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Autoregressive-Type Models for the Analysis of Bark Beetle Tracks

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SUMMARY

When the progress of female bark beetles is followed in a small arena as they are attracted to a source emitting male pheromones, the variate that is of interest to biologists is the heading angle, i.e., the angle between the direction toward the source and the direction of forward motion. In the present paper we model the resulting angular time series variate using autoregressive-type models with von Mises random errors. Estimates of parameters for four data sets were obtained by maximizing a von Mises likelihood function. Plots of residuals developed after fitting first order models indicated some interesting behavioral differences between beetles in control groups and those in bioassays with strong pheromone attractants.

1. Introduction

This paper is concerned with the development of autoregressive-type models to study the effects of various stimuli on the orientation of animals with respect to a goal. Models are developed to study chemotaxis (orientation in relation to gradients of chemicals) by walking female *Ips paraconfusus* bark beetles when they respond to compounds involved in their chemical communication (i.e., pheromone) system. The pheromone systems of insects have been of intense concern to entomologists over the last 30 years, because they appear to be promising as nontoxic alternatives to insecticides for insect control.

Commonly, insect pheromones control the orientation of one individual with respect to another. Probably the most widely known example of these chemicals is the sex attractants. Chemicals emitted by the female guide the flight of the male to her for the purpose of mating. In most such instances, the trend of an animal's movements is directed toward the source of stimulation, although this is not absolutely necessary for an animal to eventually cease motion near a source (Fraenkel and Gunn, 1961). Because the movements of the responding animal are usually directed with respect to the source in some way, one reasonable means to measure response is to measure the angle between the direction toward the source and the direction of a track segment at various points along the animal's path. We term such an angle a "heading."

Tests where the response variable is angular are common in living systems. Examples from biology include studies of the relationships between the direction of movement of intertidal gastropods and the distance moved (Fisher and Lee, 1992; Underwood and Chapman, 1985), homing in crows (Matthews, 1955), and flower location and the dance language of bees (von Frisch, 1967). In physical systems, examples from meteorology include the dependence of wind direction on wind speed (Breckling, 1989).

In Section 3 we present some autoregressive-type models that describe the distribution of the angular response at a given time, given the past history of a beetle's movement. In Section 4, estimates of the parameters in the autoregressive models are obtained by maximizing a von Mises likelihood function. We experienced no difficulties with the estimation of the parameters or the convergence of the likelihood to apparent global maxima. This may well be because of the large samples we were analyzing (samples sizes were greater than 500). Diagnostic plots of residuals led

Key words: Angular variates; Chemotaxis; Maximum likelihood; Pheromones; von Mises distribution.

us to consider second order autoregressive models. A discussion of the biological implications of the fitted models is given in Section 5.

2. Experimental Background

The compounds used as stimuli, the experimental arena, the observation chamber and recording procedures, and the handling of the experimental animal have all been extensively described by Akers and Wood (1989) and Akers (1989). In summary, five female beetles were introduced successively within a period of approximately 15 min into the center of a circular arena (15-in diameter). As much as possible, each beetle was initially placed roughly perpendicularly to the direction toward the source of pheromone. Each beetle was tracked by marking its position at 1-s intervals until it contacted the pheromone source, or the wall of the arena, or 3 min had elapsed. Preliminary experiments suggested the beetles did not interact within the arena, and that the concentration gradient remained stable over the time the beetles were tested (Akers and Wood, 1989). Each beetle was used only once. In this paper we analyze data from three treatment groups (T1, T2, T3) and one control group (C). The treatments differed in the composition and concentration of the pheromone at the source. Each treatment was replicated 20 times. Figure 1 shows examples of individual tracks from the control and the treated groups.

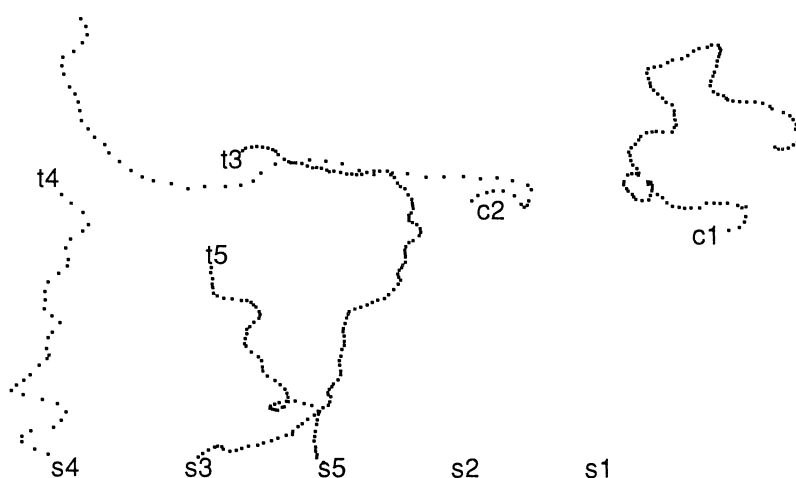


Figure 1. Individual trails of five female bark beetles; c1, c2 = starting points of two beetles in the control group; t3, t4, t5 = starting points of three beetles from the treatment groups; s1, ..., s5 = locations of sources for the corresponding trails. Points on the tracks show locations of beetles at 1-s intervals.

3. Autoregressive Models and the von Mises Distribution

Assuming that the source of the pheromone is at the origin, $S = (0, 0)$, we are interested in modeling the observed heading angle, θ_t , of an insect between times $t - 1$ and t , given the history of the insect's movements up to time $t - 1$. The heading angle θ_t is defined as the angle between the vectors \mathbf{SP}_{t-1} and $\mathbf{P}_{t-1}\mathbf{P}_t$, where $\mathbf{P}_t = (x_t, y_t)$ is the position of the insect at time t (Figure 2). We assume the variate Θ_t to be a random angular variate ranging from $-\pi$ to π , with counter-clockwise turns defined as positive. The von Mises distribution is commonly used to describe angular variates. The role of the von Mises distribution in statistical inference on the circle is as important as that of the normal distribution on the line. This distribution shares many of the properties for angles that the normal distribution has for linear data (Mardia, 1972).

A circular random variate Θ is said to have a von Mises $\text{VM}(\mu, \kappa)$ distribution if its probability density function is given by

$$f(\theta; \mu, \kappa) = \frac{1}{2\pi I_0(\kappa)} e^{\kappa \cos(\theta - \mu)}, \quad -\pi < \theta, \mu < \pi, \kappa \geq 0, \quad (3.1)$$

where $I_0(\kappa)$ is the modified Bessel function of the first kind and order zero, μ is the mean direction of the angular variate, and κ is the concentration parameter. The value $\kappa = 0$ corresponds to the circular uniform distribution. For $\kappa > 0$, the distribution is unimodal, symmetrical around the mode $\theta = \mu$, and larger values of κ correspond with greater clustering around the mode. For large κ , the

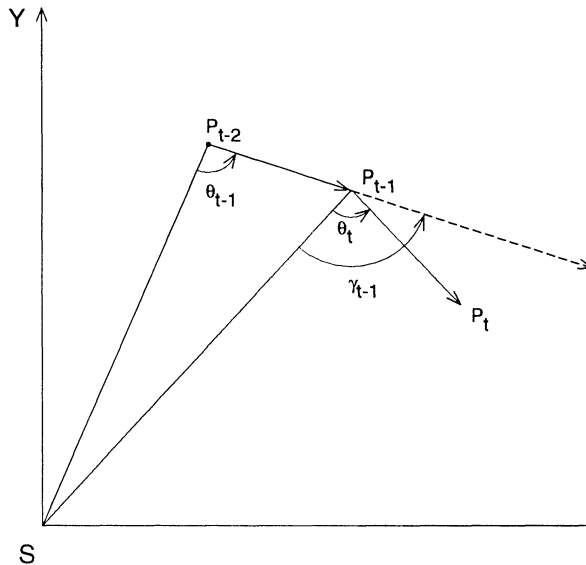


Figure 2. The heading angle θ_t is defined as the angle between the direction toward the source (S) and the direction of the track between time $t - 1$ and t . The angle γ_{t-1} is the heading angle of a beetle traveling in a straight line starting at P_{t-2} , i.e., $\gamma_{t-1} = \theta_{t-1} + \angle P_{t-2}SP_{t-1}$.

von Mises distribution is well approximated by a normal distribution with variance $1/\kappa$ (Mardia (1972), p. 60).

In the discussion that follows, we will model the mean direction μ_t and the dispersion parameter κ_t given the history of the beetle's movements up to time $t - 1$. The simplest model considered is the first order model

$$\Theta_t = \beta_1 \gamma_{t-1} + \varepsilon (\text{mod } 2\pi) \quad \text{with} \quad \varepsilon \sim \text{VM}(0, \kappa), \quad (3.2)$$

where γ_{t-1} is the heading angle the beetle would have had between times $t - 1$ and t if it continued walking in the same direction as it walked between $t - 2$ and $t - 1$, i.e., if it continued walking in a straight line (see Fig. 2). Specifically, $\gamma_{t-1} = \theta_{t-1} + \angle P_{t-2}SP_{t-1}$, where $\angle P_{t-2}SP_{t-1}$ is the angle between the vectors SP_{t-2} and SP_{t-1} . Some special cases of (3.2) are defined by

- A: $\kappa = 0$. This corresponds with a random walk model with no mean direction.
- B: $\beta_1 = 1$ and $\kappa \rightarrow \infty$. This situation represents no attraction towards the source. In terms of behavior, beetles walk in a straight line in the direction they were oriented at time zero.
- C: $\beta_1 = 0$ and $\kappa \rightarrow \infty$. This situation represents the beetle's heading directly toward the source.
- D: $0 < \beta_1 < 1$ and $\kappa \rightarrow \infty$. In this case, beetles will approach the source S along an arc.

Higher order models are given by

$$\Theta_t = \sum_{j=1}^J \beta_j \gamma_{t-j} + \varepsilon (\text{mod } 2\pi). \quad (3.3)$$

The mean direction μ_t can also be related to explanatory variables such as distance to source or concentration level of pheromon at the source. Such covariates could be added to the autoregressive models described above. Fisher and Lee (1992) recommend transforming nonangular explanatory variates by using a monotone function that maps the real line \mathfrak{R} onto the circle $(-\pi, \pi)$. This transformation avoids the problems of nonidentifiability of maximum likelihood estimates that seem to exist when regression models analogous to normal linear regression are used to model angular data (Gould, 1969; Johnson and Wehrly, 1978).

A final model of interest is one in which the dispersion parameter κ is also a function of covariates. An intuitively appealing model is

$$\kappa_t = e^{\alpha_0 + \alpha_1 d_t}, \quad (3.4)$$

where d_t is the distance between the beetle and the source at time t . For values of $\alpha_1 < 0$, the dispersion parameter $\kappa_t \in (0, \infty)$ is a decreasing function of the distance to the source, i.e., the

angular variates are increasingly concentrated around the mean direction as the beetle approaches the source of the stimulus. Thus, as the distance to the source gets smaller, the beetle might be expected to be less likely to make large turns away from the source.

3.1 Maximum Likelihood Estimation

Let θ_t be the observed heading angle for a given beetle between times $t - 1$ and t . Let \mathbf{H}_t be the history of the beetle's movements up to time t . \mathbf{H}_t includes the heading angles, θ_t , and the step sizes, r_t , up to time t and the coordinates of the beetle's position at $t = 0$. We will assume that the conditional density function $f_{t|\mathbf{H}_{t-1}}$ of Θ_t given \mathbf{H}_{t-1} is a von Mises density with mean direction $\mu_t = \sum_{j=1}^J \beta_j x_{t-j}$ and dispersion parameter $\kappa_t = \exp(\alpha_0 + \sum_{j=1}^J \alpha_j x_{t-j})$, where x_{t-j} is a known function of θ_{t-j} and r_{t-j} for $j = 1, \dots, J$. The full likelihood of the angular time series $\theta_{J+1}, \dots, \theta_T$ can be obtained by multiplying the successive conditional probability density functions $f(\theta_t|\mathbf{H}_{t-1}, \mu_t, \kappa_t)$ for $t = J + 1, \dots, T$, the joint density, $f(\theta_1, \dots, \theta_J)$, of the first J heading angles, and the density of the past j step sizes. However, for large T , the effect of $f(\theta_1, \dots, \theta_J)$ is negligible (see Harvey, 1981). The density of the step sizes can also be ignored as long as it does not depend on the parameters μ_t and κ_t . For the bark beetle tracks data, T is mostly greater than 50. Also, plots of step sizes against heading angles did not suggest any relationships between the two variables. Consequently, we can calculate effectively the maximum likelihood estimates of the parameters in μ_t and κ_t by maximizing the function

$$\log L = \sum_{t=J+1}^T \log f(\theta_t|\mathbf{H}_{t-1}, \mu_t, \kappa_t) = - \sum_{t=J+1}^T [\log I_0(\kappa_t) - \kappa_t \cos(\theta_t - \mu_t)]. \quad (3.5)$$

The estimates are then obtained by solving the equations

$$\frac{\partial \log L}{\partial \beta_j} = \sum_t \kappa_t x_{t-j} \sin(\theta_t - \mu_t) = 0, \quad (3.6)$$

$$\frac{\partial \log L}{\partial \alpha_j} = \sum_t \kappa_t x_{t-j} [-A(\kappa_t) + \cos(\theta_t - \mu_t)] = 0, \quad (3.7)$$

where $A(\kappa_t) = I_0(\kappa_t)/I_1(\kappa_t)$ and $I_1(\kappa_t)$ is the modified Bessel function of the first kind and first order.

Given the asymptotic properties of MLEs, an estimate of the variance-covariance matrix of the parameter estimates can be based on the inverse of the information matrix $I(\boldsymbol{\beta}) = E\{-\partial^2 L / \partial \boldsymbol{\beta} \partial \boldsymbol{\beta}'\}$, where $\boldsymbol{\beta}$ is the vector of parameters. From (3.6) and the fact that $\partial^2 \mu_t / \partial \beta_j \partial \beta_r = 0$,

$$\begin{aligned} E\left\{-\frac{\partial^2 L}{\partial \beta_j \partial \beta_r}\right\} &= \sum_t \kappa_t x_{t-j} x_{t-r} E[\cos(\theta_t - \mu_t)] \\ &= \sum_t \kappa_t x_{t-j} x_{t-r} A(\kappa_t). \end{aligned} \quad (3.8)$$

Similarly, from (3.6) and (3.7) we have

$$\begin{aligned} E\left\{-\frac{\partial^2 L}{\partial \alpha_j \partial \alpha_r}\right\} &= \sum_t \kappa_t^2 x_{t-j} x_{t-r} E\left\{\frac{\partial A(\kappa_t)}{\partial \kappa_t}\right\} \\ &= \sum_t \kappa_t^2 x_{t-j} x_{t-r} \left[1 - \frac{A(\kappa_t)}{\kappa_t} - A^2(\kappa_t)\right]. \end{aligned} \quad (3.9)$$

and

$$E\left\{-\frac{\partial^2 L}{\partial \beta_j \partial \alpha_r}\right\} = 0. \quad (3.10)$$

Therefore, an estimate of the asymptotic variance-covariance matrix can be obtained by substituting the MLE $\hat{\mu}_t$ and $\hat{\kappa}_t$ values in (3.8) through (3.10) and then inverting the information matrix $\mathbf{I}(\hat{\boldsymbol{\beta}})$. In the next section we used a FORTRAN program to obtain the solutions of the normal equations (3.6) and (3.7) and to calculate estimates of the standard errors.

4. Analysis of Bark Beetle Tracks

Table 1 lists the MLEs of the parameters for a first order autoregressive-type model with mean direction $\mu_t = \beta_1 \gamma_{t-1} (\text{mod } 2\pi)$ and dispersion $\kappa_t = e^{\alpha_0}$. All beetles in experiments T1 and T2, and 15 out of 20 beetles in experiment T3 reached the source. Within each experimental group in Table 1 no significant difference in the parameters between individual beetle tracks was apparent (p values for likelihood ratio tests for the equality of the β_1 parameters were $>10\%$ in each case). Estimates of the parameter β_1 were significantly <1 for those beetles that reached the source and equal to 1 (not significantly different from 1) for the beetles in the control group or for the beetles in T3 that did not reach the pheromone source. Tracks of beetles that did not reach a source emitting a chemical attractant appeared to be similar to the tracks in the control group which had no chemical attractant at the source. This phenomenon was also observed by Akers and Wood (1989) in their analysis of

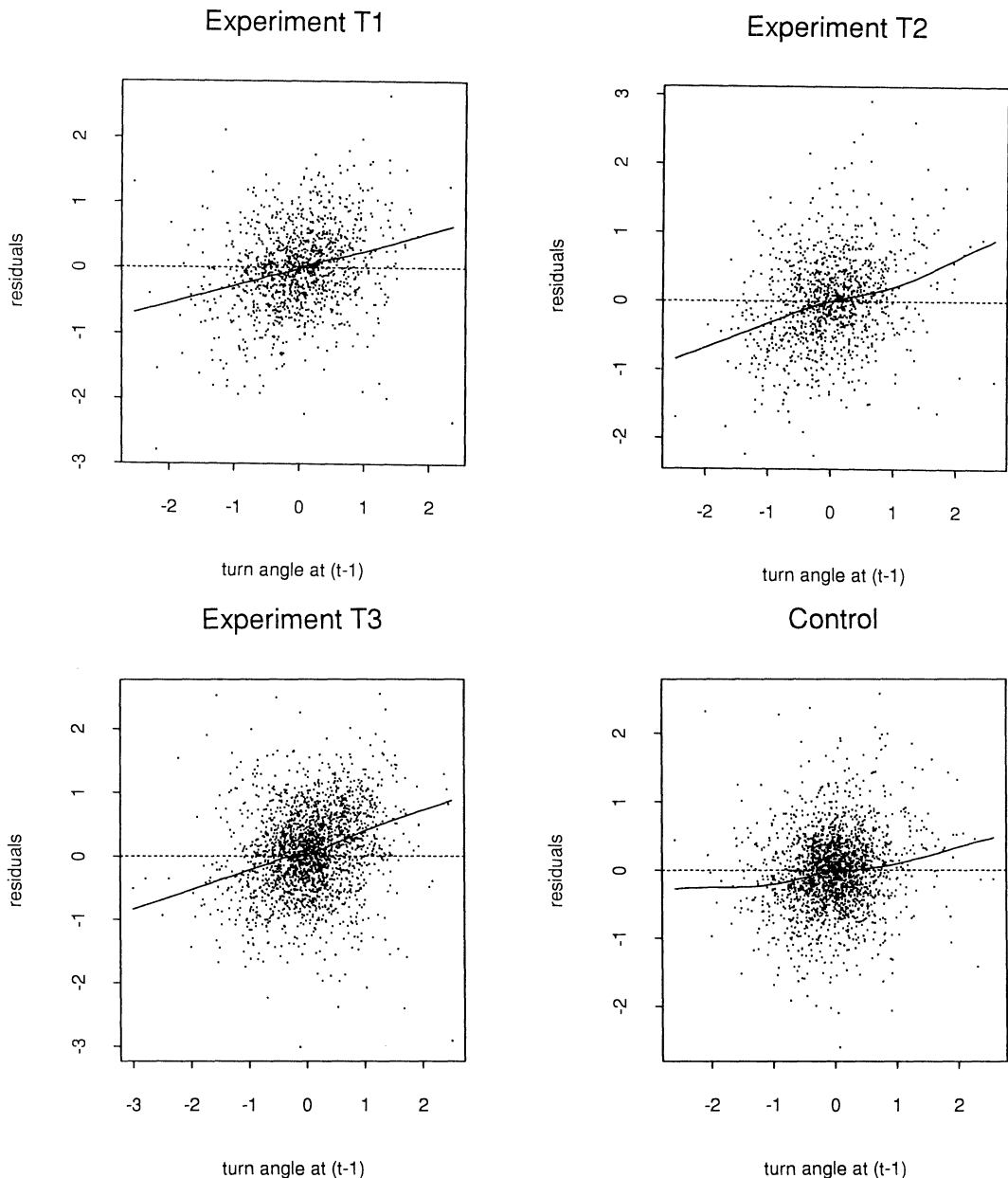


Figure 3. Plots of residuals against turn angle, $(\theta_{t-1} - \gamma_{t-2}) \text{mod } 2\pi$, developed by fitting a first order autoregressive type model with a constant dispersion parameter. The smooth curve through the points was generated by the nonparametric local regression routine *loess* (Cleveland and Devlin, 1988).

Table 1
Maximum likelihood estimates of parameters for the von Mises error model with $\mu_t = \beta_1 \gamma_{t-1}$ and $\kappa_t = e^{\alpha_0}$

Data	<i>n</i>	−log <i>L</i>	$\hat{\beta}_1$ (SE)	$\hat{\alpha}_0$ (SE)
T ₁	1200	−1071.1	.887 (.0135)	1.171 (.035)
T ₂	1076	−939.9	.894 (.0134)	1.142 (.036)
T ₃ ^a				
rs	1597	−1300.6	.952 (.0102)	1.053 (.033)
nrs	584	−568.0	.988 (.0141)	1.296 (.047)
Control	1952	−1951.5	1.001 (.0073)	1.339 (.025)

^a rs, data from beetles that reached the source; nrs, data from beetles that did not reach the source.

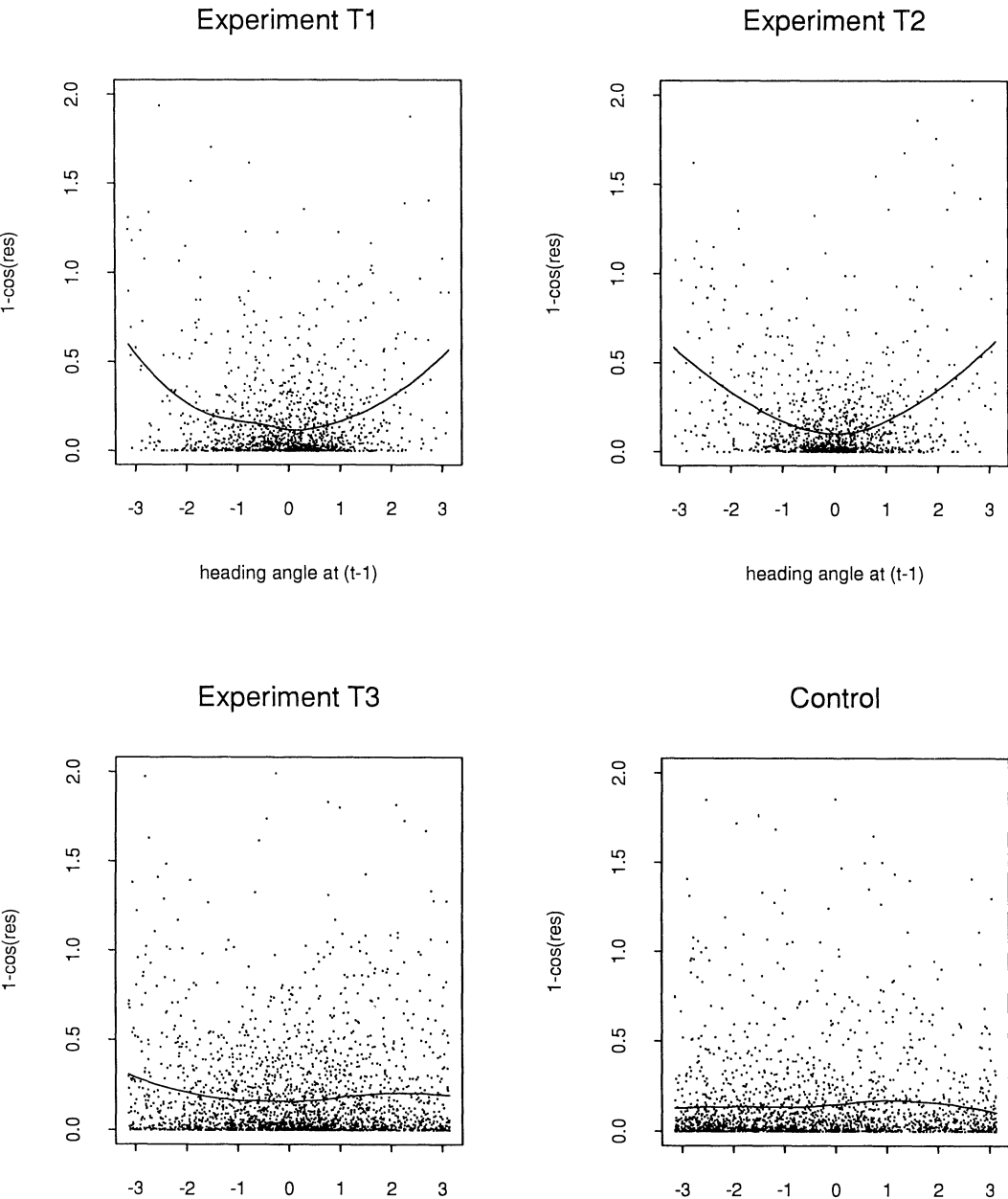


Figure 4. Plots of circular residuals against heading angle θ_{t-1} . The smooth curves through the points were generated by fitting nonparametric local regression models using *loess*.

a series of chemotaxis assay experiments from which the present data sets were drawn. By studying mean heading, mean walking and turning rates, Akers and Wood (1989) concluded that the behavior of beetles that did not reach the source “was so dissimilar to that of beetles that reached the source . . . , [that] most of this group was probably not responding to the pheromone.”

We studied the goodness-of-fit of the first order autoregressive model by producing plots of residuals against various covariates, where residual = $(\theta_t - \hat{\mu}_t)(\text{mod } 2\pi)$. The most obvious pattern in the residual plots was the relationship between the residuals and the turn angle $(\theta_{t-1} - \gamma_{t-2})(\text{mod } 2\pi)$ at a previous time point (Figure 3). When the absolute value of the turn angle at $t - 1$ is large (i.e., when the beetle makes a large turn at $t - 1$), the absolute difference between the observed and expected heading angles is apparently larger than expected under the first order model. This pattern was observed in all four data sets including the control. A relationship was also observed between the dispersion of the residuals and the heading angle at a previous time point. The scatter of the residuals appeared to be greatest when the absolute value of the heading angle at $t - 1$ was large. This relationship between the variance of the angular variable and the direction of motion was clearly apparent in plots of the circular residuals, $1 - \cos(\theta_t - \hat{\mu}_t)$, against θ_{t-1} in all cases except the control (Fig. 4).

Another interesting relationship was seen in the plots of the residuals for the control group against distance from source. The dispersion of the residuals appeared to be larger at around 7 in (the approximate distance at which the beetles were released at the start of the experiment) than at other distances from the source. Finally, contrary to our intuition (equation (3.4)), we observed no relationship between the dispersion of the heading angles and distance to source in any of the treatment experiments.

The relationships observed between turn angle and the residuals in our plots suggested the need to fit higher order models with dispersion parameters dependent on θ_t . When higher order models

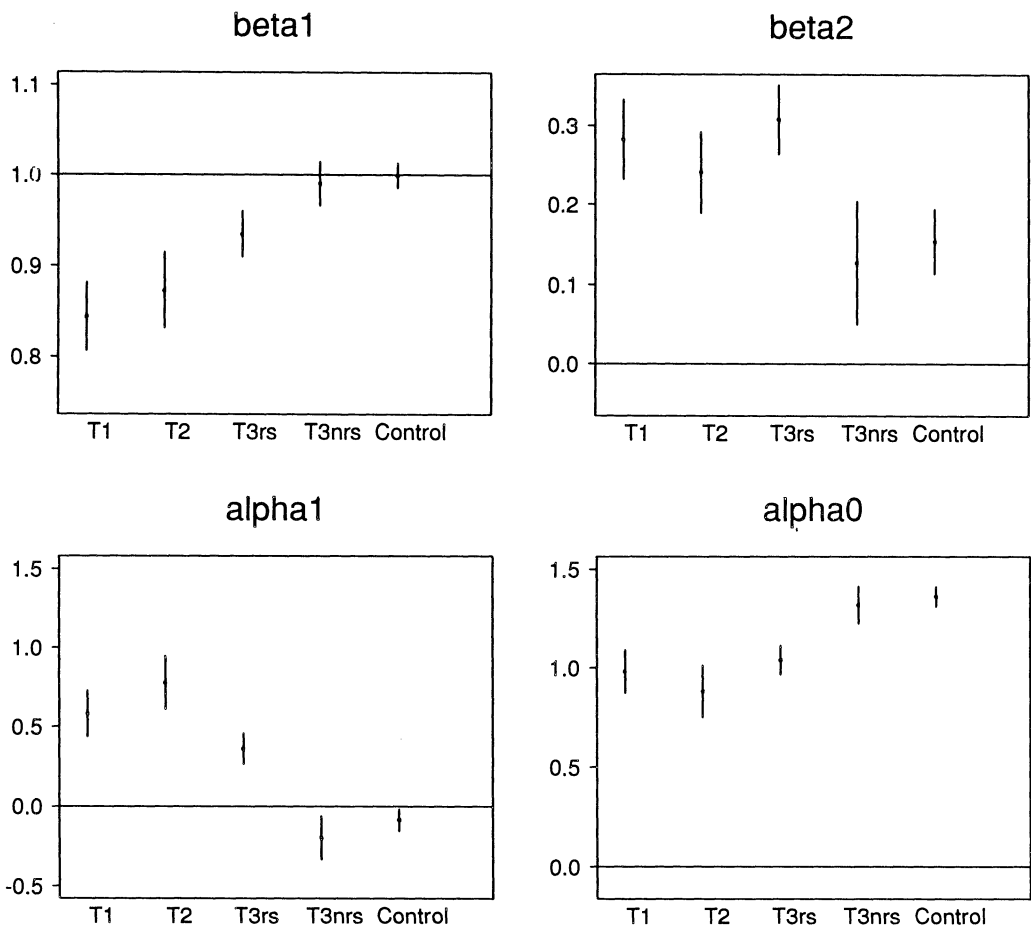


Figure 5. Estimates of parameters (± 2 SE) for the von Mises model with $\mu_t = \beta_1 \gamma_{t-1} + \beta_2 (\theta_{t-1} - \gamma_{t-2})$ and $\kappa_t = e^{\alpha_0 + \alpha_1 \cos(\theta_{t-1})}$.

were fitted to the five data groups, only the first and second order coefficients appeared to be significant when the estimates were compared with their corresponding standard errors. Figure 5 gives plots of the estimates of the parameters (± 2 SE) in the second order autoregressive type model given by

$$\Theta_t = \beta_1 \gamma_{t-1} + \beta_2 (\theta_{t-1} - \gamma_{t-2}) + \varepsilon (\text{mod } 2\pi) \quad \text{with} \quad \varepsilon \sim \text{VM}(0, \kappa)$$

and

$$\kappa_t = e^{\alpha_0 + \alpha_1 \cos(\theta_{t-1})}$$

Once more, we observed that the parameter estimates for beetles reaching the source (T1, T2, T3rs) were similar to each other, and those not reaching the source (T3nrs) were similar to the parameters in the control group. As expected from the residual plots (Figure 4), the estimates of α_1 were significant and positive only for beetles that reached the source.

5. Discussion

In this article, we used autoregressive-type models for angular variables to study the characteristics of female beetle tracks as they orient and move towards a point source emitting aggregation pheromones (i.e., attractants). We found the maximum likelihood approach and exploratory analysis of residual plots helpful tools for the fitting of autoregressive models with biologically useful parameters. We found no difficulties in maximizing a von Mises likelihood, particularly when the sample sizes were large.

Results of our analysis seemed to be consistent with the following mechanisms for the orientation of beetles in relation to the pheromone: 1) Models fitted to beetles that did not reach the odor source were similar to those of beetles in the control group and dissimilar to those of beetles reaching the source, therefore, it seemed reasonable to conclude that beetles that did not reach the odor source never detected the stimulus (odor) in the period of time they were under observation. 2) At each step, beetles in the control group and those in experiment T3 that did not respond to the pheromone appeared to be walking in a mean direction equal to the heading angle at the previous step. The random fluctuation around this mean direction was adequately explained by a von Mises variable with a constant dispersion parameter ($\hat{\kappa} = 3.73 \pm .19$). 3) Beetles that responded to the stimulus appeared to make gradual turns toward the source at each step. The mean heading angle at each step was equal to 88% (± 1.8) of the heading angle at the previous step when the turn angle at a previous step was small. If at any given step, however, the beetle made a large turn, then the momentum of that turn seemed to keep the beetle moving in large turns for at least one more recorded time point. 4) Random fluctuations around the mean direction was adequately explained by a von Mises variable with dispersion parameter $\kappa_t = e^{.97 + .57 \cos(\theta_{t-1})}$. The equation for κ_t seemed to indicate that the heading angle with respect to the source, rather than distance to source, was the important factor characterizing the beetles' motion. When the absolute value of the heading angle was large (i.e., when the beetle was heading away from the source) the fluctuation around the mean direction was larger than when the beetle was heading toward the source.

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RÉSUMÉ

Les biologistes qui suivent le trajet de cafards femelles soumises à l'attraction d'une source de phéromones mâles dans une petite arène, s'intéressent à l'angle *d'approche*; c'est à dire l'angle entre la direction de la source et celle du mouvement. Dans l'article suivant, nous modélisons la série temporelle de cette variable angulaire en utilisant des modèles autorégressifs avec des erreurs aléatoires de type von Mises. Des estimations des paramètres sont obtenues sur 4 séries de données, par maximisation d'une fonction de vraisemblance de von Mises. Des graphes des résidus, obtenus après ajustement de modèles du premier ordre, indiquent des différences de comportement intéressantes entre les groupes de contrôle et ceux soumis à l'attraction de phéromones.

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