CHAPTER 11

Speed and change of direction in larvae of *Drosophila melanogaster*

11.1 Introduction

Holzmann *et al.* (2006) have described, *inter alia*, the application of HMMs with circular state-dependent distributions to the movement of larvae of the fruit fly *Drosophila melanogaster*. It is thought that locomotion can be largely summarized by the distribution of speed and direction change in each of two episodic states: 'forward peristalsis' (linear movement) and 'head swinging and turning' (Suster *et al.*, 2003). During linear movement, larvae maintain a high speed and a low direction change, in contrast to the low speed and high direction change characteristic of turning episodes. Given that the larvae apparently alternate thus between two states, an HMM in which both speed and turning rate are modelled according to two underlying states might be appropriate for describing the pattern of larval locomotion. As illustration we shall examine the movements of two of the experimental subjects of Suster (2000) (one wild larva, one mutant) whose positions were recorded once per second. The paths taken by the larvae are displayed in Figure 11.1.

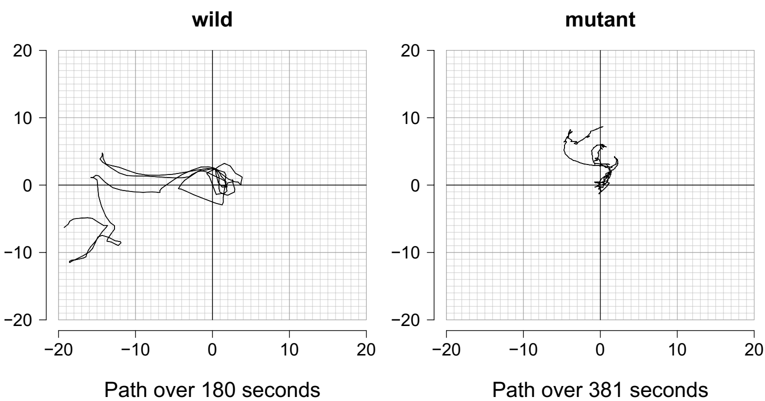

Figure 11.1 *Paths of two larvae of* Drosophila melanogaster.

First we examine the univariate time series of direction changes for the two larvae; then in Section 11.5 we shall examine the bivariate series of speeds and direction changes.

11.2 Von Mises distributions

We need to discuss here an important family of distributions designed for circular data, the von Mises distributions, which have properties that make them in some respects a natural first choice as a model for unimodal continuous observations on the circle; see e.g. Fisher (1993, pp. 49–50, 55). The probability density function of the von Mises distribution with parameters $\mu \in (-\pi, \pi]$ (location) and $\kappa > 0$ (concentration) is

$$f(x) = (2\pi I_0(\kappa))^{-1} \exp(\kappa \cos(x - \mu)) \quad \text{for } x \in (-\pi, \pi]. \tag{11.1}$$

Here I_0 denotes the modified Bessel function of the first kind of order zero. More generally, for integer n, I_n is given in integral form by

$$I_n(\kappa) \quad = \quad (2\pi)^{-1} \int_{-\pi}^{\pi} \exp(\kappa \cos x) \cos(nx)\, \mathrm{d}x; \tag{11.2}$$

see e.g. Equation (9.6.19) of Abramowitz *et al.* (1984). But note that one could in the p.d.f. (11.1) replace the interval $(-\pi, \pi]$ by $[0, 2\pi)$, or by any other interval of length 2π.

The location parameter μ is not in the usual sense the mean of a random variable X having the above density; instead (see Exercise 3) it satisfies

$$\tan \mu = \mathrm{E}(\sin X)/\mathrm{E}(\cos X),$$

and can be described as a directional mean, or circular mean. We use the convention that $\arctan(b, a)$ is the angle $\theta \in (-\pi, \pi]$ such that $\tan \theta = b/a$, $\sin \theta$ and b have the same sign, and $\cos \theta$ and a have the same sign. (But note that if $b = a = 0$, $\arctan(b, a)$ is not defined.) With this convention, $\mu = \arctan(\mathrm{E} \sin X, \mathrm{E} \cos X)$, and indeed this is the definition we use for the directional mean of any circular random variable X, not only one having a von Mises distribution. The sample equivalent of μ, based on the sample x_1, x_2, $\ldots$, x_T, is $\hat{\mu} = \arctan(\sum_t \sin x_t, \sum_t \cos x_t)$.

In modelling time series of directional data one can consider using an HMM with von Mises distributions as the state-dependent distributions, although any other circular distribution is also possible. For several other classes of models for time series of directional data, based on ARMA processes, see Fisher and Lee (1994).

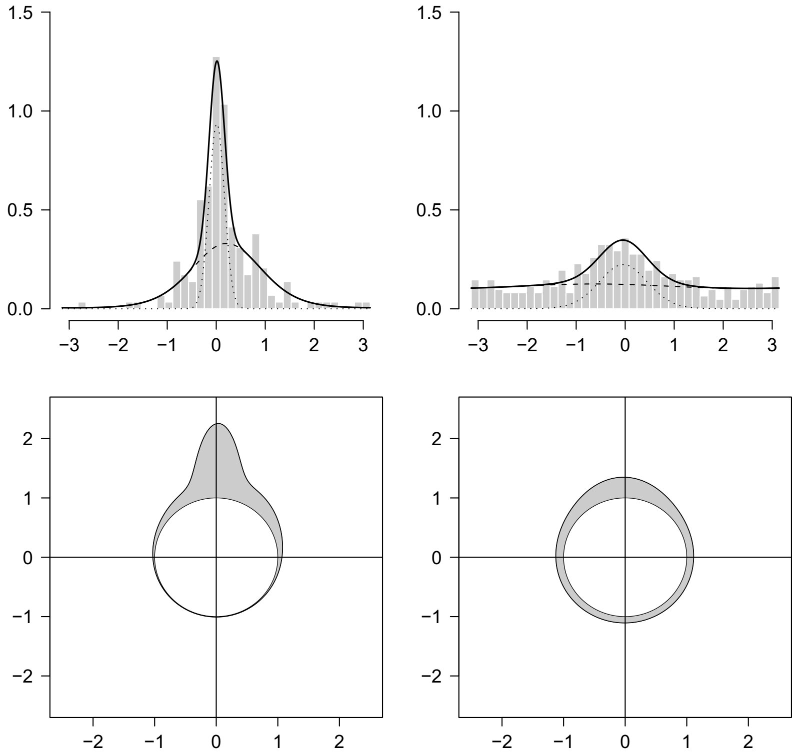

Figure 11.2 *Marginal density plots for two-state von Mises–HMMs for direction change in* Drosophila melanogaster*: wild subject (left) and mutant (right). In the plots in the first row angles are measured in radians, and the state-dependent densities, multiplied by their mixing probabilities* δ_i*, are indicated by dashed and dotted lines. In the circular density plots in the second row, North corresponds to a zero angle, right to positive angles, left to negative.*

11.3 Von Mises–HMMs for the two subjects

Here we present a two-state von Mises–HMM for the series of changes of direction for each of the subjects, and we compare those models, on the basis of likelihood, AIC and BIC, with the corresponding three-state models which we have also fitted. Table 11.1 presents the relevant comparison. For the wild subject, both AIC and BIC suggest that the two-state model is adequate, but they disagree in the case of the mutant; BIC selects the two-state and AIC the three-state.

The models are displayed in Table 11.2, with μ_i, for instance, denoting

Table 11.1 *Comparison of two- and three-state von Mises–HMMs for changes of direction in two* Drosophila melanogaster *larvae.*

subject	no. states	no. parameters	$-\log L$	AIC	BIC
wild	2	6	158.7714	**329.5**	**348.7**
	3	12	154.4771	333.0	371.3
mutant	2	6	647.6613	1307.3	**1331.0**
	3	12	638.6084	**1301.2**	1348.5

Table 11.2 *Two-state von Mises–HMMs for the changes of direction in two* Drosophila melanogaster *larvae.*

	wild, state 1	wild, state 2	mutant, state 1	mutant, state 2
μ_i	0.211	0.012	−0.613	−0.040
κ_i	2.050	40.704	0.099	4.220
$\mathbf{\Gamma}$	$\begin{pmatrix} 0.785 & 0.215 \\ 0.368 & 0.632 \end{pmatrix}$		$\begin{pmatrix} 0.907 & 0.093 \\ 0.237 & 0.763 \end{pmatrix}$	
δ_i	0.632	0.368	0.717	0.283

the location parameter in state i, and the marginal densities are depicted in Figure 11.2. Clearly there are marked differences between the two subjects, for instance the fact that one of the states of the wild subject, that with mean close to zero, has a very high concentration.

11.4 Circular autocorrelation functions

As a diagnostic check of the fitted two-state models one can compare the autocorrelation functions of the model with the sample autocorrelations. In doing so, however, one must take into account the circular nature of the observations.

There are (at least) two proposed measures of correlation of circular observations: one due to Fisher and Lee (1983), and another due to Jammalamadaka and Sarma (1988), which we concentrate on. Using the latter one can find the ACF of a fitted von Mises–HMM and compare it with its empirical equivalent, and we have done so for the direction change series of the two subjects. It turns out that there is little or no serial correlation in these series of angles, but there is non-negligible ordinary autocorrelation in the series of absolute values of the direction changes.

The measure of circular correlation proposed by Jammalamadaka and Sarma is as follows (see Jammalamadaka and SenGupta, 2001, (8.2.2), p. 176). For two (circular) random variables Θ and Φ, the circular correlation is defined as

$$\frac{\mathrm{E}(\sin(\Theta-\mu_\theta)\sin(\Phi-\mu_\phi))}{[\mathrm{Var}\sin(\Theta-\mu_\theta)\,\mathrm{Var}\sin(\Phi-\mu_\phi)]^{1/2}},$$

where μ_θ is the directional mean of Θ, and similarly μ_ϕ that of Φ. Equivalently, it is

$$\frac{\mathrm{E}(\sin(\Theta-\mu_\theta)\sin(\Phi-\mu_\phi))}{[\mathrm{E}\sin^2(\Theta-\mu_\theta)\,\mathrm{E}\sin^2(\Phi-\mu_\phi)]^{1/2}};$$

see Exercise 1 for justification.

The autocorrelation function of a (stationary) directional series X_t is then defined by

$$\rho(k)=\frac{\mathrm{E}(\sin(X_t-\mu)\sin(X_{t+k}-\mu))}{[\mathrm{E}\sin^2(X_t-\mu)\,\mathrm{E}\sin^2(X_{t+k}-\mu)]^{1/2}};$$

this simplifies to

$$\rho(k)=\frac{\mathrm{E}(\sin(X_t-\mu)\sin(X_{t+k}-\mu))}{\mathrm{E}\sin^2(X_t-\mu)}. \tag{11.3}$$

Here μ denotes the directional mean of X_t (and X_{t+k}), that is

$$\mu=\arctan(\mathrm{E}\sin X_t,\mathrm{E}\cos X_t).$$

An estimator of the ACF is given by

$$\sum_{t=1}^{T-k}\sin(x_t-\hat\mu)\sin(x_{t+k}-\hat\mu)\Big/\sum_{t=1}^{T}\sin^2(x_t-\hat\mu),$$

with $\hat\mu$ denoting the sample directional mean of all T observations x_t.

With some work it is also possible to to use Equation (11.3) to compute the ACF of a von Mises–HMM as follows. Firstly, note that, by Equation (2.10), the numerator of (11.3) is

$$\sum_{i=1}^{m}\sum_{j=1}^{m}\delta_i\gamma_{ij}(k)\mathrm{E}(\sin(X_t-\mu)\mid C_t=i)\mathrm{E}(\sin(X_{t+k}-\mu)\mid C_{t+k}=j), \tag{11.4}$$

and that, if $C_t=i$, the observation X_t has a von Mises distribution with parameters μ_i and κ_i. To find the conditional expectation of $\sin(X_t-\mu)$ given $C_t=i$ it is therefore convenient to write

$$\begin{aligned}\sin(X_t-\mu) &= \sin(X_t-\mu_i+\mu_i-\mu)\\ &= \sin(X_t-\mu_i)\cos(\mu_i-\mu)+\cos(X_t-\mu_i)\sin(\mu_i-\mu).\end{aligned}$$

The conditional expectation of $\cos(X_t-\mu_i)$ is $I_1(\kappa_i)/I_0(\kappa_i)$, and that of $\sin(X_t - \mu_i)$ is zero; see Exercise 2. The conditional expectation of $\sin(X_t - \mu)$ given $C_t = i$ is therefore available, and similarly that of $\sin(X_{t+k} - \mu)$ given $C_{t+k} = j$. Hence expression (11.4), i.e. the numerator of (11.3), can be computed once one has μ.

Secondly, note that, by Exercise 4, the denominator of (11.3) is

$$\mathrm{E}\sin^2(X_t - \mu) = \frac{1}{2}\Big(1 - \sum_i \delta_i A_2(\kappa_i)\cos(2(\mu_i - \mu))\Big),$$

where, for positive integers n, $A_n(\kappa)$ is defined by $A_n(\kappa) = I_n(\kappa)/I_0(\kappa)$.

All that now remains is to indicate how to compute μ for such a von Mises–HMM. This is given by

$$\mu = \arctan\left(\mathrm{E}\sin X_t, \mathrm{E}\cos X_t\right) = \arctan\left(\sum_i \delta_i \sin\mu_i, \sum_i \delta_i \cos\mu_i\right).$$

The ACF, $\rho(k)$, can therefore be found as follows:

$$\rho(k) = \frac{\sum_i \sum_j \delta_i \gamma_{ij}(k) A_1(\kappa_i)\sin(\mu_i - \mu) A_1(\kappa_j)\sin(\mu_j - \mu)}{\frac{1}{2}(1 - \sum_i \delta_i A_2(\kappa_i)\cos(2(\mu_i - \mu)))}.$$

As a function of k, this is of the usual form taken by the ACF of an HMM; provided the eigenvalues of $\mathbf{\Gamma}$ are distinct, it is a linear combination of the k th powers of these eigenvalues.

Earlier Fisher and Lee (1983) proposed a slightly different correlation coefficient between two circular random variables. This definition can also be used to provide a corresponding (theoretical) ACF for a circular time series, for which an estimator is provided by Fisher and Lee (1994), Equation (3.1). For details, see Exercises 5 and 6.

We have computed the Jammalamadaka–Sarma circular ACFs of the two series of direction changes, and found little or no autocorrelation. Furthermore, for series of the length we are considering here, and circular autocorrelations (by whichever definition) that are small or very small, the two estimators of circular autocorrelation appear to be highly variable.

An autocorrelation that does appear to be informative, however, is the (ordinary) ACF of the *absolute values* of the series of direction changes; see Figure 11.3. Although there is little or no circular autocorrelation in each series of direction changes, there is non-negligible ordinary autocorrelation in the series of absolute values of the direction changes, especially in the case of the mutant. This is rather similar to the 'stylized fact' of share return series that the ACF of returns is negligible, but not the ACF of absolute or squared returns. We can therefore not conclude that the direction changes are (serially) independent.

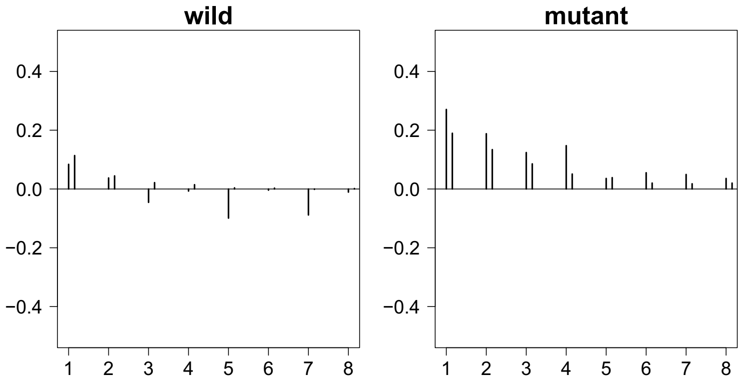

Figure 11.3 *ACFs of absolute values of direction changes. In each pair of ACF values displayed, the left one is the (ordinary) autocorrelation of the absolute changes of direction of the* sample, *and the right one is the corresponding quantity based on 50 000 observations generated from the two-state* model.

11.5 A bivariate series with one component linear and one circular: *Drosophila* speed and change of direction

We begin our analysis of the bivariate time series of speed and change of direction (c.o.d.) for *Drosophila* by examining a scatter plot of these quantities for each of the two subjects (top half of Figure 11.4). A smooth of these points is roughly horizontal, but the funnel shape of the plot in each case is conspicuous. We therefore plot also the speeds and absolute changes of direction, and we find, as one might expect from the funnel shape, that a smooth now has a clear downward slope.

We have also plotted in each of these figures a smooth of 10 000 points generated from the three-state model we describe later in this section. In only one of the four plots do the two lines differ appreciably, that of speed and absolute c.o.d. for the wild subject (lower left); there the line based on the model is the higher one. We defer further comment on the models to later in this section.

The structure of the HMMs fitted to this bivariate series is as follows. Conditional on the underlying state, the speed at time t and the change of direction at time t are assumed to be independent, with the former having a gamma distribution and the latter a von Mises distribution. In the three-state model there are in all 18 parameters to be estimated: six transition probabilities, two parameters for each of the three gamma distributions, and two parameters for each of the three von Mises distributions; more generally, $m^2 + 3m$ for an m-state model of this kind.

These and other models for the *Drosophila* data were fairly difficult

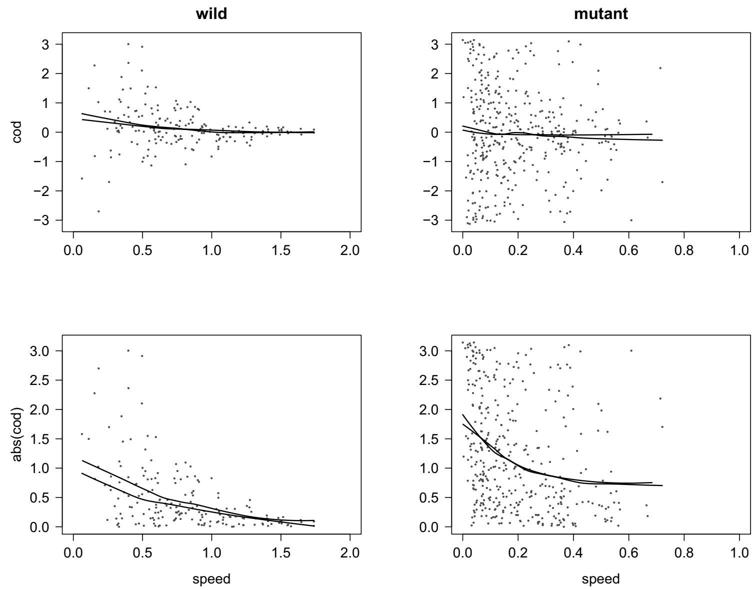

Figure 11.4 *Each panel shows the observations (change of direction against speed in the top panels, and absolute change of direction against speed in the bottom panels). In each case there are two nonparametric regression lines computed by the* **R** *function* `loess`*, one smoothing the observations and the other smoothing the 10 000 realizations generated from the fitted model.*

Table 11.3 *Comparison of two- and three-state bivariate HMMs for speed and direction change in two larvae of* Drosophila*.*

subject	no. states	no. parameters	$-\log L$	AIC	BIC
wild	2	10	193.1711	406.3	438.3
	3	18	166.8110	**369.6**	**427.1**
mutant	2	10	332.3693	684.7	724.2
	3	18	303.7659	**643.5**	**714.5**

to fit in that it was easy to become trapped at a local optimum of the log-likelihood which was not the global optimum.

Table 11.3 compares the two- and three-state models on the basis of likelihood, AIC and BIC, and indicates that AIC and BIC select three states, both for the wild subject and for the mutant. Figure 11.5 depicts the marginal and state-dependent distributions of the three-state

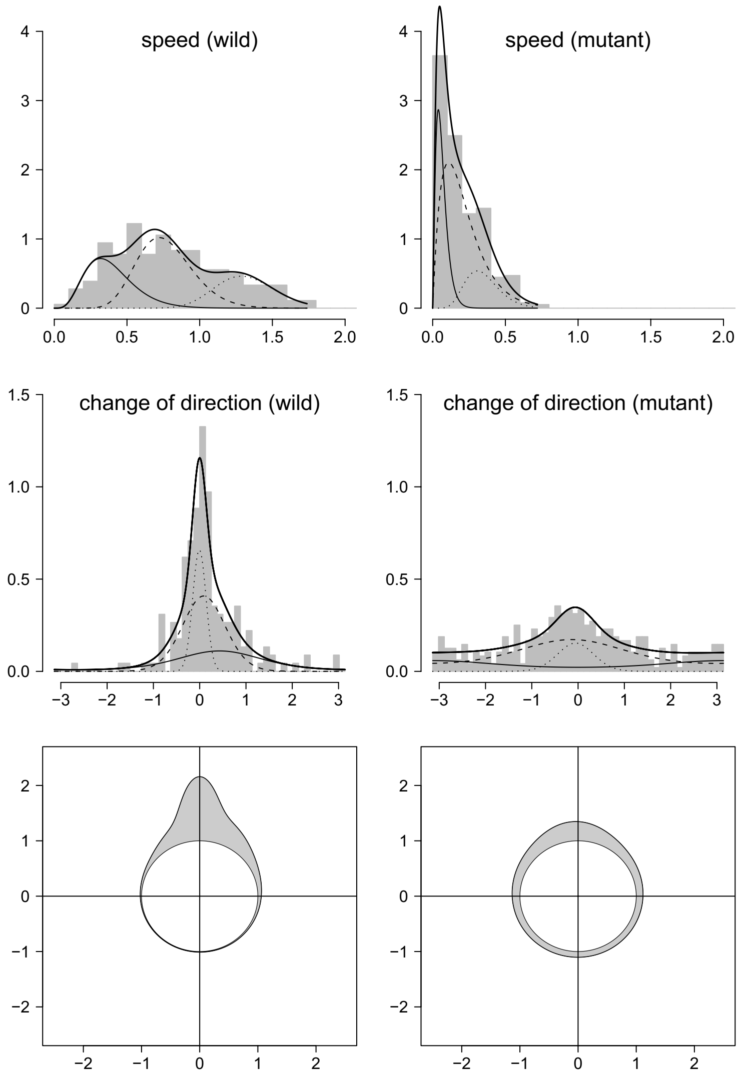

Figure 11.5 *Three-state (gamma–von Mises) HMMs for speed and change of direction in* Drosophila melanogaster*: wild subject (left) and mutant (right). The top panels show the marginal and the state-dependent (gamma) distributions for the speed, as well as a histogram of the speeds. The middle panels show the marginal and the state-dependent (von Mises) distributions for the c.o.d., and a histogram of the changes of direction. The bottom panels show the fitted marginal densities for c.o.d.*

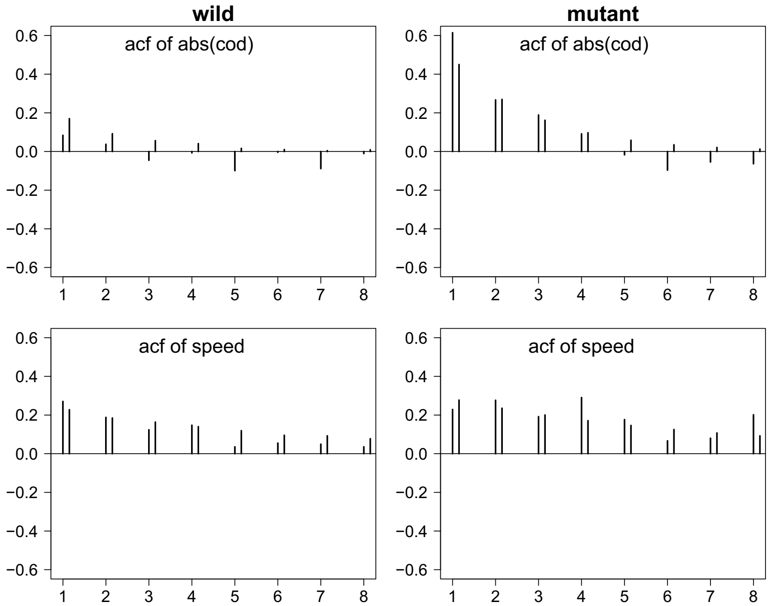

Figure 11.6 *Sample and 3-state-HMM ACFs of absolute change of direction (top panels) and speed (bottom panels). The ACFs for the absolute change of direction under the model were computed by simulation of a series of length 50 000.*

model. Figure 11.6 compares the sample and three-state model ACFs for absolute c.o.d. and for speed; for the absolute c.o.d. the model ACF was estimated by simulation, and for the speed it was computed by using the results of Exercise 3 of Chapter 2.

What is noticeable about the models for c.o.d. depicted in Figure 11.5 is that, although not identical, they are visually very similar to the models of Figure 11.2, even though their origin is rather different. In one case there are two states, in the other three; in one case the model is univariate, and in the other it is one of the components of a bivariate model.

This application illustrates two attractive features of HMMs as models for bivariate or multivariate time series. The first is the ease with which different data types can be accommodated — here we modelled a bivariate series with one circular-valued and one (continuous) linear-valued variable. Similarly it is possible to model bivariate series in which one variable is discrete-valued (even categorical) and the other continuous-valued. The second feature is that the assumption of contemporaneous conditional independence provides a very simple means of modelling dependence between the contemporaneous values of the component series, whether these are bivariate or multivariate. Although the range of dependence structures which can be accommodated in this way is limited, it seems to be adequate in some applications.

Exercises

1. Let μ be the directional mean of the circular random variable Θ, as defined on p. 156. Show that $\mathrm{E}\sin(\Theta - \mu) = 0$.

2. Let X have a von Mises distribution with parameters μ and κ. Show that
$$\mathrm{E}\cos(n(X-\mu)) = I_n(\kappa)/I_0(\kappa) \text{ and } \mathrm{E}\sin(n(X-\mu)) = 0,$$
and hence that
$$\mathrm{E}\cos(nX) = \cos(n\mu)I_n(\kappa)/I_0(\kappa)$$
and
$$\mathrm{E}\sin(nX) = \sin(n\mu)I_n(\kappa)/I_0(\kappa).$$
More compactly,
$$\mathrm{E}(e^{inX}) = e^{in\mu}I_n(\kappa)/I_0(\kappa).$$

3. Again, let X have a von Mises distribution with parameters μ and κ. Deduce from the conclusions of Exercise 2 that
$$\tan\mu = \mathrm{E}(\sin X)/\mathrm{E}(\cos X).$$

4. Let $\{X_t\}$ be a stationary von Mises–HMM on m states, with the i th state-dependent distribution being von Mises (μ_i, κ_i), and with μ denoting the directional mean of X_t.

   Show that
$$\mathrm{E}\sin^2(X_t - \mu) = \frac{1}{2}\Big(1 - \sum_i \delta_i A_2(\kappa_i)\cos(2(\mu_i - \mu))\Big),$$
where $A_2(\kappa) = I_2(\kappa)/I_0(\kappa)$. Hint: use the following steps.
$$\mathrm{E}\sin^2(X_t - \mu) = \sum \delta_i \mathrm{E}(\sin^2(X_t - \mu) \mid C_t = i);$$
$$\sin^2 A = (1 - \cos(2A))/2; \quad X_t - \mu = X_t - \mu_i + \mu_i - \mu;$$
$$\mathrm{E}(\sin(2(X_t - \mu_i)) \mid C_t = i) = 0;$$
and
$$\mathrm{E}(\cos(2(X_t - \mu_i)) \mid C_t = i) = I_2(\kappa_i)/I_0(\kappa_i).$$
Is it necessary to assume that μ is the directional mean of X_t?

5. Consider the definition of the circular correlation coefficient given by Fisher and Lee (1983): the correlation between two circular random variables Θ and Φ is
$$\frac{\mathrm{E}(\sin(\Theta_1 - \Theta_2)\sin(\Phi_1 - \Phi_2))}{[\mathrm{E}(\sin^2(\Theta_1 - \Theta_2))\mathrm{E}(\sin^2(\Phi_1 - \Phi_2))]^{1/2}},$$
where (Θ_1, Φ_1) and (Θ_2, Φ_2) are two independent realizations of (Θ, Φ).
Show that this definition implies the following expression, given as Equation (2) of Holzmann *et al.* (2006), for the circular autocorrelation of order k of a stationary time series of circular observations X_t:
$$\frac{\mathrm{E}(\cos X_0 \cos X_k)\mathrm{E}(\sin X_0 \sin X_k) - \mathrm{E}(\sin X_0 \cos X_k)\mathrm{E}(\cos X_0 \sin X_k)}{(1 - \mathrm{E}(\cos^2 X_0))\mathrm{E}(\cos^2 X_0) - (\mathrm{E}(\sin X_0 \cos X_0))^2}. \tag{11.5}$$

6. Show how Equation (11.5), along with Equations (2.8) and (2.10), can be used to compute the Fisher–Lee circular ACF of a von Mises–HMM.