



# Are foraging patterns of aerial predators influencing diurnal activity of their prey?

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## Abstract

There is often a reciprocal relationship between predators and their dominant prey. This results in continuous co-evolution, where the prey selects more efficient ways to avoid predation and the predator selects more efficient ways of catching prey. The aim of this study was to determine if aerial predators (raptors) influence diurnal activity patterns of their prey (mice). Sampling of both raptors and mice was done simultaneously during autumn, winter and spring at two different study sites in three different habitats on South Africa's arid west coast. Sixty PVC mouse traps were checked every half hour throughout all daylight hours and raptors were observed using scan sampling every two minutes. A total of 1228 rodents were trapped consisting mainly of the diurnal mouse, *Rhabodmys pumilio* and a total of 197 hours was spent observing hunting behaviour of four raptor species: Black and African Marsh Harriers (*Circus maurus* and *C. ranivorus*), Black-shouldered Kite (*Elanus caeruleus*) and Rock Kestrel (*Falco rupicolus*). All birds hunt rodents on a regular basis and all were beginning to breed towards the end of my study. Results showed significantly higher small mammal activity during winter and in habitats with dense vegetation. Diurnal small mammal activity peaks appeared to shift randomly between sites, habitats and seasons, thereby avoiding predation through unpredictability of activity. Small mammal activity patterns deliberately avoided peak foraging times of raptors during winter at the Pelican site; however this relationship was not linked to any climatic variables to explain how mice avoid high predation periods. Raptors selected peak foraging times during periods of high small mammal activity at the Dune site during winter; however wind speed and cloud cover were correlated with both raptor foraging and small mammal activity, thereby influencing the relationship between the predator and the prey. In conclusion, no re-occurring diurnal peaks in small mammal activity were seen across the three seasons and this may have been an anti-predation strategy, because predators would find it more difficult to predict high prey activity. However the raptors it seemed were selecting periods of high mice activity at one site when weather conditions allowed.

## 1. Introduction

Aerial predators such as raptors spend many hours hunting small mammal prey. These birds as well as small mammal carnivores exert a considerable pressure on small mammals such as mice and shrews. There should therefore be considerable selection pressure on small mammal prey to avoid capture by this array of predators. There is a continuous “arms race” between predators selecting efficient adaptations of catching prey and prey selecting efficient “counter-adaptations” to avoid predation (Dawkins and Krebs, 1979). According to the Life-Dinner Principle, prey should be under stronger selection pressure than their principal predators, and will tend to have some evolutionary advantage over their pursuers (Dawkins and Krebs, 1979). Selection imposed by the predator on the prey is greater, because failure to avoid predation results in loss of “Life-”. This compares to selection imposed by the prey on the predator where failure in capturing prey merely results in the loss of a meal, i.e. “-Dinner” (Dawkins and Krebs, 1979; Griffiths, 1981; Vermeij, 1982).

The efficiency of predators to detect or capture prey depends on the extent to which anti-predatory advantages are effective (Vermeij, 1982). Anti-predatory advantages such as shifts in foraging times are an effective method for prey to avoid predation. However, this is only advantageous in environments where predator-free periods exist or where predation-avoidance periods decrease capture success (Vermeij, 1982; Schmitt, 1982).

Other effective methods of avoiding predation are through habitat selection according to the intensity of predation pressure and type of predators in an area. Korpimäki et al. (1996) found that voles selected different micro-habitats according to the probability of survival from different predators in each habitat. In environments with aerial predators the probability of small mammal survival in sparsely vegetated areas was generally lower than in dense vegetation (Korpimäki et al. 1996; Simmons, 2000; Jacob and Brown, 2000). This is due to the reliance of raptors on seeing and hearing to detect prey therefore greater probability of capturing prey in less dense vegetation (Korpimäki et al. 1996).

There are multiple external variables which influence the behaviour of both predator and prey. For example, climatic factors may highly affect the activity and therefore the trappability of small mammals (Bowland, 1987; Hensbergen and Martin, 1993). High relative humidity for example decreased the activity of some mice populations (Hensbergen and Martin 1993). Windy conditions also increased trap success of small mammal communities in Natal (Bowland, 1987). Furthermore, temperature may be greatly influence small mammal activity, due to their small size, and high surface area to body size ratio. Climate influences foraging activity of raptorial predators as well. For

example, it was found that prey deliveries were significantly reduced during still days compared to windier conditions for African Marsh Harriers (Simmons, 2000). In addition, cloud cover and rain were found to play an important role in hunting success (Simmons, 2000). For example, hunting success of Red-chested Sparrowhawks decreases dramatically during rain (Simmons, 1986).

There are numerous studies on the impact of prey *abundance* on aerial predator numbers and breeding success; however there is little research on the influence of prey *activity* on raptor behaviour (Simmons, 2000; Vermeij, 1982). In a previous study by Simmons (2000), the daily foraging times of African Marsh Harriers (*Circus ranivorus*) were examined and related to the activity patterns of Striped Mice (*Rhabdomys pumilio*) and Vlei Rat (*Otomys irroratus*) populations. Results showed that there were distinct high peaks of Striped Mice activity during dusk and dawn, but no Harriers were seen foraging during these active rodent peaks. However, two more rodent activity peaks were also seen during the day and Harriers not only delivered more prey to their nests at such times but appeared to select these peak activity periods for active foraging (Simmons 2000).

The aim of this study was to re-examine the association between activity of rodents and foraging behaviour for a suite of aerial predators including African Marsh Harriers. The first of such prey-predator relationships were tested with the additional three raptor species: Black Harriers (*Circus maurus*), Black-shouldered Kites (*Elanus caeruleus*) and Rock Kestrels (*Falco rupicolus*). These raptor species are predominately small mammal specialists and their ranges and breeding habitats coincide over certain areas of the west coast, South Africa (Hockey et al., 2005).

Predictions of this study are as follows:

- Based on the Life-Dinner Principle, peak activity periods of small mammals should differ from the foraging times of their aerial predators.
- Small mammal activity in predation-vulnerable habitats would be more affected by raptor activity than in less vulnerable habitats.
- Contrary to the first two predictions, raptors should show tendencies to forage in prey-vulnerable habitats and during periods of high prey activity assuming prey are easier to hunt when they are more active.
- Lastly, temporal anti-predatory patterns of prey were expected to be enhanced when predation pressure is greatest during raptor breeding season in spring.

## 2. Methods

### 2.1 Study Site

Jakkalsfontein Private Nature Reserve (JPNR) is approximately 70Km from Cape Town following the Route 27 on the west coast of South Africa (S 33° 25", E 018° 14"). The reserve was previously used by farmers for low intensity grazing. Since the land was bought in 1989, this area has been protected in a private nature reserve and alien vegetation removed, thus ecosystem processes and behaviour should be close to natural. The dominant vegetation type along this coastal plain consists of strandveld with patches of fynbos further inland (Mucina and Rutherford, 2006). There are a number of pristine wetlands at Jakkalsfontein, which provide favoured breeding areas for both African Marsh Harriers and Black Harriers (Simmons, 2000). Rock Kestrels and Black-shouldered Kites are known to breed within the reserve as well, making sightings of aerial predators more likely in the study area.

Three types of habitats were selected; (i) dense broad-leafed shrubland called strandveld habitat, (ii) wetland habitat and (iii) coastal dune habitat consisting of less than 50% vegetative cover and will be referred to as open habitat. These habitats were selected, because rodent activity patterns may differ within them, thereby potentially influencing patterns of aerial predation. The dominant strandveld habitat is predicted to exhibit greater rodent activity due to greater availability of cover (and thus a lower risk of predation). Wetland habitats are also important to sample, because they are known to act as refugia for mice populations and should have high numbers and activity (Bowland and Perrin, 1993). The open vegetation is expected to have low mice activity; partly because these areas have higher raptor predation success at least for African Marsh Harriers (Simmons, 2000).

To replicate samples I selected two sites that held similar combinations of wetland, strandveld, and open dune habitats. The sites were called Dune and Pelican, and there was approximately one kilometre distance between them (Figure 1). The sites differed according to the following characteristics. The Pelican site had denser strandveld vegetation and the wetland had a larger body of water relative to the Dune site. The open habitat at the Dune site was between two coastal dunes and the open habitat at the Pelican site was near a tarred road which was seldom used. During September a pair of Rock Kestrels and African Marsh Harriers nested near the Pelican site and a pair of Black Harriers nested in the wetland at the Dune site.



Figure 1. Google Earth image of Jakkalsfontein Private Nature Reserve indicating the Pelican study site (S 33°25'04" E 018°14'52") and Dune study site (S 33°25'27" E 018°15'20") which were around 1 km apart.

## 2.2 Sampling methods

The association between raptors and small mammals may change over different seasons. This may be due to increased predation pressure during the raptor breeding season, possibly altering the behaviour of their prey to avoid predation. Therefore, sampling was done over three discrete periods of time. i) During autumn (April and May) which was prior to raptor breeding and predation pressure should be low. ii) During winter (July) as raptors began breeding and predation pressure should increase. iii) During spring (September) when predation pressure should be high from breeding raptors and mice start to breed as well (David and Jarvis, 1985). At least three full days of small mammal trapping and raptor observations were done for each site over each season, except during spring at the Pelican site and during autumn at the Dune site (Table 1). A total of 87 hours of observation were undertaken for raptor hunting at the Pelican site and 110 hours at the Dune site.

Table 1. The number of rodent trapping days and hours observing raptors for the different seasons sampled at each site.

Season	Number of sampling days trapping rodents		Number of hours observing raptors	
	Pelican site	Dune site	Pelican site	Dune site
Autumn	4	2.5	33.3	36.2
Winter	3	3	31.0	41.9
Spring	2	3	22.7	32.2

### *Daily activity of rodents*

It was assumed that rodents are more likely to enter a live trap during periods of increased activity compared to periods of reduced activity. The activity of the rodents was measured by using 60 PVC live traps (Willan, 1979) with 20 traps per habitat. There were 10 trapping stations per habitat which were 10 meters apart and two traps per station which were placed within 1 meter distance. Trapping was done from sunrise to sunset and traps were set and baited with a mixture of oats, apple, and peanut butter in the early mornings at first light. Traps were checked every half hour interval by walking along a circuit which encompassed each habitat transect (Figure 2). The traps were checked 22 times per day in autumn and spring and 21 times per day in winter. One concern was the influence of human disturbance on the activity of the rodents. However mice could be heard going into traps when only two meters away and other studies have found Striped Mice to become accustomed to human presence (Schradin, 2006).

The captured rodents were marked with non-toxic permanent marker to indicate recaptured individuals, which were then released and traps re-baited and set. Total of 1228 small mammals were trapped. Striped Mice were the dominant species caught as well as a few individuals of Vlei Rats, Forest Shrews (*Myosorex varius*) and Hairy-footed Gerbils (*Gerillurus paeba*).

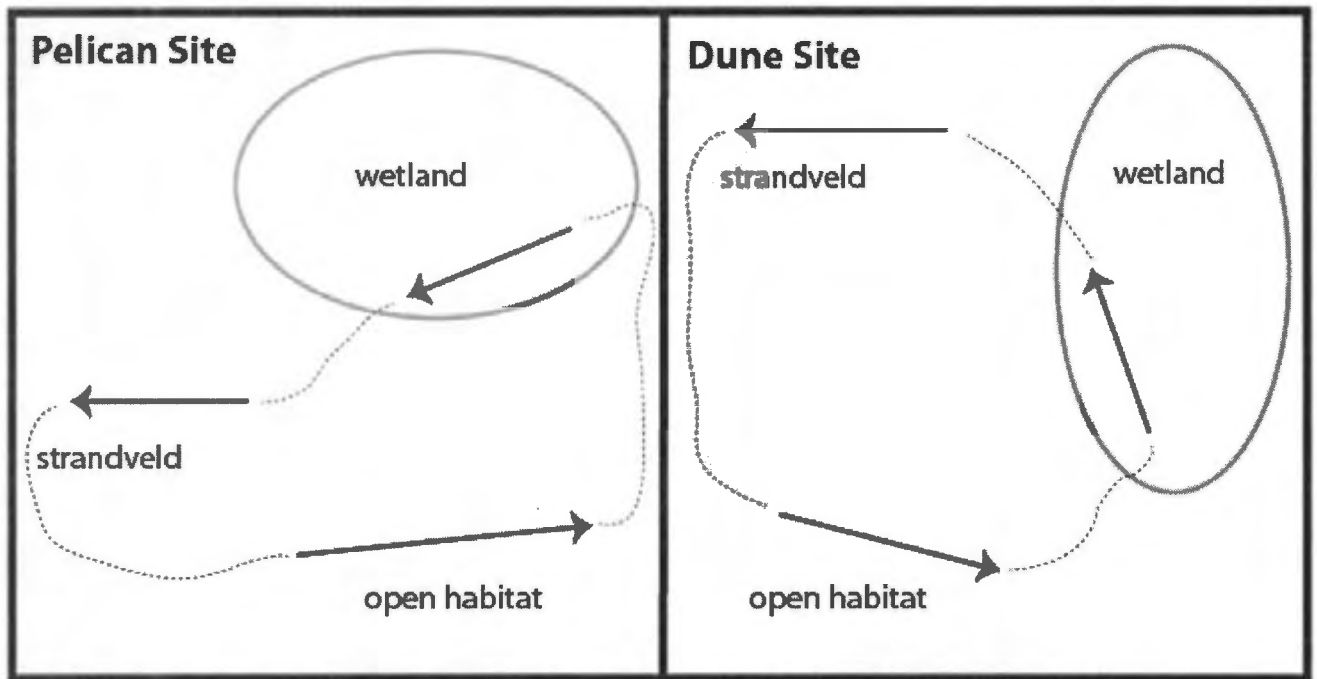


Figure 2. Diagram of experimental set-up and direction walked when monitoring the traps at the Pelican and Dune sites. The solid arrows indicate where the transects were placed, and represent 100m.

### *Raptor sampling*

Raptor observations were viewed either from the top of the highest dune or from the top of a 6 meter look-out post overlooking the study sites. Scan or instantaneous sampling (see Altman, 1974) was done every 2 minutes of the day using 8x42 binoculars. Scan sampling allows for the diurnal variation in activities for all four raptor species (African Marsh Harrier, Black Harrier, Black-shouldered Kite and Rock Kestrel) to be studied together. When a raptor was within 500 meters of the study site the activity was placed into one of the following categories: perched, hunting, hovering and other. The vegetation type and distance from observer in which the activity occurred was captured as well.

### *Climate variables*

Gauging of average wind speeds (km/hr), temperature (°C) and humidity (%) were taken every half hour of the day with a Kestrel® hand held anemometer. The Kestrel® anemometer is claimed to be accurate to 0.1m/s for wind speed readings and  $\pm 0.1^{\circ}\text{C}$  for temperature readings (Russel, 2008). Cloud cover was estimated with ranks from 0 (no cloud cover) to 10 (overcast or misty) and rain was noted as absent or present every half hour.

## 2.3 Data Analysis

### *Climate Variables*

Average wind speed, humidity and temperature were correlated with each other in the program STATISTICA, to determine associations between the different climatic variables. The climatic variables were then grouped into categories. Average wind speed was grouped into 8 categories of 2km/hr intervals, humidity was grouped into 8 categories of 10% intervals and temperature was grouped into 9 categories of 3°C intervals. The number of small mammals trapped was divided by the number of half hours that traps were set within each climatic category. The number of 2 minute intervals that raptors were seen hunting was divided by the total number of 2 minute intervals spent observing within each climatic category. This proportion was then converted into a percentage. The rate of small mammal trapping and percentage time spent foraging by raptors were correlated with each climatic variable in the program STATISTICA. A Mann-Whitney U test was used to compare small mammal activity in the absence and presence of rain. The percentage time raptors spent foraging with rain present and absent could not statistically be compared, due to the way the data was set up.

### *Raptor data*

To be able to analyse foraging behaviour a sample size of at least 30 individuals is recommended in each habitat over each season for each activity (Morrison, 1984). Hovering and hunting were amalgamated into one category called active hunting to increase sample sizes. Wetland habitats were smaller areas compared to open and strandveld habitats, and even pooling across seasons there were insufficient observations to determine foraging behaviour. Therefore the association of small mammal activity cannot be related to foraging patterns of raptors in wetlands and will be excluded from further analysis. Similarly, hunting activity in open areas could also not be analysed for the Dune site and during spring time at the Pelican site due to small sample sizes.

The remaining raptor observations were grouped into half hour time intervals in order to make it comparable to the small mammal data. The amount of time raptors were seen actively hunting per half hour was divided by the amount of time spent observing which gave the proportion of time spent actively hunting per half hour (Altman, 1974). This proportion was converted into a percentage and calculated for each site over all seasons as well as for each habitat.

In the program STATISTICA a Mann-Whitney U test was used to compare the percentage time spent foraging between the two study sites for each season and habitat. A Kruskal-Wallis non-

parametric ANOVA was used to determine the difference in time spent foraging over the three seasons. If there was a significant difference in foraging time then a multiple comparisons test of mean ranks was done to determine where the difference lay. The association between the percentage time raptors spent foraging and daily half hour intervals could not be tested for significance, because replicates were included into the calculation of the percentage time spent foraging.

#### *Small mammal data*

The most suitable method for analysing small mammal count data is through a Poisson General Linear Models (GLM), due to the high number of zeros in the data (O'Hara and Kotze, 2010). "Use of the Poisson distribution implies that the behaviour occurs randomly at a constant rate, that the chance of two or more simultaneous occurrences of the behaviour is negligible, and that the chance that a particular behaviour will occur during an interval is independent of the time that has elapsed since the last occurrence of that behaviour" (Altman and Wagner, 1970).

Using the program RGui 2.13.0 and the packages MASS, *stats* and *sandwich* a Poisson GLM, adjusted Poisson GLM and Quasi-Poisson GLM were done following methods by Zeileis *et al.*, (2011). The Poisson GLM is estimated using Maximum Likelihood and is restricted by the assumption that variance and means are equal. Therefore the coefficient estimates were recalculated using an adjusted Poisson GLM in the *sandwich* package, which also reduces the standard error. To determine if results were influenced by overdispersion due to high number of zeros in the data a Quasi-Poisson GLM was run and the dispersion factor determined.

The Poisson GLM was used to compare the probability of trapping small mammals between study sites and for each study site between seasons and habitats. The model was also run for strandveld and open habitats at each site for each season using hourly time intervals as the parameters. Hourly time intervals were used instead of half hour time intervals to increase replicates when comparing between time categories. This was to avoid comparing between time intervals with only two replicates as well as reduce the number of parameters used in the model. Due to the small sample sizes in the open habitat at the Dune site, the probability of catching small mammals through the day could not be tested.

#### *Association between small mammal and raptor activity*

Correlation analysis was done between the percentage raptor activity and average small mammal activity per half hour using the program STATISTICA. The small mammal activity and raptor activity results were compared over time to determine patterns of activity through the day. In open

habitats the relationship between small mammal activity and raptor activity could not be determined for all the seasons at the Dune site and for spring at the Pelican site due to small sample sizes. If there were significant correlations between small mammal activity and raptor activity, then the climatic variables for that relationship would be analysed further using correlations. This should determine whether or not climatic variables were having an influence on the relationship between small mammal activity and raptor activity.

### 3. Results

#### 3.1 Weather variables

##### *Climatic variables*

Humidity showed a strong positive correlation to cloud cover (Table 2:  $r= 0.814$ ,  $p<0.01$ ,  $N=11$ ). Both humidity and cloud cover were negatively correlated to temperature (Table 2). Wind speed showed a significant negative correlation to humidity (Table 2:  $r= -0.449$ ,  $p<0.001$ ,  $N=112$ ), however wind speed was not correlated to cloud cover (Table 2).

##### *Rodent activity and climate*

There was a significant positive correlation between mice trapped per half hour and temperature (Table 2:  $r= 0.809$ ,  $p<0.05$ ,  $N=9$ ), therefore mice activity increases with increasing temperature and vice versa. Wind speed, percentage humidity and cloud cover showed no significant influence on the number of mice trapped per half hour, even though humidity and temperature were strongly correlated (Table 2).

There was a greater rate of mice trapped in the absence rather than in the presence of rain (Table 2). To determine if lower temperatures (during rain) caused this effect I tested for differences in the temperature when mice were trapped in the rain and with no rain: there was non-significant difference (Mann-Whitney U test: U-value= 771.5;  $N= 140, 15$ ;  $p>0.05$ ). Therefore the decrease in rate of mouse captures during rain was not due to lower temperatures.

##### *Raptor activity and climate*

Wind speed and humidity were significantly correlated to the percentage time spent actively hunting by raptors (Table 2). Raptor activity was found to increase as wind speed increased (Table 3:  $r= 0.783$ ,  $p<0.05$ ), but decrease in activity as humidity increased (Table 3:  $r= -0.892$ ,  $p<0.05$ ). However

humidity decreases with increasing wind speeds and vice versa, due to the significantly negative correlation between humidity and average wind speed (Table 2). Temperature and cloud cover did not influence the percentage of time spent actively hunting (Table 3). Raptors spent 3.5% longer hunting during rain compared to when it was not raining (Table 3).

Table 2. Results for correlations between different climate variables, the average number of trapped rodents per half hour and the percentage of time raptors spent foraging.

<b>Correlation between different climate variables</b>			
<b>Climate variables</b>	<b>r</b>	<b>p</b>	<b>N</b>
Wind speed (km/hr) and average humidity (%)	-0.449	<0.001	112
Temperature (°C) and average humidity (%)	-0.892	<0.001	148
Cloud cover and average wind speed (Km/hr)	0.272	>0.05	11
Cloud cover and average temperature (°C)	-0.679	<0.05	11
Cloud cover and humidity (%)	0.814	<0.01	11
<b>Rodent activity in relation to weather</b>			
<b>Climate variables</b>	<b>r</b>	<b>p</b>	<b>N</b>
Wind speed (Km/hr)	-0.407	>0.05	8
Temperature (°C)	0.809	<0.01	9
Humidity (%)	-0.531	>0.05	8
Cloud cover	0.074	>0.05	11
<b>Rain</b>	<b>Average capture per 1/2 hour</b>		<b>hours</b>
present	0.81 (max=5)		13.5
absent	3.04 (max=13)		196.5
<b>Raptor activity in relation to weather</b>			
<b>Climate variables</b>	<b>r</b>	<b>p</b>	<b>N</b>
Wind speed (Km/hr)	0.783	<0.05	8
Temperature (°C)	0.414	>0.05	9
Humidity (%)	-0.892	<0.01	8
Cloud cover	0.316	>0.05	11
<b>Rain</b>	<b>Percentage activity per time</b>		<b>hours</b>
present	12.58		207.3
absent	9.10		10.1

### 3.2 Raptor data analysis

There was no significant difference between the Pelican and Dune sites for the overall percentage foraging time and over the different seasons (Table 3). In addition, there was no significant difference in the time raptors spent foraging over strandveld habitat between the two study sites

(Table 3). However, there was a significantly greater amount of time spent foraging by raptors in open habitats at the Pelican site than at the Dune site (Table 3:  $U=112$ ,  $N=22,22$ ,  $p<0.05$ ).

Significantly more time was spent actively hunting in autumn than in winter and spring within the Pelican site (Table 4). Percentage time spent hunting was significantly shorter in spring than in winter at the dune site, however this was not significant when only observing strandveld habitat (Table 4). There was no difference in the time spent hunting between autumn and winter in open areas at each site (Pelican:  $U=188$ ,  $N=22,21$ ,  $p>0.05$ ; Dune:  $U=219.5$ ,  $N=22,22$ ,  $p>0.05$ ).

Raptors spent significantly more time hunting in strandveld habitat than open habitat at both sites (Pelican:  $U=72.5$ ,  $N=22,22$ ,  $p<0.05$ ; Dune:  $U=98$ ,  $N=22,22$ ,  $p<0.05$ ). However this takes no account of the relative size of each habitat observed, and the strandveld habitat type covered by far the largest area.

Table 3. Difference in the percentage time raptors spent hunting according to season and habitat between the Pelican and Dune sites using a Mann-Whitney U test.

Mann-Whitney U test between Pelican and Dune sites			
Variables tested	U-value	N1; N2	p-value
All foraging activity	160	22; 22	>0.05
Autumn	170	22; 22	>0.05
Winter	208	21; 22	>0.05
Spring	159	22, 22	>0.05
Strandveld habitat in Autumn	182	22; 22	>0.05
Strandveld habitat in Winter	220	21; 22	>0.05
Strandveld habitat in Spring	182	22; 22	>0.05
Open habitat over all seasons	112	22; 22	<0.05

Table 4. Difference in the percentage time raptors spent hunting between autumn, winter and spring within the Dune and Pelican sites using Kruskal-Wallis non-parametric ANOVA and multiple comparison of mean ranks test.

Kruskal-Wallis non-parametric ANOVA						
	Sum of ranks for seasons			df, N	H-value	P-value
	Autumn	Winter	Spring			
Dune site	802	867.5 <sup>a</sup>	541.5 <sup>b</sup>	2, 66	7.44	<0.05
Pelican site	937 <sup>a</sup>	600.5 <sup>b</sup>	607.5 <sup>b</sup>	2, 65	8.64	<0.05
Strandveld habitat at Dune site	839.5	733.5	638	2, 66	2.61	>0.05
Strandveld habitat at Pelican site	951.5 <sup>a</sup>	544.5 <sup>b</sup>	649 <sup>b</sup>	2, 65	10.36	<0.05

### 3.3 Mouse data analysis

There was a greater chance of trapping fewer small mammals at the Pelican site compared to the Dune site (Table 5: coefficient estimate= -0.849,  $p < 0.001$ ). Therefore rodent activity for each site was analysed separately. Although the dispersion parameter was greater than 1, the coefficient estimates between the Poisson, Quasi-Poisson and adjusted Poisson GLMs were not different, therefore over dispersion should not be problematic. The probability of trapping small mammals in winter and spring was significantly greater than during autumn at the Pelican site (Table 6). At the Dune site there was a greater probability of trapping more small mammals in winter than during autumn (Table 7: coefficient estimate= 0.566,  $p < 0.001$ ). Furthermore, there was a significantly greater probability of trapping small mammals in strandveld and wetland habitats than in open habitats at both sites (Table 6 and 7). This is expected if mice avoid open habitat due to high predation levels or low food resources.

Table 5. Summary of Poisson GLM and coefficients of Quasi-Poisson for small mammal data at the Pelican site compared to the Dune site over all seasons.

Coefficients from quasipoisson	Estimate	Std.Error	z value	Pr(> z )	significance
intercept	0.408	0.035	11.688	0.001	<0.001
Pelican site	-0.849	0.061	-14.035	0.001	<0.001
<b>Dispersion parameter for quasipoisson: 1.422</b>					
AIC: 3254.1					
Null deviance: 1885.0 on 1181 degrees of freedom					
Residual deviance: 1674.3 on 1180 degrees of freedom					

Table 6. Summary of adjusted Poisson, Quasipoisson and Poisson GLM for small mammal data at the Dune site with seasons and habitats as parameters. Strandveld and wetland habitats were compared to open habitat over all seasons and winter and spring were compared to autumn over all habitats.

Coefficients from Adjusted Poisson	Estimate	Std.Error	z value	Pr(> z )	significance
Intercept	-0.549	0.112	-4.897	0.0001	<0.001
Habitat: strandveld	0.775	0.104	7.422	0.0001	<0.001
Habitat: wetland	0.964	0.1	9.665	0.0001	<0.001
Season: winter	0.513	0.103	4.986	0.0001	<0.001
Season: spring	0.261	0.098	2.658	0.0001	<0.001
<b>Dispersion parameter from Quassipoisson GLM: 1.09</b>					
<b>Poisson GLM</b>					
Null deviance: 814.40 on 536 degrees of freedom					
Residual deviance: 670.48 on 532 degrees of freedom					

Table 7. Summary of adjusted Poisson, Quasi-Poisson and Poisson GLM for small mammal data at the Pelican site with seasons and habitats as parameters. Strandveld and wetland habitat were compared to open habitat over all seasons and winter and spring were compared to autumn over all habitats.

Coefficients from Adjusted Poisson	Estimate	Std.Error	z value	Pr(> z )	significance
Intercept	-1.564	0.159	-9.825	0.0001	<0.001
Habitat: strandveld	1.196	0.161	7.449	0.0001	<0.001
Habitat: wetland	1.167	0.165	7.062	0.0001	<0.001
Season: winter	0.566	0.127	4.475	0.0001	<0.001
Season: spring	0.025	0.159	0.154	0.877	>0.05
Dispersion parameter from Quassipoisson: 1.203					
Poisson GLM					
Null deviance: 798.66 on 599 degrees of freedom					
Residual deviance: 686.94 on 595 degrees of freedom					

### 3.4 Association between small mammal and raptor activity

#### *Pelican site*

Two significant peaks in small mammal activity were seen at 10:30-11:30 (coefficient estimate= 1.609,  $p < 0.05$ ) and 13:30-14:30 (coefficient estimate= 1.928,  $p < 0.01$ ) during autumn in the strandveld habitat (Figure 3 and Appendix A: Table A.1). The raptor activity peaks during 12:00 - 12:30 and 13:00-14:30 roughly corresponded to these higher small mammal activity peaks (Figure 3). However, the raptor activity peaks noted during the periods 15:00-16:30 and 17:00-17:30 did not correspond to higher small mammal activity (Figure 3). There was no significant relationship between activity of small mammals and raptors during autumn in the strandveld habitat at the Pelican site (Table 8).

#### *Dune site*

There were no significant peaks of small mammal activity in the strandveld habitat during autumn (Figure 4 and Appendix A: Table A.2). However, the time period 17:00-17:30 appeared to have a high peak in small mammal activity if compared over half hour intervals instead of hourly intervals (Figure 4). There was a high proportion of time spent hunting by raptors at 13:00-14:00 and 16:00 - 18:00 (Figure 4). No significant relationship between small mammal and raptor activity were seen during the day (Table 8).

Table 8. Results from correlation between the activity of small mammals and foraging times of raptors.

	N	r	p
<b>Pelican site</b>			
Open vegetation in autumn	23	0.134	>0.05
Open vegetation in winter	21	-0.271	>0.05
Strandveld habitat in autumn	22	-0.058	>0.05
Strandveld habitat in winter	21	<b>-0.441</b>	<b>&lt;0.05</b>
Strandveld habitat in spring	22	-0.047	>0.05
<b>Dune site</b>			
Strandveld habitat in autumn	22	-0.136	>0.05
Strandveld habitat in winter	21	<b>0.463</b>	<b>&lt;0.05</b>
Strandveld habitat in spring	22	-0.142	>0.05

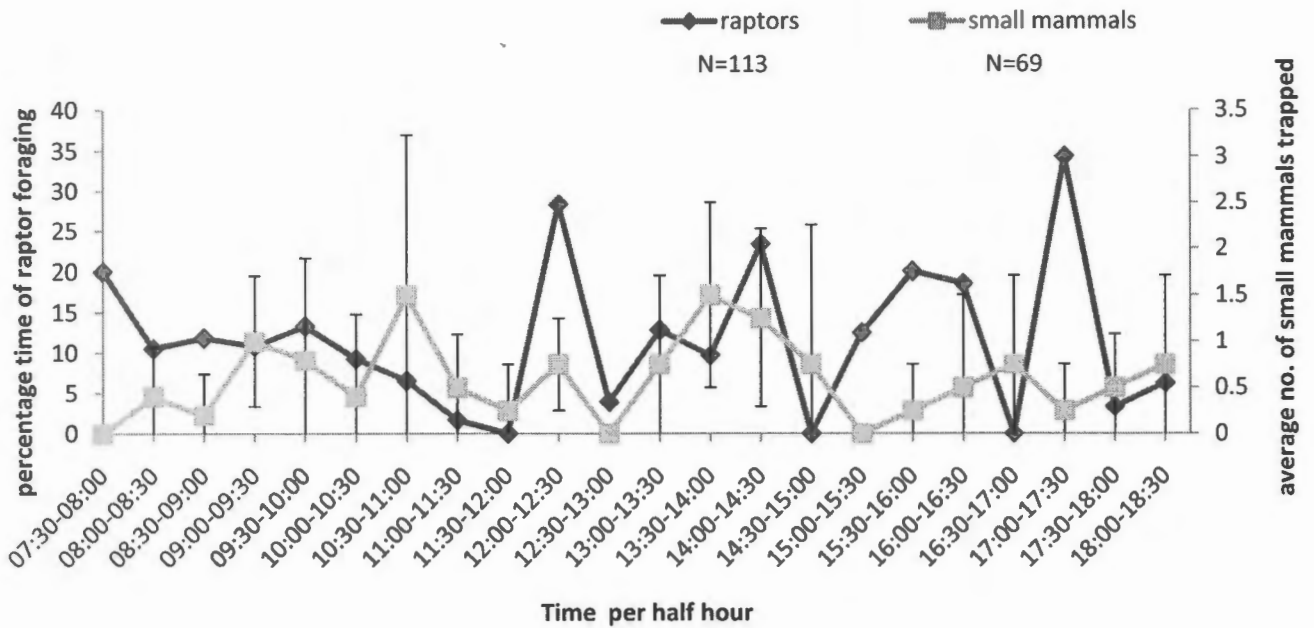


Figure 3. The relationship between raptor foraging time and small mammal activity (with standard deviations) during autumn in strandveld habitat at the Pelican site.

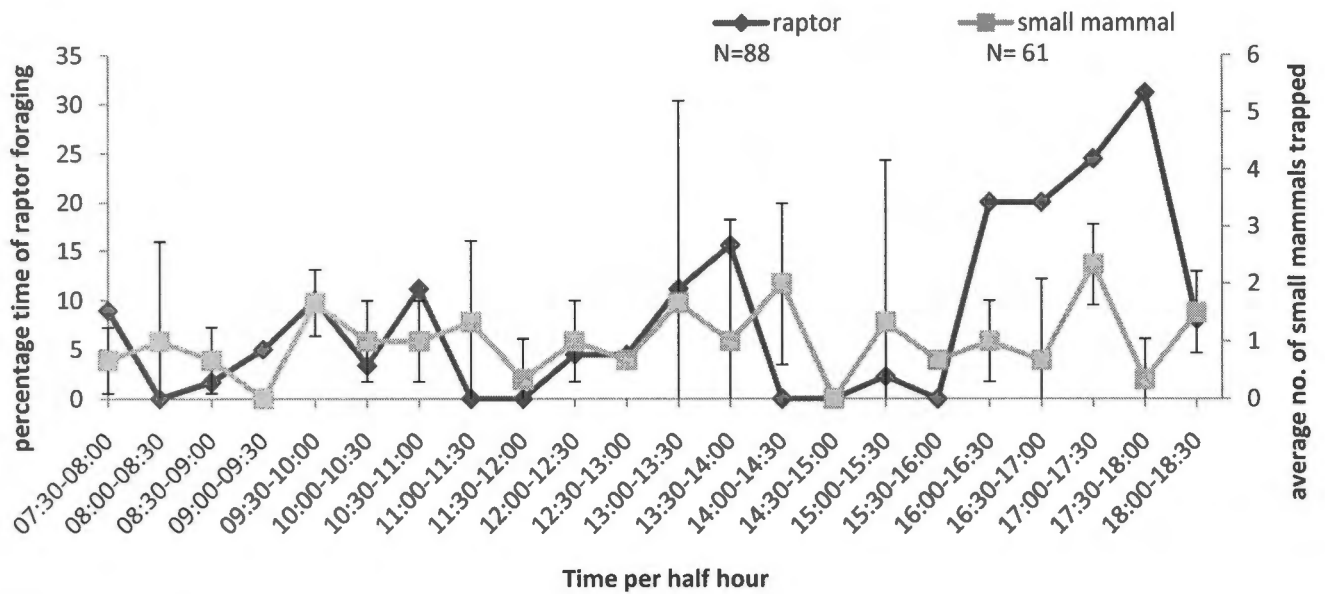


Figure 4. The relationship between raptor foraging time and small mammal activity (with standard deviations) during autumn in strandveld habitat at the Dune site.

#### *Pelican site*

There was a significant negative correlation between small mammal and raptor diurnal activity in the strandveld habitat during winter (Figure 5 and Table 8:  $r=-0.441$ ,  $p<0.05$ ). There was a high peak in small mammal activity from 9:00-13:00, which decreased just before raptor activity increased at 14:00-15:30 and 17:00-18:00 (Figure 5). However the small mammal activity peak was not significantly different from the subsequent decline in activity (Appendix A: Table A.3).

None of the climatic variables tested could explain the changes seen in activity patterns between the small mammals and raptors (Table 9). Therefore small mammals may deliberately avoid predation when predator pressure increases (Figure 5).

#### *Dune site*

The opposite trend was seen in the strandveld habitat at the Dune site during winter. There was a significant positive correlation between small mammal and raptor diurnal activity (Table 8:  $r=0.463$ ,  $p<0.05$ ). The high peak in raptor activity corresponded to the period of high activity in small mammals from 11:30 to 14:00 (Figure 6). The small mammal activity through the day was significantly different from activity during 08:00 to 08:30 (Appendix A: Table A.4).

Wind speed was positively correlated to small mammal activity and the percentage time raptors spent foraging (Table 9). Both small mammal activity and raptor activity were negatively correlated to

cloud cover (Table 9). Furthermore, the percentage time raptors spent foraging was positively correlated to temperature but negatively correlated to humidity (Table 9).

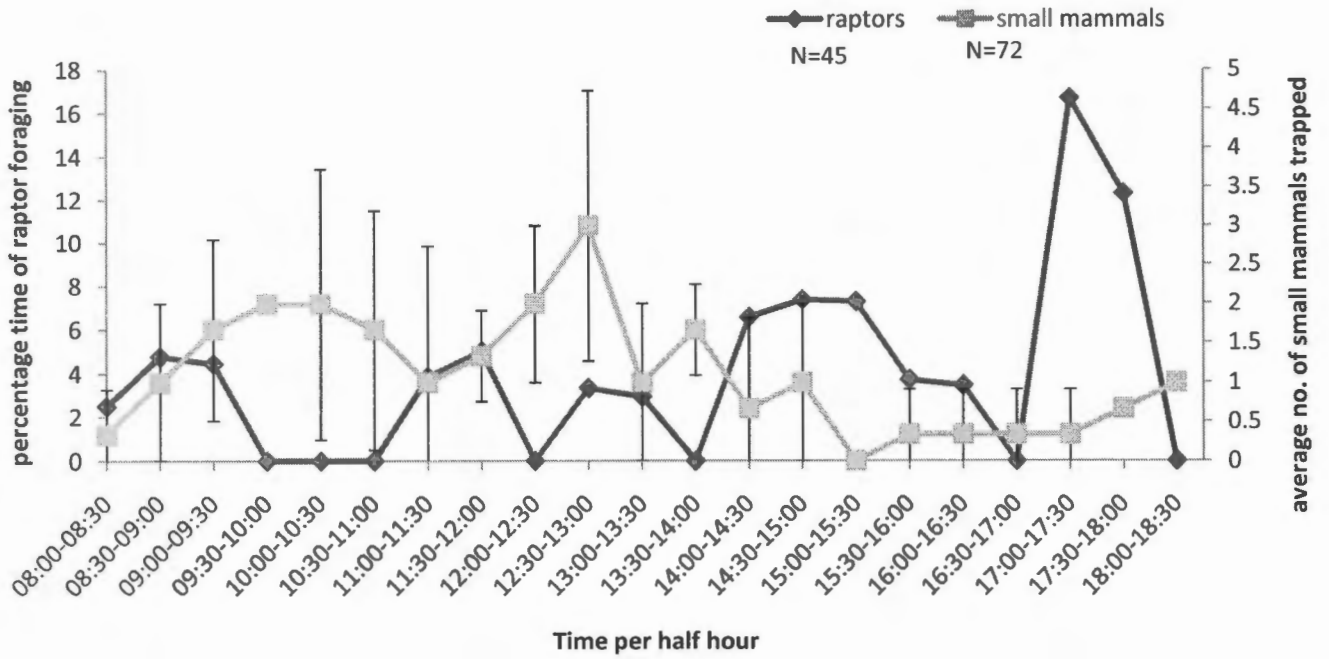


Figure 5. The relationship between small mammal activity (with standard deviations) and percentage time of raptor foraging during winter in strandveld habitat at the Pelican site ( $r = -0.441$ ,  $p = 0.045$ ,  $N = 21$ ).

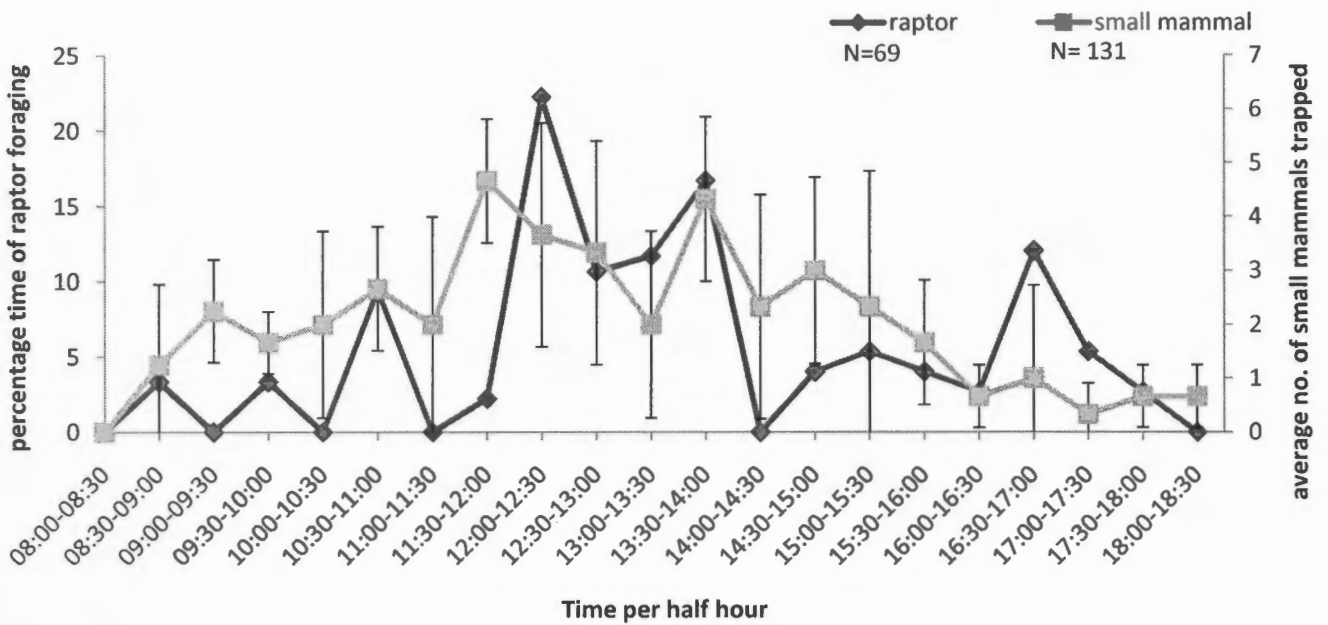


Figure 6. The relationship between small mammal activity (with standard deviations) and percentage time of raptor foraging during winter in strandveld habitat at the Dune site ( $r = 0.463$ ,  $p < 0.05$ ,  $N = 21$ ).

Table 9. Correlation analysis of average small mammal activity and percentage time raptors spent foraging per half hour with the different climatic variables, during winter at the Dune and Pelican sites.

<b>Pelican site</b>			
<b>Variables</b>	<b>r</b>	<b>p</b>	<b>N</b>
Average humidity (%) and rodent activity	0.156	>0.05	21
Average temperature (°C) and rodent activity	-0.124	>0.05	21
Average wind speed (Km/hr) and rodent activity	-0.402	>0.05	21
Average cloud cover and rodent activity	0.417	>0.05	21
Average humidity (%) and raptor activity	-0.06	>0.05	21
Average temperature (°C) and raptor activity	0.009	>0.05	21
Average wind speed (Km/hr) and raptor activity	0.213	>0.05	21
Average cloud cover and raptor activity	-0.102	>0.05	21
<b>Dune site</b>			
<b>Variables</b>	<b>r</b>	<b>p</b>	<b>N</b>
Average humidity (%) and rodent activity	-0.233	>0.05	21
Average temperature (°C) and rodent activity	0.344	>0.05	21
Average wind speed (Km/hr) and rodent activity	<b>0.645</b>	<b>&lt;0.01</b>	21
Average cloud cover and rodent activity	<b>-0.502</b>	<b>&lt;0.05</b>	21
Average humidity (%) and raptor activity	<b>-0.542</b>	<b>&lt;0.05</b>	21
Average temperature (°C) and raptor activity	<b>0.456</b>	<b>&lt;0.05</b>	21
Average wind speed (Km/hr) and raptor activity	<b>0.575</b>	<b>&lt;0.01</b>	21
Average cloud cover and raptor activity	<b>-0.487</b>	<b>&lt;0.05</b>	21

*Pelican site*

There were no significant peaks of activity during spring for small mammals in the strandveld habitat at the Pelican site (Appendix A: Table A.5). There was a high peak in raptor activity during 14:30-15:30, however there was no significant correlation between raptor and small mammal activity (Table 8 and Figure 7).

*Dune site*

There was a significant peak in small mammal activity from 16:30 -17:30 (coefficient estimate= 0.916 ,  $p < 0.01$ ) and an almost significant peak from 09:30-10:30 (coefficient estimate= 0.56,  $Pr|z|=0.061$ ,  $p < 0.05$ ) in the strandveld habitat during spring (Appendix A: Table A.6). Raptor's peak foraging time was between 11:00 and 13:30, during which three peaks occurred (Figure 8). There was no significant relationship between the activity of raptors and small mammals during the day (Table 8). However Figure 8 indicates that small mammal activity peaks were avoiding raptor activity peaks.

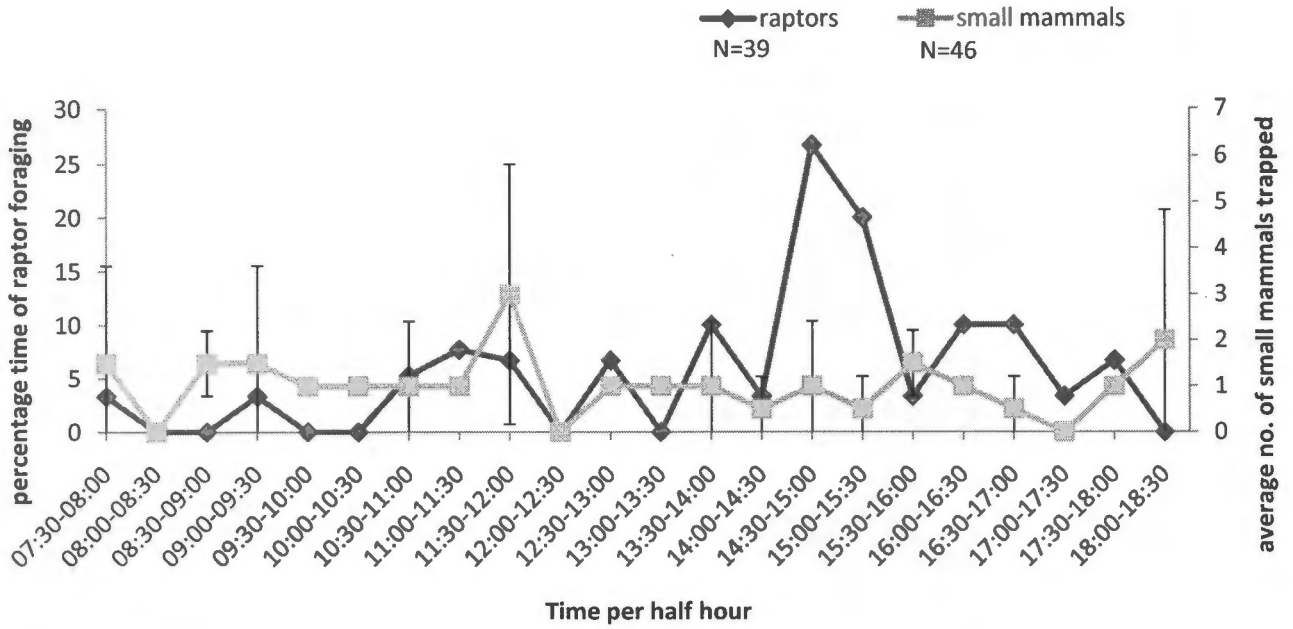


Figure 7. The relationship between raptor foraging time and small mammal activity (with standard deviations) during spring in strandveld habitat at the Pelican site.

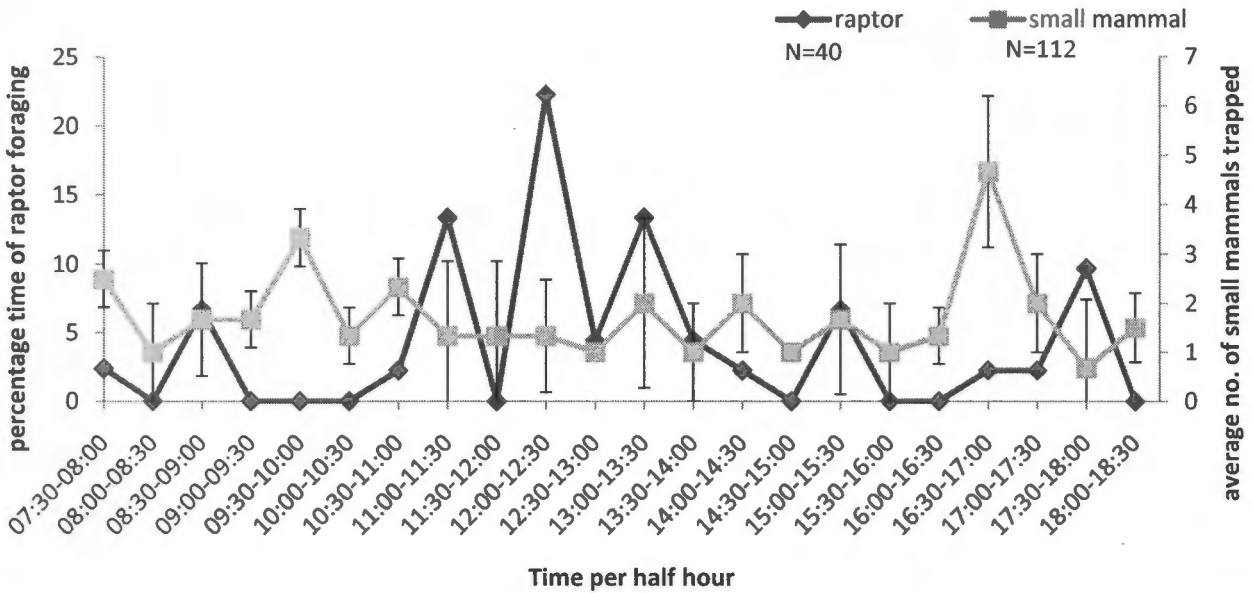


Figure 8. The relationship between raptor foraging time and small mammal activity (with standard deviations) during spring in strandveld habitat at the Dune site.

### *Pelican site*

There were no significant small mammal activity peaks in open habitats during autumn, possibly due to the small sample size (Appendix B: Table B.1). There were four foraging peaks for raptors. The first two peaks occurred over periods of higher small mammal activity from 09:30-11:00 and 12:00-13:00, but the second two peaks occurred over lower small mammal activity from 16:00-16:30 and 17:00-17:30 (Figure 9). However, small mammal activity and raptor foraging activity were not correlated (Table 8).

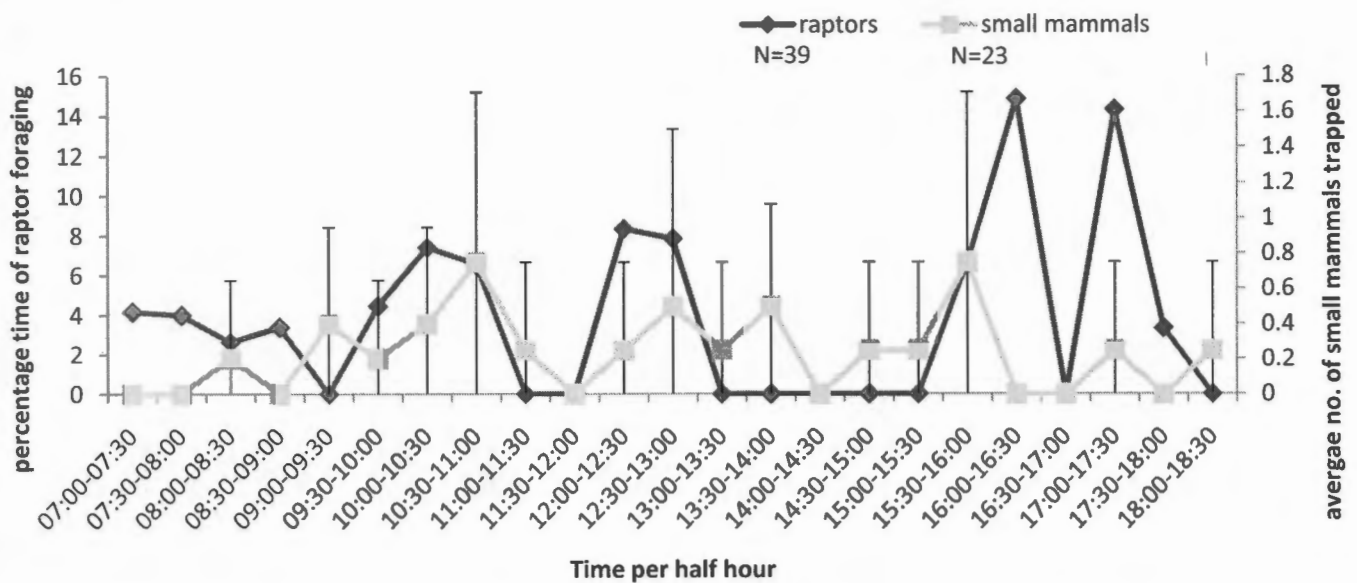


Figure 9. The relationship between raptor foraging time and small mammal activity (with standard deviations) during autumn in open habitat at the Pelican site.

### *Pelican site*

During winter in the open habitat, small mammal activity was significantly higher from 9:30 through to 16:30 than before 09:30 and after 16:30 where no activity was seen (Figure 10 and Appendix B: Table B.2). There were two peaks in raptor activity. One was at 8:30-9:00 during which no small mammals were active and the second was at 11:30-12:00, during which small mammals were active (Figure 10). There was a negative correlation between small mammal activity and raptor activity (Table 8:  $r = -0.271$ ,  $p > 0.05$ ), however it was not significant.

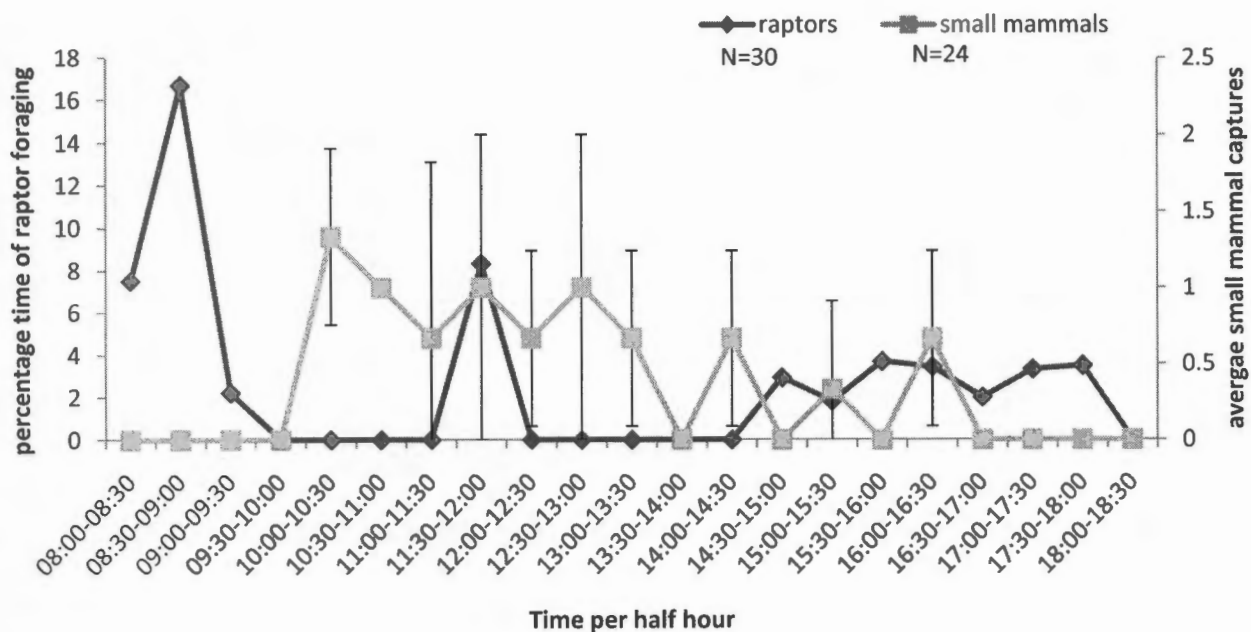


Figure 10. The relationship between raptor foraging time and small mammal activity (with standard deviations) during winter in open habitat at the Pelican site.

#### 4. Discussion

Understanding temporal interactions between aerial predators and their prey will provide insight into their evolutionary relationship and increase our knowledge on behavioural patterns seen. It was predicted that peak activity periods of small mammals should differ from the foraging times of aerial predators if the prey are winning the “arms race” between predators and prey (Dawkins and Krebs, 1979; Simmons, 2000). Furthermore these activity periods may change in different habitats as well as over different seasons depending on predation pressure (Vermeij, 1982; Schmitt, 1982; Jacob and Brown, 2000).

This study found that small mammals were most active during winter at both sites (Table 6 and 7). David and Jarvis (1985) found high seasonal variability in striped-mice populations, with population peaks during breeding season in late spring to summer and low populations during winter and early spring. The high number of striped mice caught in winter may be due to increased activity of mice in search of mates or new territories at the beginning of the breeding season (Hensbergen and Martin, 1993). Another explanation may be an increase in foraging distances and times due to decreased food resources. Temperature was found to significantly influence small mammal activity (Table 2:  $r=$

0.809,  $p < 0.01$ ). Thus small mammals which are active at night, dawn or dusk during autumn and spring may be forced to be active during the warmer temperatures of the day. Therefore, temperature limited activity may explain the higher small mammal activity during winter.

Seasonal shifts in mouse activity may also be due to changes in the probability of surviving predation during different seasons. Raptors spent significantly more time foraging in autumn than during winter and spring at the Pelican site (Table 4). This possibly explains the higher small mammal activity during winter when the predation risk was reduced (Table 7). However there was no difference in time spent foraging by raptors between autumn and winter at the Dune site, yet small mammal activity still increased during winter (Table 4 and 6). Therefore the seasonal changes seen in small mammal activity were more likely due to previously mentioned factors than risk of aerial predation.

Striped Mice generally start their breeding season in spring, however extremely few juvenile mice were seen during this study (David and Jarvis, 1985). Despite the high number of trapped rodents, there was a marked decrease in the number of small mammals trapped from winter to spring (Table 6 and 7). Low mice populations and lack of breeding during breeding season is not abnormal, because mice go through cyclical high and low population peaks over different years (David and Jarvis, 1985). The number of breeding Black Harriers within Jakkalsfontein was very low as well, with only one out of five possible breeding sites which were active. Thus the lack of breeding raptors may be a reflection of low small mammal populations within the area.

It was expected that foraging times of raptors would increase during their breeding season. However there was a decrease in raptor foraging time from winter to spring (during breeding season) at the Dune site (Table 4). This was possibly due to territorial boundaries from the pair of Black Harriers breeding in the wetland. This is a plausible explanation as there was no difference in raptor foraging time when only considering strandveld habitat at the Dune site (Table 4).

Small mammal activity was much greater in strandveld and wetland habitats than open habitats at both sites (Table 6 and 7). This was expected because there was greater vegetative cover in strandveld and wetlands habitats compared to open habitats, thus lower risk of predation (Korpimaki et al. 1996, Simmons, 2000). Raptors spent significantly more time foraging over strandveld habitat than open habitat which was contrary to what was expected from a predation risk point of view (Korpimaki et al. 1996; Simmons, 2000; Jacob and Brown, 2000). However a better indication of predation pressure in habitats would be the number of successful prey captures in each habitat rather than the time spent foraging. Furthermore, strandveld habitat was the dominant vegetation type and

the amount of time spent foraging per unit area would be a better indication of which habitats were preferred. This data could not be collected however.

The peak diurnal foraging times of raptors in autumn were similar over both sites and habitats. There was roughly one peak around midday to early afternoon and another peak in the late afternoon (Figure 3, 4 and 9). However these peaks in raptor activity did not always correspond to small mammal activity peaks (Figure 3, 4 and 9). Therefore, mice activity peaks appeared to occur in no predictable pattern when comparing between sites and habitats during autumn. A similar result was found during spring in the strandveld habitat at the Pelican site: the high peak in raptor activity did not relate to any shifts of small mammal activity (Figure 7 and Table 8). However the lower sample size during spring at the Pelican site possibly resulted in no obvious patterns of small mammal activity. At the Dune site in the strandveld habitat during spring, small mammal activity avoided peak foraging times of raptors (Figure 8). However this relationship was weakly correlated and not significant (Table 8:  $r = -0.142$ ,  $p > 0.05$ ). Furthermore there was an early morning peak in raptor foraging during which no small mammals were active, and a late morning peak in raptor foraging which coincided with high small mammal activity at the Pelican site during winter in the open habitat (Figure 10).

Comparing the small mammal activity over all the seasons and habitats there were no reoccurring time periods of higher or lower activity. Although there were definite peaks in small mammal activity, these seemed to be highly variable. Other studies have found high variability in Striped Mouse activity through the day as well (Choate, 1972; Christian, 1977; Perrin, 1981). These random peaks of small mammal activity may be a strategy to avoid predation, because raptors would be less likely to predict peak activity times of their prey. Therefore on some occasions the prey may be “lucky” and other occasions not so “lucky”. However, there may be some “signal” that small mammals were using to actively avoid predation, as evidence from the negative correlation at the Pelican site during winter (Table 8).

There was a significant correlation between small mammal activity and raptor foraging times at both sites during winter in the strandveld habitat, however these trends were contradictory. Small mammal activity was highest during low raptor activity at the Pelican site (Table 8:  $r = -0.411$ ,  $p < 0.05$ ) compared to high small mammal activity during high raptor activity at the Dune site (Table 8:  $r = 0.463$ ,  $p < 0.05$ ). None of the climatic variables were significantly related to the diurnal activity patterns of rodents and raptors at the Pelican site (Table 9 and Figure 5). Therefore the factor that had the most direct impact on small mammal activity was foraging times of raptors. At the Dune site,

wind speed and cloud cover influenced small mammal activity and raptor foraging times through the day significantly (Table 9). Furthermore temperature and humidity were also correlated to foraging times of raptors but not to small mammal activity (Table 9). Thus the positive relationship between raptor foraging and small mammal activity may be due to their strong association with climatic variables and not necessarily due to raptors selecting foraging times of high small mammal activity.

Some studies have suggested that predator activity patterns and prey avoidance patterns may be linked to humidity (Hensbergen and Martin, 1993). The percentage time raptors spent foraging was negatively correlated with humidity and positively correlated with wind speed (Table 3 and 9). However the association between hunting activity and humidity was most likely due to humidity being negatively correlated to wind speed (Table 2:  $r = -0.339$ ,  $p < 0.05$ ). Wind speed was previously found to be correlated to hunting activity of African Marsh Harriers (Simmons, 2000) as well as positively correlated to small mammal capture rate at night (Bowland, 1987). Although neither wind speed or humidity were related to small mammal activity over all sampling days, there was a significant increase in small mammal activity with wind speed and cloud cover during winter at the Dune site (Table 2 and 9). Therefore when mice activity was correlated to the same climatic variables as raptor activity, their diurnal activity patterns co-occurred. However climatic variables could not explain how small mammal activity avoided peak foraging times of raptors at the Pelican site during winter (Figure 5 and Table 9). Therefore, how rodents avoid peak raptor hunting activity remains unexplained for this study.

The association of diurnal activity between African Marsh Harriers and Striped Mice by Simmons (2000) differed from this study's results. There were no consistent peaks of small mammal activity which raptors were able to select during the day. There was also no early morning and late evening mouse activity peak during which raptors were not foraging. One plausible reason for this difference may be due to the higher predation pressure placed on small mammals by multiple aerial predators coinciding in the same area. This relates to the Life-Dinner Principle, therefore as predation pressure increases, anti-predator advantages become more effective (Dawkins and Krebs, 1979; Vermeij, 1982). Thus it may be more effective for mice to avoid predation by having random peaks of high activity during the day which raptors are unable to predict.

Understanding the relationship between diurnal foraging times of raptors and small mammal activity is complex due to the many variables that may influence behaviour of rodents and raptors. There is not only the influence of season, habitat, time and climate, but also the influence of inter annual cycles, e.g. David and Jarvis (1985). Therefore future long term data is necessary to truly understand

interactions between prey and predator behaviour as well as the influence of environmental change on this relationship.

## **5. Conclusions**

This study shows that the highest small mammal activity was during winter due to increased foraging distances in search of food and new territories, and due to temperature limited foraging times during the day. The low mice populations as indicated from the decrease in the number of trapped rodents from winter to spring and lack of juveniles may explain the low raptor breeding this year. Small mammals were more active in denser habitats than open habitats as expected. However there was no obvious shift in diurnal activity patterns between habitats or over different seasons, due to the variability of peak activity times. There were roughly similar peaks in raptor activity during different seasons and in different habitats. However these peaks were probably influenced by wind speed and other behavioural activities than activity peaks of small mammals. During winter at the Dune site the diurnal patterns of raptor foraging times and small mammal activity co-occurred when they were correlated to the same climatic variables. Small mammal activity patterns deliberately avoided peak foraging times of raptors during winter at the Pelican site; however this relationship was not linked to any climatic variables. Diurnal small mammal activity peaks appeared to shift randomly between sites, habitats and seasons, thereby avoiding predation through unpredictability of activity. In conclusion, the relationship between small mammal activity and raptor foraging times was not as obvious as found by Simmons (2000) possibly due to the greater predation pressure placed on small mammals from multiple aerial predators. Thus results indicate that the prey was more likely to win the “arms race” between predators and prey.

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## Appendix A: Strandveld habitat

Table A.1. Summary of adjusted Poisson, Quasi-Poisson and Poisson GLM for small mammal data in strandveld habitat at the Pelican site during autumn with time as parameters.

Coefficients from Adjusted Poisson	Estimate	Std.Error	z value	Pr(> z )	significance
Intercept	-1.609	0.632	-2.545	0.011	<0.05
08:30-09:30	1.099	0.723	1.52	0.128	>0.05
09:30-10:30	1.099	0.796	1.38	0.167	>0.05
10:30-11:30	1.609	0.766	2.1	0.036	<0.05
11:30-12:30	0.916	0.725	1.265	0.206	>0.05
12:30-13:30	0.629	0.911	0.69	0.49	>0.05
13:30-14:30	1.928	0.67	2.879	0.004	<0.01
14:30-15:30	0.629	1.129	0.557	0.578	>0.05
15:30-16:30	0.629	0.911	0.69	0.49	>0.05
16:30-17:30	0.916	0.806	1.137	0.256	>0.05
17:30-18:30	1.139	0.745	1.529	0.126	>0.05
Dispersion parameter from quasipoisson: 1.27					
Poisson GLM					
Null deviance: 112.681 on 93 degrees of freedom					
Residual deviance: 98.863 on 83 degrees of freedom					

Table A.2. Summary of adjusted Poisson, Quasi-Poisson and Poisson GLM for small mammal data in strandveld habitat at the Dune site during autumn with time as parameters.

Coefficients from Adjusted Poisson	Estimate	Std.Error	z value	Pr(> z )	significance
Intercept	-0.182	0.523	-0.349	0.727	>0.05
08:30-09:30	-0.916	0.779	-1.176	0.239	>0.05
09:30-10:30	0.652	0.54	1.207	0.227	>0.05
10:30-11:30	0.742	0.574	1.293	0.196	>0.05
11:30-12:30	0.182	0.631	0.289	0.773	>0.05
12:30-13:30	0.742	0.758	0.979	0.328	>0.05
13:30-14:30	0.993	0.618	1.608	0.108	>0.05
14:30-15:30	0.182	1.012	0.18	0.857	>0.05
15:30-16:30	0.405	0.551	0.736	0.462	>0.05
16:30-17:30	0.993	0.618	1.608	0.108	>0.05
17:30-18:30	0.182	0.631	0.289	0.773	>0.05
Dispersion parameter from quasipoisson: 1.245					
Poisson GLM					
Null deviance: 66.501 on 48 degrees of freedom					
Residual deviance: 52.289 on 38 degrees of freedom					

Table A.3. Summary of adjusted Poisson, Quasi-Poisson and Poisson GLM for small mammal data in strandveld habitat at the Pelican site during winter with time as parameters.

Pelican site season:winter in the strand only					
Coefficients from Adjusted Poisson	Estimate	Std.Error	z value	Pr(> z )	significance
Intercept	0	0.612	0	1	>0.05
08:30-09:30	0.288	0.677	0.425	0.671	>0.05
09:30-10:30	0.693	0.645	1.074	0.283	>0.05
10:30-11:30	0.288	0.743	0.387	0.699	>0.05
11:30-12:30	0.511	0.639	0.799	0.424	>0.05
12:30-13:30	0.693	0.687	1.009	0.313	>0.05
13:30-14:30	0.154	0.688	0.224	0.823	>0.05
14:30-15:30	-0.693	0.874	-0.793	0.428	>0.05
15:30-16:30	-1.099	0.842	-1.305	0.192	>0.05
16:30-17:30	-1.099	0.842	-1.305	0.192	>0.05
17:30-18:30	0	0.612	0	1	>0.05
Dispersion parameter from quasipoisson: 0.973					
Poisson GLM					
Null deviance: 79.520 on 61 degrees of freedom					
Residual deviance: 59.149 on 51 degrees of freedom					

Table A.4. Summary of adjusted Poisson, Quasi-Poisson and Poisson GLM for small mammal data in strandveld habitat at the Dune site during winter with time as parameters.

Coefficients from Adjusted Poisson	Estimate	Std.Error	z value	Pr(> z )	significance
Intercept	-17.303	0.529	-32.725	0.0001	<0.001
08:30-09:30	17.862	0.623	28.67	0.0001	<0.001
09:30-10:30	17.909	0.57	31.406	0.0001	<0.001
10:30-11:30	18.15	0.621	29.204	0.0001	<0.001
11:30-12:30	18.73	0.574	32.607	0.0001	<0.001
12:30-13:30	18.283	0.672	27.215	0.0001	<0.001
13:30-14:30	18.507	0.683	27.1	0.0001	<0.001
14:30-15:30	18.283	0.59	31.011	0.0001	<0.001
15:30-16:30	17.457	0.72	24.249	0.0001	<0.001
16:30-17:30	16.897	0.912	18.535	0.0001	<0.001
17:30-18:30	16.897	0.589	28.673	0.0001	<0.001
Dispersion parameter from quasipoisson: 0.999					
Poisson GLM					
Null deviance: 118.312 on 65 degrees of freedom					
Residual deviance: 67.237 on 55 degrees of freedom					

Table A.5. Summary of adjusted Poisson, Quasi-Poisson and Poisson GLM for small mammal data in strandveld habitat at the Pelican site during spring with time as parameters.

Coefficients from Adjusted Poisson	Estimate	Std.Error	z value	Pr(> z )	significance
Intercept	-0.288	0.866	-0.332	0.74	>0.05
08:30-09:30	0.693	0.943	0.735	0.462	>0.05
09:30-10:30	0.288	0.866	0.332	0.74	>0.05
10:30-11:30	0.288	0.935	0.308	0.758	>0.05
11:30-12:30	0.693	1.106	0.627	0.531	>0.05
12:30-13:30	0.288	0.866	0.332	0.74	>0.05
13:30-14:30	0	1.027	0	1	>0.05
14:30-15:30	0	1.027	0	1	>0.05
15:30-16:30	0.511	0.883	0.578	0.563	>0.05
16:30-17:30	-1.099	1.225	-0.897	0.37	>0.05
17:30-18:30	0.693	1	0.693	0.488	>0.05
<b>Dispersion parameter from quasipoisson: 1.29</b>					
<b>Poisson GLM</b>					
<b>Null deviance: 52.208 on 43 degrees of freedom</b>					
<b>Residual deviance: 45.354 on 33 degrees of freedom</b>					

Table A.6. Summary of adjusted Poisson, Quasi-Poisson and Poisson GLM for small mammal data in strandveld habitat at the Dune site during spring with time as parameters.

Coefficients from Adjusted Poisson	Estimate	Std.Error	z value	Pr(> z )	significance
Intercept	0.288	0.228	1.261	0.207	>0.05
08:30-09:30	0.223	0.292	0.764	0.445	>0.05
09:30-10:30	0.56	0.299	1.871	0.061	>0.05
10:30-11:30	0.318	0.329	0.967	0.334	>0.05
11:30-12:30	0	0.408	0	1	>0.05
12:30-13:30	0.118	0.38	0.31	0.757	>0.05
13:30-14:30	0.118	0.346	0.34	0.734	>0.05
14:30-15:30	0	0.368	0	1	>0.05
15:30-16:30	-0.134	0.332	-0.403	0.687	>0.05
16:30-17:30	0.916	0.309	2.966	0.003	<b>&lt;0.01</b>
17:30-18:30	-0.065	0.403	-0.16	0.873	>0.05
<b>Dispersion parameter from quasipoisson: 0.743</b>					
<b>Poisson GLM</b>					
<b>Null deviance: 59.522 on 63 degrees of freedom</b>					
<b>Residual deviance: 47.370 on 53 degrees of freedom</b>					