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40 A common problem in animal behavior is determining whether the rate at which a certain 41 behavioural event occurs is affected by an environmental or other factor. In the example 42 considered later in this paper, the event is a vocalization by an individual sperm whale 43 and the factor is the operation or non-operation of an underwater sound source. A typical 44 experiment to test for such effects involves observing animals during control and 45 treatment periods and recording the times of the events that occur in each. In statistical 46 terminology, the data arising from such an experiment - the times at which events of a 47 specified type occur – represent a point process (Cox & Lewis 1978). Events in a point 48 process are treated as having no duration. Although this is not strictly correct for 49 behavioural events, the approximation is reasonable when the duration of events is small 50 in relation to the interval between them.

51 In some cases, under the null hypothesis of no treatment effect, behavioural 52 events can be assumed to follow a stationary Poisson process. Under this model, the 53 intervals between successive events are independent and, conditional on their number, the 54 events are uniformly distributed over the observation period. As described below, when 55 the Poisson assumption is valid, a statistical test to determine whether event rate changes 56 under treatment can be based on the binomial distribution. In many cases, however, the 57 Poisson model has been shown to be invalid for behavioural events. This is the case, for 58 example, when events occur in bouts (Slater & Lester 1982; Sibly et al. 1990; Haccou & 59 Meelis 1992). As illustrated below, when behavioural events do not follow a Poisson 60 process, the binomial test can give misleading results. A number of methods are 61 available to test whether a point process is Poisson based on the uniformity result 62 mentioned above (Stephens 1986). If a point process cannot be assumed to be Poisson,

one option is to use a test that is valid under a particular alternative to the Poisson model.
Unfortunately, while it is often easy to show that a point process is not Poisson, it can be
difficult to specify an appropriate alternative model. The purpose of this paper is to
describe and illustrate the use of a simple nonparametric method that can be used to
analyze behavioural point process data even if the process generating the data is
unknown.

69

#### 70 A Rotation Test

71

72 Suppose that events are observed over the period (0, T), and that the total times under 73 control and treatment conditions are  $T_c$  and  $T_T$ , respectively (with  $T = T_c + T_T$ ). Assume that, under control conditions, events follow a stationary Poisson process with rate  $\lambda_c$ 74 75 and that, under treatment conditions, events follow an independent Poisson process with rate  $\lambda_T$ . Under this model, interest centers on testing the null hypothesis  $H_o: \lambda_C = \lambda_T$  of 76 no treatment effect. Let the random variables  $N_c$  and  $N_T$  be the numbers of events 77 78 occurring under control and treatment conditions, respectively, and let  $N = N_C + N_T$  be the total number of events. Conditional on the observed value n of N, under  $H_o$ ,  $N_c$  has 79 a binomial distribution with n trials and success probability  $T_C / T$ . The null hypothesis 80 can be rejected at significance level  $\alpha$  if the observed value of  $N_c$  is below the lower 81 82  $(\alpha/2)$  quantile or above the upper  $(\alpha/2)$  quantile of this binomial distribution. Provided *n* is not too small and  $T_C/T$  is not too close to 0 or 1, the binomial distribution 83

can be approximated by a normal distribution with mean  $nT_C/T$  and variance  $nT_C T_T/T^2$ , so that  $H_o$  can be rejected at approximate significance level  $\alpha$  if: 86

87 
$$\left|\frac{TN_{c} - nT_{c}}{\sqrt{nT_{c}T_{T}}}\right| > \Phi^{-1}(\alpha/2)$$
(1)

88

89 where  $\Phi^{-1}(\alpha/2)$  is the upper  $(\alpha/2)$  quantile of the standard normal distribution.

90

91 Behavioral events often exhibit clustering in time beyond what is expected under 92 a Poisson process. As illustrated below, the binomial test may fail in such cases because 93 the underlying randomization scheme – distributing n events at random over the 94 observation period – fails to capture internal structure in the events that is present even 95 under the null hypothesis. A randomization procedure that does preserve this internal 96 structure can be visualized in the following way. Transform the observation period into a 97 circle by joining its end to its beginning. This is sometimes referred to as imposing a 98 periodic boundary condition. Keeping the partition of the observation period into control and treatment segments fixed, displace the events by the same random rotation. Let  $t_j$  be 99 100 the time of the *i*th event. Its time under this rotation scheme is given by:

101

102 
$$t_{j}^{*} = t_{j} + U \qquad t_{j} + U < T \\ t_{j} + U - T \qquad t_{j} + U > T$$
(2)

104	where $U$ is a uniform random variate over the interval (0, $T$ ). By displacing each event				
105	by the same random angle, this procedure preserves the internal structure of the events				
106	except at the beginning of the original observation period, where events originally near $T$				
107	are now in proximity to events originally near 0. Provided $n$ is not too small, the effect of				
108	this concatenation is negligible. The test proceeds by approximating the distribution of				
109	$N_c$ under the null hypothesis from values produced by a large number of random				
110	rotations. The null hypothesis is then rejected at significance level $\alpha$ if the observed				
111	value of $N_c$ lies below the lower or above the upper $\alpha/2$ quantile of this distribution.				
112	This general approach was originally proposed by Harkness & Isham (1983) for testing				
113	association between two two-dimensional point processes observed on a rectangle. The				
114	test has been applied by Miller et al (2004a, b), but a detailed description of the test				
115	including assessment of its validity and power has not previously been published.				
116					
117	To summarize, the steps involved in the rotation test are:				
118					
119	1. Express the data as a set of behavioral event times over the observation period (0,				
120	T).				
121	2. Calculate the number $N_c$ of events occurring during the control period.				
122	3. Generate a rotated set of behavioural event times according to (6).				
123	4. Calculate the number $N_{c\_rot}$ , of events in the rotated set falling in the original				
124	control time period.				

125	5.	Repeat steps 3-5 many times to obtain a distribution for $N_{c_{rot}}$ and assess
126		significance by comparing the the observed value of $N_c$ to the quantiles of this
127		distribution.
128		

130

129

**Test Performance** 

131 In this section, we assess the performance of the binomial and rotation tests under three 132 point process models: the stationary Poisson process, the one-dimensional Thomas 133 process (Thomas 1949), and an exponential autoregressive (EAR) model (Lawrance & 134 Lewis 1979). The Thomas process is a classical model of clustering in point process 135 data, while the EAR model gives rise to clustering through positive autocorrelation in the 136 intervals between events. No claim is made that either of these models is necessarily 137 appropriate for a particular behavioural point process. Instead, they are used here as 138 plausible alternatives to the Poisson process.

139

140 In a Thomas process, initiating events follow a stationary Poisson process with 141 rate  $\mu$ . Each initiating event gives rise to an additional number of offspring events. The 142 numbers of these offspring are independent Poisson random variables with mean  $\theta$ . Let  $s_a$  be the time of an initiating event and suppose that it gives rise to k offspring. The 143 times of these offspring are given by  $s_j = s_o + \delta_j$ , j = 1, 2, ..., k, where  $\delta_1, \delta_2, ..., \delta_k$  are 144 145 independent random intervals with common distribution function F. The process consists 146 of the union of the initiating events and their offspring. The Thomas process is stationary 147 with overall rate  $\mu(1+\theta)$ . However, it is over-dispersed in relation to the Poisson

process with the same rate. For example, for the Thomas process, the variance of the number of events occurring in a unit interval is  $\mu(1+3\theta+\theta^2)$  instead of  $\mu(1+\theta)$  for the Poisson process with the same overall rate.

151

In contrast to the Thomas process, which is a model of the event times, the EAR process is a model for the intervals between events. Let  $d_j = t_j - t_{j-1}$  be the interval between events j - 1 and j. Under the Poisson model, the intervals  $d_1, d_2, ...$  are independent exponential random variables. In contrast, under the EAR model, the sequence of intervals follows the autoregressive process:  $d_i = \rho d_{i-1} + \varepsilon_i$  (3)

159

160 where  $\varepsilon_j$  is equal to 0 with probability  $\rho$  and equal to an exponential random variable 161 with mean  $1/\lambda$  with probability  $1 - \rho$ . The EAR process is stationary with overall rate 162  $\lambda$  and autocorrelation function  $Corr(d_j, d_{j-h}) = \rho^h$ . The positive dependence between 163 successive intervals gives rise to clustering of events.

164

Although it is possible to make some progress analytically, for the purpose of this paper we present some results from a small simulation study. The goal of the first part of this study was to assess the validity of the nominal significance levels of the binomial and rotation tests under the three point process models outlined above. This involved repeatedly simulating point process data from these models under the null hypothesis and

170 applying both tests at the nominal 0.05 significance level. For a valid test, the null 171 hypothesis should be rejected at a rate equal to the nominal significance level. In the 172 study described here, the observation period was taken to be the unit interval, with the 173 first half corresponding to the control period and the second half to the treatment period. 174 Results are presented in Table 1 for overall mean rates of 500 and 1000. For the Thomas 175 process, the parameter  $\theta$  was fixed at 1 while for the EAR process the parameter  $\rho$  was 176 fixed at 0.5. Each entry in Table 1 was based on 1000 simulated data sets and each 177 rotation test was based on 1000 random rotations. In the case of the Thomas process, we 178 assumed that offspring events fell into the same sub-period as their initiating event. In 179 practical terms, this amounts to the assumption that the displacements between offspring 180 and initiating events are negligible in relation to the length of the periods of control and 181 treatment conditions.

182

Turning to Table 1, it is clear that the binomial test is invalid for point process data generated by the Thomas and EAR processes. For these models, the estimated true rate at which the null hypothesis is falsely rejected is well above the nominal significance level. In contrast, the estimated true significance level for the rotation test is not significantly different from the nominal level for all three point process models.

188

189 The goal of the second part of the simulation study was to assess the power of the 190 rotation test. Power is defined as the probability of rejecting the null hypothesis when the 191 alternative hypothesis is correct. This probability will depend on the nature and 192 magnitude of the departure from the null hypothesis, as well as on the amount of data.

193 As a rough guide, a test has good power if this probability is at least 0.8. The power 194 study was based on the same general simulation procedure outlined above except that, for 195 each of the point process models, the overall rate under treatment conditions was 196 increased by a multiplicative factor f over its value under control. For the Thomas 197 process, this was accomplished by increasing the rate  $\mu$  of initiating events. As before, let  $\lambda_c$  and  $\lambda_T$  be the rates under control and treatment conditions, respectively. For the 198 199 case here where the observation period is evenly divided between control and treatment, 200 the overall rate  $\lambda$  is simply the average of  $\lambda_c$  and  $\lambda_T$ . Throughout this power study, this overall rate was held fixed by taking  $\lambda_c = 2\lambda/(1+f)$  and  $\lambda_T = f \lambda_c$ . 201

202

203 The results of the power study are shown in Table 2. Results are presented for 204 overall rates 500 and 1000 with the parameter  $\theta$  of the Thomas process fixed at 1, the 205 parameter  $\rho$  of the EAR process fixed at 0.5, and f = 1.5, 2, and 3. As before, each entry in this table was based on 1000 simulated data sets and for each data set the rotation 206 test was based on 1000 random rotations. For the Poisson case, results are presented for 207 208 both the binomial test and the rotation test. In this case, the rotation test is less powerful 209 than the binomial test, although it achieves good power in most of the cases considered 210 here. As the binomial test is not valid for the Thomas and EAR processes, for these 211 processes results are presented only for the rotation test. The power of the rotation test is 212 quite similar for the two cluster processes. In general, the rotation test achieves good 213 power provided the magnitude of the treatment effect and the overall rate of events are 214 not too small.

216	In addition to the results presented in Table 2, we determined by simulation the
217	minimum detectable effect size $f_{\min}$ – defined as the value of f for which the test at 0.05
218	significance level achieves a power of $0.8$ – for the cases considered in Table 2. Results
219	are presented in Table 3. In overall terms, the rotation test has good power once $f$ reaches
220	approximately 2.
221	
222	
223	An Application to Sperm Whale Response to Airgun Sounds
224	
225	In this section, we apply the rotation test to some experimental data involving the
226	exposure of a sperm whale to air-gun sounds. Air-guns are a source of loud, impulsive
227	low-frequency underwater sound. They are generally deployed in towed arrays for
228	geophysical exploration (Richardson et al. 1995). Air-gun arrays have very high source
229	levels (Richardson et al. 1995; Caldwell & Dragoset 2000) and there is a concern that
230	exposing sperm whales and other marine mammals to air-gun noise may have adverse
231	impacts on their behavior (Gordon et al. 2003).
232	
233	Because sperm whales use echolation to locate prey, one hypothesized behavioral
234	impact of air-gun sound is a reduction in whale foraging rate. Sperm whales produce
235	regular echolocation clicks almost continuously while foraging, interrupted only by short
236	pauses and buzzes (short series of rapid echolocation clicks indicative of attempted prey
237	capture (Whitehead 2003, Miller et al. 2004a)). Whales begin producing echolocation

238 clicks during the descent phase of deep dives, stop clicking during or just prior to ascent,

239	and do not generally produce series of regular echolocation clicks while at the surface or
240	during shallow dives (Watwood et al. 2006). We therefore defined foraging periods as
241	the portions of deep dives between the start and end of regular echolocation clicks. The
242	behavioral event of interest was the production of echolocation buzzes, which serve as a
243	proxy for foraging rate.
244	
245	The data used here were collected during controlled exposure experiments
246	conducted on the 2002 and 2003 Sperm Whale Seismic Study cruises. During the
247	experiments, dtags (Johnson & Tyack 2003) were attached to individual whales to record
248	sound and movement data during control conditions (no air-gun sound exposure) and
249	treatment conditions (air-gun sound exposure). Air-guns were fired every 15 seconds
250	during the treatment period. Detailed information on these experiments can be found in
251	Jochens & Biggs (2003, 2004) and Madsen et al. (2006). Here, we present data from a
252	single individual.
253	

The behavioural record is shown in Figure 1. For this whale, the total time spent foraging during the observation period was T = 5.89 hours, of which  $T_c = 4.74$  hours was under control conditions (the air-gun array was not operating) and  $T_T = 1.15$  hours was under treatment conditions (the air-gun array was in operation). A total of n = 153echolocation buzzes were recorded, of which  $N_c = 139$  occurred during control conditions and  $N_T = 14$  occurred during treatment conditions. The empirical rate of events during control conditions was 29.3 events h<sup>-1</sup> and the corresponding rate during treatment conditions was only 12.2 events h<sup>-1</sup>. The value of the binomial test statistic in
(1) is 3.43, which is significant at approximately the 0.0006 level.

263

264 For reasons connected to the spatial distribution of prey and whale foraging 265 behavior, we expected that the Poisson model underlying the binomial test was unlikely to apply to this time-series of sperm whale foraging events. This expectation was 266 267 confirmed by an analysis of the intervals between events, which revealed positive 268 autocorrelation at short lags. As the intervals in a Poisson process are independent, this 269 autocorrelation is evidence of non-Poisson behaviour in the point process. We therefore applied the rotation test to these data. The histogram of values of  $N_c$  based on 10,000 270 271 rotations is shown in Figure 2. Of these, 647 exceeded the observed value of 139 for an 272 estimated two-sided significance level of approximately 0.13. In contrast to the binomial test, by conventional standards, the null hypothesis cannot be rejected by the rotation test. 273 274 It is not possible to calculate a priori power estimates for the sperm whale data set, since 275 we do not know the true process generating the buzz time series data, and thus we can not 276 produce the simulated data needed for power estimation.

277

## 278 Discussion

279

The rotation test is a general nonparametric approach that can be used when data exhibit serial dependence. The purpose of this paper has been to describe, evaluate, and illustrate this test in the specific context of testing for a treatment effect on the rate of a behavioural point process. We have shown that, in this context, the rotation test works well, maintaining the nominal significance level while providing high power when the
data do not follow a Poisson process. In contrast, the binomial test is invalid in this case.

287 A common approach to analyzing behavioural point processes is to reduce the 288 data to empirical rates within time bins (e.g. Cherry 1989; Mooring 1995; Paredes et al. 289 2005; Fernández-Juricic & Tran 2007). As a general proposition, binning point process 290 data entails a loss of power (Dean & Balshaw 1997) and is not recommended. Moreover, 291 the analysis of binned data is also affected by non-Poisson behaviour in the underlying 292 point process. Briefly, if the underlying point process is Poisson, then the counts within 293 bins will have Poisson distributions. Statistical methods for analyzing Poisson count data 294 are reviewed in McCullagh & Nelder (1989). However, if the underlying point process is 295 not Poisson, then the distribution of bin counts is also not Poisson and the results of these 296 methods can be misleading (Paul & Banerjee 1998). A common alternative to the 297 Poisson distribution for count data is the negative binomial distribution. Parametric 298 methods for analyzing negative binomial data are available (e.g., Barnwal & Paul 1988; 299 Paul & Banerjee 1998). The rotation test provides a nonparametric alternative.

300

Turning to the results of the previous section, it is clear that no general conclusion about the effect of air-gun noise on sperm whales can be drawn from the results of the single test presented here. However, it is also worth pointing out that the hypothesized effect of air-gun nose is a *reduction* in foraging. Had a one-sided test for such a reduction been performed, the significance level would have been around 0.065 which, in light of power considerations, is certainly suggestive of an effect.

308	Finally, although this paper has focused on the rotation test in the context of
309	analyzing behavioural point process data, the same general method could be used in other
310	situations. For example, Shapiro (2008) used a rotation test to determine whether the
311	frequencies of different types of vocalizations in killer whales differed between
312	behavioural states. In this case, the approach was used to account for serial dependence
313	in vocalization type.
314	
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316	
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326	

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399	Tables		
400			
401	Table 1. Validity of the binomia	al and rotation tests	
402			
403		overall mean rate	
404		500	1000
405	Poisson		
406	binomial	0.05	0.05
407	rotation	0.042	0.054
408			
409	Thomas		
410	binomial	0.221	0.233
411	rotation	0.045	0.049
412			
413	EAR		
414	binomial	0.247	0.251
415	rotation	0.052	0.052
416			
417	The rate at which the null hypoth	nesis of no treatment effect was	s falsely rejected in testing

418 at the 0.05 significance level using the binomial test and the rotation test for data

419 simulated from the Poisson, Thomas, and EAR models with overall mean rates of 500

420 and 1000. For the Thomas model,  $\theta = 1$  and for the EAR model  $\rho = 0.5$ . Results are

- 421 based on 1000 simulations except for the binomial test under the Poisson model where
- 422 the theoretical result is given.

424 Table 2. Power of the rotation test

425

426				ove	rall mean rate	•		
427			500				1000	
428			f				f	
429		1.5	2	3		1.5	2	3
430	Poisson							
431	binomial	1	1	1		1	1	1
432	rotation	0.61	0.90	0.99	(	0.82	0.98	1
433								
434	Thomas							
435	rotation	0.34	0.63	0.88	(	).56	0.86	0.97
436								
437	EAR							
438	rotation	0.37	0.64	0.86	(	).54	0.83	0.98
439								
440	The power of the rotation	test at	the 0.0	)5 signi	ficance level	is pre	esented	, for data
441	simulated under the Poiss	on, The	omas, a	and EA	R models wh	en the	e mean	rate under
442	treatment is a factor $f$ greater the factor $f$ greater the factor $f$ greater the factor f	ater tha	n that u	under c	ontrol and wh	nen th	e over	all mean rate is
443	fixed at 500 and 1000. Fo	or the T	Thomas	s model	, we always u	ised 6	) = 1; f	or the EAR model
444	we always used $\rho = 0.5$ .	For th	e Poiss	son moo	del, results are	e also	given	for the binomial

445 test. Results are based on 1000 simulations.

448		overall 1	mean rate	
449		500	1000	
450	Poisson			
451	binomial	1.3	1.2	
452	rotation	1.7	1.5	
453				
454	Thomas			
455	rotation	2.5	1.8	
456				
457	EAR			
458	rotation	2.7	2.0	
459				
460	The minimum detectable	e effect size $f_{\min}$ – define	d as the value of $f$ for which the te	st at
461	0.05 significance level a	chieves a power of $0.8 - f$	for the cases considered in Table 2	•
462	Results are based on 100	00 simulations.		

447 Table 3. Minimum detectable effect levels.

# **Figure Legends**

465	Figure 1. Top panel: Dive profile of the tagged sperm whale. The grey line indicates
466	whale depth, and black circles indicate the times of echolocation buzzes. Airgun
467	exposure periods are shaded gray. Black lines connecting the top and bottom panels
468	illustrate how dive ascents, descents and surface periods were cut from the dataset to
469	produce the buzz time-series we analyzed. Only foraging periods (indicated by yellow
470	shading) were included in the buzz time-series. Bottom Panel: Time-series of
471	echolocation buzzes produced by the sperm whale during foraging periods. Black dots
472	indicate the times of buzzes, and gray shaded areas indicate airgun exposure periods.
473	
474	Figure 2. Histogram of values for $N_c$ , the number of creaks during the control period,
475	obtained in 10,000 rotations of the sperm whale dataset. (The value of $N_c$ was 139 for
476	the original, non-rotated dataset.)

