describing the  
339 movement as it implies that the turning angles across the elephant's path  
340 came from two distinct distributions. With the value of  $\omega$  indicating that 29%  
341 of angles were drawn from a highly peaked distribution and 71% from a flatter,  
342 more uniform distribution.

343 The possible presence of a mixed distribution could indicate two distinct  
344 movement behaviours over the path, with one behaviour admitting turning  
345 angles drawn from a distribution tightly peaked around 0 and the other be-  
346 haviour with angles taken from a flatter distribution. However, it should be  
347 noted that one cannot use this analysis as a method of predicting such multi-  
348 ple state behaviour, as it provides no information of the movement state any  
349 given part of the path is likely to be in, neither does it provide a 'switching'  
350 parameter which determines the likelihood of switching between states; as is  
351 expected in behavioural state analyses although  $\omega$  acts as a proxy for this  
352 (Johnson et al (2008); Patterson et al (2009); Parton and Blackwell (2017);  
353 McClintock and Michelot (2018)). Similarly, it does not consider any other  
354 covariates or parameters of the movement path typically used in CRW move-  
355 ment models, such as step-length or bout distribution, nor any correlation  
356 between these parameters (i.e. having smaller step lengths when the variation  
357 in turning angle is large and vice-versa). All of which can be considered by the  
358 use of cylindrical distributions (Abe and Ley (2017); Imoto et al (2019)).

359 A method of analysis which does consider switching parameters and other  
360 covariates to predict behavioural states is the *momentuHMM* package in *R*  
361 which was introduced in McClintock and Michelot (2018) and used to analyse  
362 the companion elephant dataset from Wall et al (2014a). The results found by  
363 applying this analysis to these data gives the best-fitting mixed distribution

formed from WN distributions to be one with concentration parameters  $\rho_1 = 0.11$ ,  $\rho_2 = 0.80$  and a mixing parameter of  $\omega = 0.56$  (The package requires using von Mises rather than WN distributions, however, as has been discussed these distributions are known to be similar).

Whilst the results found considering a mixed distribution and those found using the *momentuHMM* package are qualitatively similar, they are not equivalent since the HMM method of McClintock and Michelot (2018) specifically attempts to identify periods of distinct behaviour taking into account various aspects of the movement path, whereas, our results simply looked for the distribution which best described the distribution of turning angles. The observation that the outcomes are similar indicates that this analysis on the distribution of turning angles can give credible results for the underlying distributions of turning angles and identifying the presence of multiple movement behaviours. Also, in the specific case where HMM techniques wish to be used to analyse movement behaviour, using the mixed analysis approach to provide an initial parameter selection for the concentration and switching parameters could be beneficial due to HMMs sensitivity to the set of initial conditions.

%%Figure 2 here%%

## 6 Discussion

Accurately identifying parameters of movement models is clearly crucial when analysing, predicting and understanding animal behaviour. Identifying the most accurate distribution in turning angles is important as differing distributions can result in noticeably different predictive outcomes (Bartumeus et al (2008); Codling et al (2010)). In movement data analyses it is often assumed that angles are drawn from a single underlying distribution, here we have demonstrated the parameter space for when a mixed distribution can be best described by a single distribution with either a normal type, WN, or a sharply peaked and slowly decaying tailed distribution, WC; two distributions commonly associated with the analysis of directional movement.

Our results indicate that a mixed distribution formed from two WN distributions will, in general, be best fitted by a WC distribution when the difference between the concentration parameters of the underlying initial WN distributions is large ( $|\rho_1 - \rho_2| \geq 0.5$ ). This has been reported when analysing and classifying animal movement behaviour into two movement states, such as “foraging” and “exploratory” (Langrock et al (2014); Nicosia et al (2017); McClintock and Michelot (2018)) The characteristic distributions found in such movement include a flat almost uniform distribution attributed to the “foraging” stage, and would be equivalent to a low concentration parameter in a SWS distribution, along with another much more peaked distribution for the “exploratory” phase, given by a distribution with a concentration parameter close to 1. Evidence of such results after model fitting have been observed in a range of animals including American lobster, *Homarus americanus*, (Bowlby et al (2007)), African elephants (McClintock and Michelot

(2018)), Cataglyphis desert ants (Dahmen et al (2017)), caribou (Nicosia et al (2017)) and elk, *C. elaphus*, (Parton and Blackwell (2017)). Specifically, Langrock et al (2014), found that reindeer in a 2 state model exhibited angular distributions described by a von Mises distribution with  $\kappa = 0.246$  (approximately equivalent to a WN with  $\rho = 0.1218$ ) for the “foraging” behaviour and  $\kappa = 3.517$  (approximately equivalent to a WN with  $\rho = 0.8389$ ) for the “exploratory” behaviour.

Here we assumed that the mixed distribution was formed from underlying distributions both centred at 0, however, it has been observed that the underlying distributions may be centred at 0 and  $\pm\pi$ . This has been found in the movement of female wolves (Mastrantonio et al (2019)), muskox (Pohle et al (2017)), American bison (Langrock et al (2012)) and elk (Patterson et al (2016)). It can be shown that, similar to the the results found here, both the WN and WC distribution are the single favoured distribution in certain cases (see Online Resource 4). However, in general, detection of such mixed behaviour is more readily observable as the resulting mixed distribution would appear bimodal, with a peak (usually higher) at 0 and another (generally lower) at  $\pm\pi$ . This bimodal behaviour would be the indicator that a mixed distribution, rather than one single distribution, should be considered. In contrast, when both distributions are centred at the same value, determining the presence of multiple underlying distributions is not usually clear. Similarly, the case for when one of the underlying distributions is centred at a point other than 0 or  $\pm\pi$ , would be expected to demonstrate bimodal behaviour. This case is not considered here and as in terms of animal movement it would imply an animal had a preference for consistent turning regardless of the direction faced, giving a helical movement path. However, this is not uncommon, and has been observed in movement data including; sunfish (Drucker and Lauder (2001)), thrushes (Da Silveira et al (2016)), elk (Fryxell et al (2008)) and wolves (Mastrantonio et al (2019)).

That this relatively straight forward approach of analysing movement data revealed results consistent with those using more complex methods is interesting as it relies solely on the angular data. However, as it gives no information as to which distribution any particular part of the movement path belongs, it cannot be used as an indicator of states of behaviour. Discovering when a period of movement comes from a particular state with prescribed model and parameter set is an active area of research, and as such there has been much work on behavioural change point analysis (BCPA) utilising a range of methods from hidden Markov models (HMMs) (Michelot et al (2016); Jonsen (2016); McClintock and Michelot (2018)), Markov chain Monte Carlo processes (McClintock et al (2012); Parton and Blackwell (2017)) and switching Markov models (Nicosia et al (2017)), to wavelet analysis (Polansky et al (2010)) and time series CUSUM techniques (Knell and Codling (2012)) (see Gurarie et al (2016), for a more complete list). Currently the analysis described here may be used to predict the values of the initial distributions required in HMM techniques (Michelot et al (2016); Jonsen (2016); McClintock and Michelot (2018)), but could also be extended to predict breaks in behaviour by includ-

ing additional ‘smoothing’ techniques in order to ascertain when a change from using one distribution to another has occurred, most likely utilising a time-series break point analysis such as that used in Knell and Codling (2012). For this to be the case, many improvements would be needed in the method for finding the  $\rho_1, \rho_2, \omega$  parameters, for example a more efficient search algorithm, (for example, the Nelder-Mead algorithm (Nelder and Mead (1965))) could be used rather than the slow parameter sweep used in section 5.

These results indicate that when techniques such as HMMs (Michelot et al (2016); McClintock and Michelot (2018)), switching Markov models (Nicosia et al (2017)) or state-space models (Patterson et al (2010)) are used to ascertain the number of movement states from telemetry data, it would be necessary to include more states when the assumed distributions for angular data are of normal-type (WN or vM) compared to using WC distributions. In such a case the resulting best-fitting model will be easier to interpret, with each single distribution more likely to describe a single movement behaviour. For example Pohle et al (2017) determined that, when considering von Mises distributions, 5 states gave the most parsimonious model in the analysis of muskox movement. Had a wrapped Cauchy been used instead of a von Mises, this work indicates that the expected number of states would have been lower, as the WC distribution can better capture distributions with slower decaying tails or bimodal behaviour.

Although only 2 distributions were considered in forming the mixed distribution here, the results generalise when including multiple underlying distributions (Online Resource 5). There are many other potential avenues for enhancing and extending the work shown here, for example, this method could be extended to mixing more than two normal distributions by simply including more  $\rho_i$  and mixing ratio terms in the summation for the mixed distribution and editing the subsequent calculations appropriately. However, interpreting the results obviously increases in difficulty due to the increasing dimension of the required parameter space. It should be noted that Jammalamadaka and Kozubowski (2017) have shown that a WC distribution can in fact be recovered precisely when one considers mixing an infinite number of WN distributions and therefore taking the mixture distribution as a continuous function across all possible concentration parameter values in  $[0, 1]$  for the initial WN distributions.

Whilst we chose to focus on two particular distributions, other wrapped distributions such as wrapped Gompertz and the wrapped exponential have also been used to describe animal movement (Roy and Adnan (2012); Ravindran and Ghosh (2011)) and could be included in a more complete analysis. Similarly, other distributions on the unit circle such as the Jones-Pewsey (Jones and Pewsey (2005)), Kato-Jones (Kato et al (2013)) and wrapped  $t$  (Pewsey et al (2007)) could have been considered, as could cylindrical distributions (see Abe and Shimatani (2018) for a discussion of common cylindrical distributions). However, these are all multi-parameter distributions and as such can prove computationally harder to fit to actual data. Since our main aim here is to illustrate a possible mechanism for how distributions, such as the wrapped

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2 499 Cauchy, may emerge in observed directional data, a full and complete  
3 500 classification of mixed circular distributions along with their combinations, is  
4 501 beyond the scope of this work. Instead, this work highlights the importance  
5 502 the choice between the most common distributions used in directional data,  
6 503 can have to practitioners.

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## 1 **Figure Legends**

2 **Figure 1:** Plots demonstrating the parameter space for where a single WC or WN is the  
3 favoured distribution for  $\rho_1, \rho_2 \in [0,1]$  calculated at 0.001 intervals with the mixing ratio  $\omega \in$   
4  $[0,0.5]$  at 0.05 intervals (due to symmetry the results for  $\omega > 0.5$  are not displayed). Areas in  
5 blue (dark grey – printed version) indicate parameter combinations for which the WC was  
6 favoured whereas areas in yellow (light grey – printed version) show combinations for which  
7 the WN was favoured. The dashed black line indicates where the transition from preferred  
8 distribution occurs.

9 **Figure 2:** Movement data analysis of African elephant (ID: *Habiba*) from Wall et al (2014a).  
10 (A) shows the recorded movement path; (B) the corresponding turning angle distribution  
11 (grey); (C) the best fitting WC distribution (black-dashed;  $\rho_{wc} = 0.4385$ ) and best fitting WN  
12 (black dotted;  $\rho_{wn} = 0.3558$ ); (D) the best fitting mixed distribution (black – dashed and  
13 dotted) determined by numerical simulations with parameters  $\rho_1 = 0.20, \rho_2 = 0.91, \omega =$   
14  $0.71$ . Thin black dashed line corresponds to a WN with concentration parameter  $\rho_1$  and the  
15 black thin dotted line corresponds to a WN with concentration parameter  $\rho_2$ .

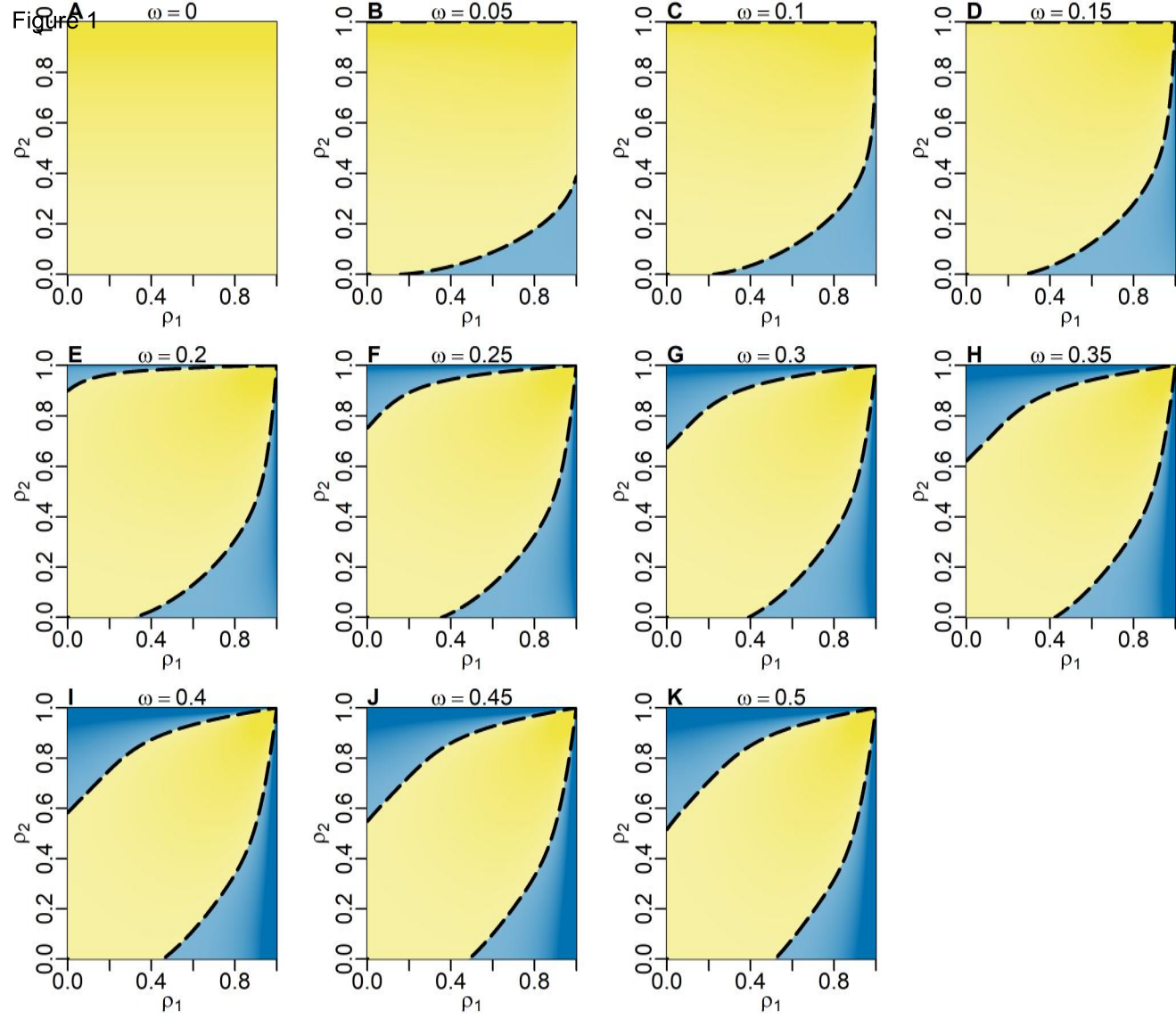


Figure 2

### Elephant Movement

