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# A multi-variate analysis of roe deer *(Capreolus capreolus)* population activity

by

**Dennis C. TURNER**

With 6 tables and 1 figure [1]

ABSTRACT

Seasonal and diurnal activity levels of a free-ranging roe deer *(Capreolus capreolus)* population were studied in an agricultural area of eastern Switzerland. For 2 h-diurnal intervals, the proportion of active deer in the population was estimated, and data on environmental factors believed to influence activity were recorded. Data from the crepuscular intervals over 16 months were analyzed separately from diurnal data, collected from dawn to dusk between May and August. ANOVA of all data from crepuscular intervals demonstrated higher population activity levels at dawn, lower levels in spring higher activity during the rut. The effect of lunar cycle on activity levels was not significant. ANOVA of diurnal data showed higher activity levels in the dawn and dusk intervals than in other daylight intervals. When two-way interactions between variables were ignored, wind speed and air temperature were negatively correlated with activity levels. However when such interactions were included in the variance model, time of day and wind speed were no longer significant factors; air temperature remained a significant negative covariable. Neither the number of human-induced, potential disturbances in an interval nor rainfall during the interval had any significant effect on population activity. These results are discussed relative to food intake and energetic constraints in models of herbivore foraging behavior.

## INTRODUCTION

The study of animal activity patterns is a relatively old theme in behavioral research. Of more recent interest are considerations of optimal foraging time, i.e. when and for what duration an animal should actively secure food (SCHOENER 1971; WESTOBY 1974),

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and of ecological factors affecting activity at both the individual and population level (BELOVSKY & JORDAN 1978; MORRISON 1978; TURNER 1975, 1978, 1979).

Most optimal foraging models to date are based on energetic considerations or constraints, assuming that behavior should be directed primarily toward net energy gain (MACARTHUR & PIANKA 1966; NORBERG 1977, PYKE *et al.* 1977; SCHOENER 1971). However WESTOBY (1974, 1978) and PULLIAM (1975) emphasize the importance of nutrient balance and digestibility as constraints in foraging models for herbivores. WESTOBY (1974) stresses the fact that large herbivores are adapted to feeding on abundant vegetation of lower quality, are limited by how fast they can digest food, and are forced to keep the gut filled at all times.

Given these theoretical considerations, a number of hypotheses could be formulated on the influence of environmental factors on population activity levels. This report analyzes the effects of such factors on the activity of a free-ranging roe deer *(Capreolus capreolus)* population. If these animals are indeed forced to feed continuously over the 24 h period (naturally with pauses for rumination), one could expect few differences in population activity levels between different times of day, different seasons, different lunar phases, at different ambient temperatures, with or without precipitation, at high or low wind velocity, etc. On the other hand, diverse selective pressures may have existed or now be operative, including energetic constraints, forcing differences in population activity levels to appear.

## MATERIALS AND METHODS

*Study site.* The study site consists of 200 ha of agricultural cropland near the village of Zizers, Canton Grisons, Switzerland. There is a small forest to the north of the open fields; otherwise only a few wind-rows interspersed over the crop field area offer permanent year-round cover. Detailed maps of the fields were made using aerial photographs, and every 2-3 weeks vegetation heights were recorded for estimates of total amount of protective cover. The entire level field-area is served by a road network, allowing census from an automobile. The study site is bordered on the east by the Swiss National Railway lines and on the other 3 sides by a freeway and the Rhine River.

*Study population.* Between 50 and 80 roe deer inhabit the site (including the small wooded area), depending on hunting pressure each September. Circa 50% of the animals in the population were individually marked at any one time during the study. Many individuals remain year-round in the crop-field area; others move back and forth between the open area and small forest to the north. Movement of animals in and out of the study site is possible, but this rarely occurs (TURNER 1979).

*Data collection.* Observations were made from an automobile, which was driven along a randomly selected route at 10 km/h while the areas to both sides were searched for animals. The extensive road network and routes taken allowed the census of up to 95% of the level field area, depending on the height of the crops. Daylight hours were partitioned into 2 h-intervals, and during each, one census-sampling trip was made throughout the entire study site. The number of standing and lying animals was recorded. To avoid double counts on the same unmarked animal, data were not taken in cases of doubt.

For each 2 h-interval the following data were also recorded: air temperature, precipitation, wind speed, and the number of human-induced, potential disturbances (pedestrians, horse riders, etc.). Censuses were conducted in spring and summer normally

2 to 3 full days each week and in fall and winter normally every second week. No censuses were conducted during or immediately following the hunting season (3 weeks in September). Data were collected between April 1976 and August 1977. To allow a meaningful comparison of activity levels between seasons, the calendar year was partitioned into five phases relevant to the socio-ecology of the deer (see TURNER 1979): The Pre-Fawn phase covered the 6 weeks before the peak in fawning (ca. first week of June). The Post-Fawn phase included the next 6 weeks. The Rut phase spanned the 4 weeks from mid-July to mid-August. Fall phase was from October to December 31; and the Winter-Transition phase was from January 1 to April 1.

Data were collected during 978 field hours, in which deer were spotted almost 5 000 times. These data were coded and keypunched onto cards for computer analysis; statistical tests were conducted using programs available in SPSS (NIE *et al.* 1975) Program Version 7.

*Estimating Population Activity*

An acceptable measure for population activity, or the proportion of the population active during any one interval, was sought. Actual number of animals standing ÷ the population size ($St_i \div PS$) was to be estimated for each 2 h-interval.

The relationship between the total amount of protective cover in the study site and 1) the number of deer seen standing per field hour, 2) lying per field hour, and 3) the total number of deer seen is shown in Figure 1. The negative correlation between the former and each of the latter was so clear that no statistical tests were performed.

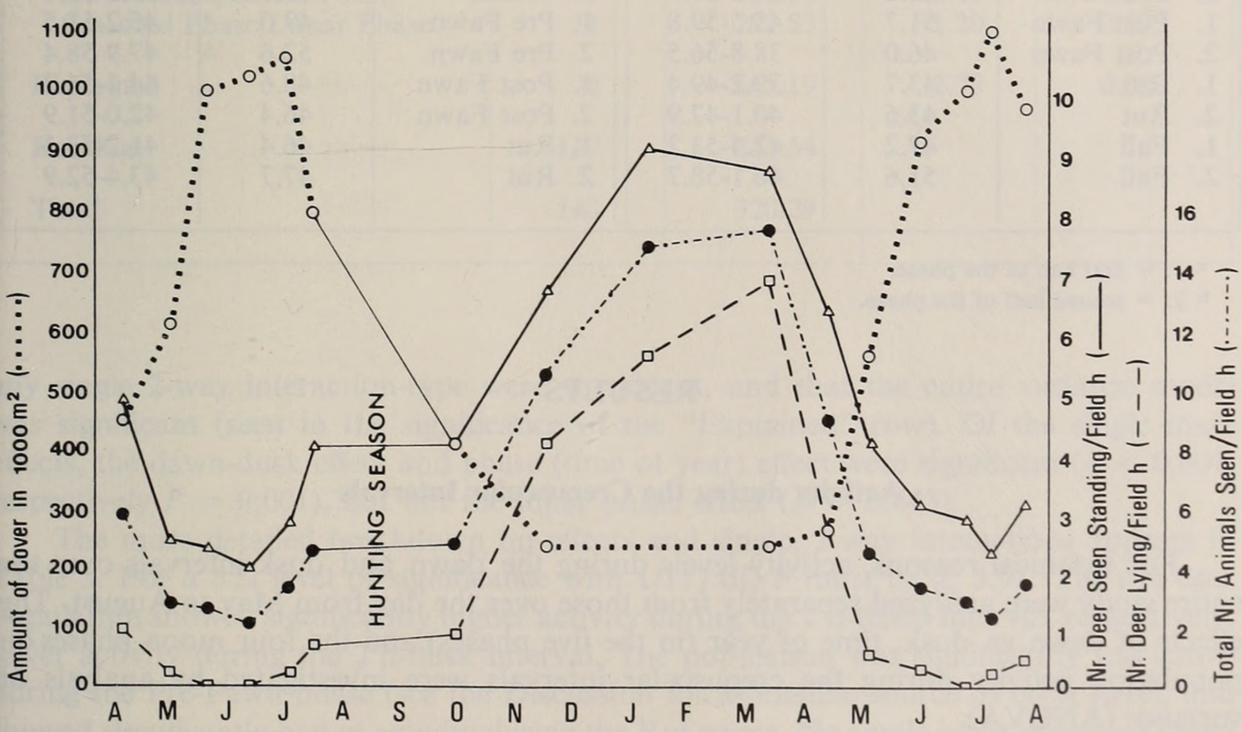


FIG. 1.

The relationship between total amount of protective cover in the study site and 1) the number of deer seen standing, 2) lying, and 3) the total number seen, per hour in the field. (Values represent averages over each half-phase.)

Obviously the optimal choice of measurement for the activity estimate had to utilize the number of deer seen standing, since any measure involving number seen lying, e.g. the ratio of standing: lying, would have resulted in either distorted, zero or undefinable numbers during the summer phase. Since the number of animals seen standing was negatively correlated with the total amount of cover in the study site, this number had to be corrected for the proportion of the site visible at that time.

Population size was estimated, and confidence limits calculated, using mark-recapture (re-sighting) data according to BAILEY (1951). These estimates appear in Table 1.

Both the correction factor for amount of cover and the population size estimates were calculated twice for each phase, i.e. for each half-phase. In the end, the measure of population activity calculated was $St^*_i \div PS^*$, where $St^*_i$ was the estimated number of animals standing in an interval (i), corrected for proportion of the study site visible, and PS* was the estimated population size during the corresponding half-phase.

TABLE 1.

*Population estimates and their confidence limits for each half-phase*

| Half-Phases 1976 | Population Size (PS*) | Confidence Limits | Half-Phases 1977 | Population Size (PS*) | Confidence Limits |
|---|---|---|---|---|---|
| 1.[a] Pre Fawn | 57.4 | 49.8-67.7 | 1. Winter | 62.9 | 58.3-68.3 |
| 2.[b] Pre Fawn | 43.2 | 37.6-50.8 | 2. Winter | 53.1 | 49.7-57.0 |
| 1. Post Fawn | 51.7 | 45.5-59.8 | 1. Pre Fawn | 49.0 | 45.2-53.5 |
| 2. Post Fawn | 46.0 | 38.8-56.5 | 2. Pre Fawn | 52.6 | 47.9-58.4 |
| 1. Rut | 43.7 | 39.2-49.4 | 1. Post Fawn | 48.6 | 44.1-54.2 |
| 2. Rut | 43.6 | 40.1-47.9 | 2. Post Fawn | 46.4 | 42.0-51.9 |
| 1. Fall | 47.2 | 42.4-53.2 | 1. Rut | 46.4 | 41.2-53.1 |
| 2. Fall | 51.6 | 46.1-58.7 | 2. Rut | 47.7 | 43.4-52.9 |

[a] 1. = first half of the phase.
[b] 2. = second half of the phase.

## RESULTS

### Activity during the Crepuscular Intervals

For technical reasons, activity levels during the dawn and dusk intervals over the entire study were analyzed separately from those over the day from May to August. The effects of dawn *vs.* dusk, time of year (in the five phases) and the four moon phases on population activity during the crepuscular intervals were investigated by analysis of variance (ANOVA).

Parametric ANOVAs make three important assumptions to be tested on the residual values: normal distribution, equality of sample variances, and independence of residuals. Independence of residuals was assumed. For the ANOVA on these data, Bartlett-Box F tests revealed no significant differences in residual variances when arranged by phase and dawn *vs.* dusk ($P = 0.262$). (A more detailed breakdown including moon phases was not necessary, since more cells would also yield no significant differences.) Problems arose when the distribution of residuals was compared with the normal distribution by a $\chi^2$-Goodness of Fit test (Pierce & Kopecky 1979; $\chi^2 = 15.9$, 4df significant). A total of 12 transformations were tested, but these showed either 1) no improvement in the $\chi^2$ value, or 2) worsened variance relationships. I therefore decided to continue the analysis of the crepuscular intervals with non-transformed data, where at least the sample variances were not significantly different.

The results of the ANOVA on population activity during dawn and dusk intervals over the entire study are presented in Tables 2 and 3. From Table 2, it can be seen that the main effects *in toto* were significant, that neither the 2-way interactions *in toto* nor

Table 2.

*Analysis of variance of population activity during the crepuscular intervals over time*

| Source of Variation | df | Mean Square | F | Significance of F |
|---|---|---|---|---|
| Main Effects | 8 | 1 403.28 | 5.76 | 0.000 |
| Dawn-Dusk Interval | 1 | 5 901.49 | 24.22 | 0.000 |
| Seasonal Phase | 4 | 1 229.07 | 5.05 | 0.001 |
| Lunar Phase | 3 | 219.58 | 0.90 | 0.443 |
| 2-Way Interactions | 18 | 210.61 | 0.86 | 0.622 |
| Dawn-Dusk/Seasonal Phase | 4 | 47.34 | 0.19 | 0.941 |
| Dawn-Dusk/Lunar Phase | 3 | 116.04 | 0.48 | 0.699 |
| Seasonal Phase/Lunar Phase | 11 | 292.83 | 1.20 | 0.293 |
| Explained | 26 | 665.19 | 2.73 | 0.000 |
| Residual | 117 | 243.64 | | |
| Total | 143 | 320.29 | | |

any single 2-way interaction-type were significant, and that the entire variance model was significant (seen in the significance of the "Explained" row). Of the single main effects, the dawn-dusk effect and phase (time of year) effect were significant ($P < 0.001$, respectively $P = 0.001$), but not the lunar phase effect ($P = 0.443$).

The more detailed breakdown on effects and single, 2-way interactions appears in Table 3. For a 5% level of significance with 1/117 df, F must be $\geqq 3.93$. The roe deer population showed significantly higher activity during the 2 h-dawn interval, respectively, lower activity during the 2 h-dusk interval. The population was significantly less active during the Pre-Fawn phase (see the Discussion for a possible source of error here), and showed significantly higher activity during the Rut phase. No single lunar phase exhibited a significant effect on activity. The effect values for winter phase, +3.326, and the last quarter of the lunar cycle, +0.884, are probably not significant. [For each contrast, e.g. phase, lunar phase, etc., one parameter had to be eliminated to hold the number of parameters equal to the number of degrees of freedom. The effect value of the omitted parameter can be calculated as the negative sum of all other corresponding effect values; but its standard error and significance cannot be determined since the model data are

TABLE 3.

*Breakdown of effects and interactions in the ANOVA of data from crepuscular intervals*

| Variable | Effect and Interactions | Standard Error | F |
|---|---|---|---|
| Dawn | 7.175 | 1.4579 | 24.22 |
| Pre Fawn Phase | −5.142 | 2.5734 | 3.99 |
| Post Fawn Phase | −1.740 | 2.5731 | 0.46 |
| Rut Phase | 9.550 | 2.5223 | 14.34 |
| Fall Phase | −5.994 | 3.9600 | 2.29 |
| Winter Phase | (3.326) | — | — |
| New Moon | −2.537 | 2.4280 | 1.09 |
| 1st-Quarter Moon | −1.590 | 2.6126 | 0.37 |
| Full Moon | 3.243 | 2.4604 | 1.74 |
| Last-Quarter Moon | (0.884) | — | — |
| Dawn/Pre Fawn | −1.380 | 2.4612 | 0.32 |
| Dawn/Post Fawn | 1.616 | 2.5128 | 0.41 |
| Dawn/Rut | 0.741 | 2.4563 | 0.09 |
| Dawn/Fall | −0.177 | 3.3937 | 0.00 |
| Dawn/Winter | (−0.800) | — | — |
| Dawn/New Moon | −0.818 | 2.1830 | 0.14 |
| Dawn/1st-Quarter Moon | 2.088 | 2.3956 | 0.76 |
| Dawn/Full Moon | −2.202 | 2.2970 | 0.92 |
| Dawn/Last-Quarter Moon | (0.932) | — | — |
| Pre Fawn/New Moon | −3.619 | 3.9400 | 0.84 |
| Pre Fawn/1st-Quarter Moon | −0.279 | 3.9147 | 0.01 |
| Pre Fawn/Full Moon | −0.617 | 4.5142 | 0.02 |
| Pre Fawn/Last-Quarter Moon | (4.515) | — | — |
| Post Fawn/New Moon | 2.167 | 4.5038 | 0.23 |
| Post Fawn/1st-Quarter Moon | −3.781 | 4.2355 | 0.80 |
| Post Fawn/Full Moon | −0.358 | 4.1648 | 0.01 |
| Post Fawn/Last-Quarter Moon | (1.973) | — | — |
| Rut/New Moon | 7.676 | 3.9918 | 3.70 |
| Rut/1st-Quarter Moon | −2.778 | 4.1097 | 0.46 |
| Rut/Full Moon | 5.165 | 4.3446 | 1.41 |
| Rut/Last-Quarter Moon | (−10.063) | — | — |
| Fall/New Moon | −7.147 | 5.1130 | 1.95 |
| Fall/Full Moon | 4.302 | 4.8474 | 0.79 |
| Fall/Last-Quarter Moon | (2.845) | — | — |
| Winter/New Moon | (0.923) | — | — |
| Winter/1st-Quarter Moon | (6.838) | — | — |
| Winter/Full Moon | (−8.491) | — | — |
| Winter/Last-Quarter Moon | (0.730) | — | — |
| Grand Mean 42.010 | | | |

not orthogonal. For two-sided comparisons, when one result is significant (e.g. the dawn interval activity, higher), the complementary result is also significant in the opposite direction (e.g. the dusk interval, lower).]

The separate 2-way interactions should be viewed with caution, since neither 2-way interactions *in toto*, nor any of the 2-way interaction-types were significant (see Table 2). The effect values of only two such interactions come into question anyway: The population may have shown less activity during the Rut phase when the moon was in its last quarter. Likewise, population activity may have been lower during the winter phase with full moon. In a preliminary ANOVA, three-way interactions were also not significant.

### Activity over the Day

Between the end of April and mid-August, the diurnal period could be divided into 8, 2 h intervals. For the analysis of environmental influences on population activity levels here, air temperature and wind speed (in classes) were treated as linear covariables; visual inspection of the data indicated that linearity could be assumed. Time of day (in intervals, from 1 to 8), rainfall (yes/no), and the number of human-induced, potential disturbances noted (in classes) were treated as factors. For the ANOVA of these data, similar statistical problems surfaced. The non-transformed residual values were not normally distributed ($\chi^2 = 98.2$, 4df); nor did any transformation produce better results. The test of residual variances also yielded significant differences. However, here the folded-natural logarithm transformation,

$$\mathrm{FLOG}\,(Y) = 50 + 25\,[\log Y - \log (100 - y)]$$

resulted in no significant differences in residual variances (Bartlett-Box F Test, $P' = 0.47$). $Y$ and FLOG ($Y$) are equal at the value 50, the transformation is symetrical around this point, true and transformed values in this range are in quite good agreement, and transformed values stretch from $-\infty$ to $+\infty$ (as in the normal distribution). Therefore, the ANOVA of diurnal data was conducted using this transformation.

TABLE 4.

*Analysis of variance of population activity during the day, excluding 2-way interactions*

| Source of Variation | df | Mean Square | F | Significance of F |
|---|---|---|---|---|
| Covariables | 2 | 12 032.02 | 26.06 | 0.000 |
| Air Temperature | 1 | 18 473.82 | 40.02 | 0.000 |
| Wind Speed | 1 | 9 111.18 | 19.74 | 0.000 |
| Main Effects | 11 | 7 809.13 | 16.92 | 0.000 |
| Interval Number | 7 | 10 853.84 | 23.51 | 0.000 |
| Disturbances | 3 | 765.09 | 1.66 | 0.176 |
| Rainfall | 1 | 1 299.56 | 2.82 | 0.094 |
| Explained | 13 | 19 872.43 | 43.05 | 0.000 |
| Residual | 333 | 461.66 | | |
| Total | 346 | 1 190.96 | | |

RAW REGRESSION COEFFICIENTS
Air Temperature – 1.600
Wind Speed – 6.950

Two-way interactions were not significant in a preliminary ANOVA of these data (Sum of Squares = 307.9; Mean Square = 592.25; F = 1.35; for 5% level of significance with 52/281 df, F $\geqq$ 1.39), and the program was run again with only the covariables and main effects. These results appear in Tables 4 and 5.

From Table 4, it can be seen that the covariables *in toto* and singularly were significant parameters in explaining population activity within the diurnal period. Main effects *in toto*, but only daily interval, as a single main effect-type, were also significant. The entire variance model was likewise significant.

TABLE 5.

*Breakdown of effects in the ANOVA of diurnal activity data*

| Variable | Effect | Standard Error | F |
|---|---|---|---|
| Interval 1 | 31.838 | 3.6830 | 74.73 |
| Interval 2 | 0.106 | 3.4107 | 0.00 |
| Interval 3 | −16.460 | 3.3474 | 24.18 |
| Interval 4 | −13.699 | 3.3048 | 17.18 |
| Interval 5 | −12.209 | 3.4187 | 12.75 |
| Interval 6 | − 8.090 | 3.5028 | 5.34 |
| Interval 7 | − 7.939 | 3.2326 | 6.03 |
| Interval 8 | (26.453) | — | — |
| No Disturbances | (0.972) | — | — |
| 1-2 Disturbances | 2.718 | 2.0843 | 1.70 |
| 3-5 Disturbances | 3.677 | 2.4031 | 2.34 |
| 6+ Disturbances | − 7.367 | 3.6283 | 4.12 |
| No Rainfall | − 2.640 | 1.5733 | 2.82 |
| Wind Speed [1] | − 6.950 | 1.5644 | 19.74 |
| Air Temperature [1] | − 1.600 | 0.2529 | 40.02 |
| Grand Mean 36.815 | | | |

[1] Regression coefficient.

When one considers the detailed breakdown of effects (Tab. 5), the crepuscular nature of roe deer population activity becomes evident. Here, the critical F value for a 5% level of significance with 1/333 df was 3.87. Time intervals 1 and (probably) 8 exhibited significantly higher population activity; intervals 3 to 7 had significantly lower activities, while that for the second daily interval was not significant. Although the effect of all disturbance classes taken together was not significant (from Tab. 4), when six or more disturbances occurred, the negative effect of population activity was significant. It can again be seen in Table 5 that rainfall during the interval had no significant effect, and that the covariables were both significant: the higher the wind speed or the air temperature, the lower the population activity.

Although it was technically incorrect to consider the separate 2-way interactions when these were not significant *in toto*, the difference in F values for significance was very close (F = 1.35 and F $\geqq$ 1.39) and I decided to present the values for just main effects and covariables when 2-way interactions were also taken into the model. These appear in Table 6, where the critical F value remained the same.

Under these conditions none of the single time intervals were significant factors, but air temperature remained as a significant covariable. All other factors and the covariable, wind speed, were, or became, insignificant; i.e. for those that were significant in Tables 4 and 5, their influence as single effects was lost when specific 2-way interactions were included. Instead, several of the single 2-way interactions were significant.

TABLE 6.

*Adjusted breakdown of main effects in the ANOVA of diurnal data, when 2-way interactions were included in the model*

| Variable | Adjusted Effect | Standard Error | F |
|---|---|---|---|
| Interval 1 | 18.353 | 12.5324 | 2.15 |
| Interval 2 | 7.488 | 14.5273 | 0.27 |
| Interval 3 | −10.255 | 16.2493 | 0.40 |
| Interval 4 | − 7.476 | 15.7403 | 0.23 |
| Interval 5 | −11.804 | 16.8838 | 0.49 |
| Interval 6 | − 9.400 | 15.0475 | 0.39 |
| Interval 7 | −10.402 | 14.4176 | 0.52 |
| Interval 8 | (23.496) | — | — |
| No Disturbances | (−13.747) | — | — |
| 1-2 Disturbances | 3.081 | 9.4097 | 0.11 |
| 3-5 Disturbances | − 5.264 | 11.8594 | 0.20 |
| 6+ Disturbances | 15.929 | 18.1696 | 0.77 |
| No Rainfall | − 0.072 | 7.4284 | 0.00 |
| Wind Speed [1] | 2.149 | 6.2004 | 0.12 |
| Air Temperature [1] | − 1.078 | 0.5035 | 4.58 |

[1] Regression coefficient.

## DISCUSSION

From the analysis of crepuscular data over 16 months, the roe deer population at Zizers showed higher activity in the dawn interval, lower activity during the Pre-Fawn phase, higher activity during the Rut and no influence of lunar cycle on diurnal activity.

PRIOR (1968), as well as numerous hunting journalists, have reported effects of the lunar cycle, particularly a negative full-moon effect, on the diurnal activity of roe populations. I instigated a complementary investigation of lunar effects on activity during the night (Baertschi & Turner, in prep.), but neither the present study, nor the nocturnal investigation found any significant effect of moonlight on population activity levels.

Higher activity levels in the dawn intervals were indicated by both analyses. Analysis of only crepuscular data showed higher levels at dawn than at dusk; but analysis of all 8 daily intervals indicated more activity at dawn and dusk than in most of the mid-day intervals. At first glance, this would support ELLENBERG's (1974) notion of "crepuscular deer". However, VON BERG (1978) and TURNER (1978) have demonstrated the periodicity of active and resting bouts for individual animals, and the former author has presented some evidence that dawn and dusk serve as cues ("Zeitgeber") to synchronize activity rhythms. My finding, that higher proportions of the population are active during the dawn and dusk intervals would support this. Rainfall during the dawn interval (and only in this interval) also significantly reduced population activity, again indicative of daybreak as a synchronizing cue. However the reader is reminded that the general interaction-type time interval/rainfall was not significant (nor presented in the results), and should be viewed with caution.

Ambient temperature might also be a synchronizing cue for population activity. When the variance model was adjusted for 2-way interactions (Tab. 6), daily time intervals were no longer significant, but air temperature remained an important negative covariable. At this time of year, heat avoidance may be critical. Whether light intensity, ambient temperature or some other cyclical phenomenon is responsible for synchronizing activity in the population cannot be determined with these data; however, de-synchronization during the day is most probably due to the variable digestion times of foods selected by the individual animals (see TURNER 1978).

Since wind speed influences evaporative cooling, I had hypothesized a positive correlation with activity between April and August. Instead, the negative correlations in Tables 4 and 5 were significant. Olfaction is an important sensory modality in roe deer, and I suspect that too much wind may disrupt their scent-localizing abilities important in predator avoidance. Qualitative inspection of the winter data indicated a negative correlation, which may be related to thermoregulation.

I hypothesized that more human-induced disturbances in an interval would result in higher population activity due to movement between fields. Although disturbances as a main effect-type were not significant (Tab. 4), their breakdown into classes (0, 1-2, 3-5, 6+) in Table 5 showed an interesting trend: It appears that up to six disturbances per interval, the population was indeed more active—a progressively higher proportion of the animals moving around between open fields and cover. At 6 or more disturbances per interval, apparently the animals disappear more permanently into protective cover; here the effect is negative and significant.

Lastly, the seasonal phase effect was significant with lower levels of population activity during the Pre-Fawn phase, and higher levels during the Rut (Tabs. 2 and 3). I have already demonstrated elsewhere, that all age-/sex-classes are involved in time-(and energy-) consuming social behaviors during the Rut phase (TURNER 1979); higher population activity levels were to be expected here. The lower levels during the Pre-Fawn phase may represent the real situation, or they may be due to a systematic error in observation. Most of the lower activity values of the Pre-Fawn phase stem from 1976 data—at the beginning of the study. Implied, is that I spotted a lower proportion of the population standing than in reality, due to beginner's observation abilities. Indeed, a second ANOVA of crepuscular data, excluding the Pre- and Post-Fawn phases of 1976, yielded no significant difference for the remaining, 1977 Pre-Fawn data. (The Rut phase still showed significantly higher activity, and the phase effect, itself, remained significant.) However, the curves for number of deer seen standing and lying (Fig. 1) and the relationship between these two curves is so similar in spring-summer 1976 and 1977, that I seriously doubt a systematic observer error. The reported reduction in population activity during the Pre-Fawn phase also coincided with a reduction in time-costs for energetically expensive behavior in the adult, pregnant females (TURNER 1979).

Although generalization from this particular study site and population to other areas and populations is perhaps unwise, this analysis of roe deer activity produced results which support the food-intake constraints proposed by WESTOBY (1974, 1978): relatively few environmental factors influenced activity levels. Those which had a significant influence were either operative as cues synchronizing activity (daylight, air temperature) or related to bioenergetics (air temperature, wind speed, seasonal differences in energy costs of social behavior and pregnancy). It appears that energetic constraints also play a role in the behavior of this herbivore.

## Zusammenfassung

In einer landwirtschaftlichen Region der östlichen Schweiz wurden jahres- und tageszeitliche Aktivitätsniveaus einer freilebenden Rehpopulation *(Capreolus capreolus)* untersucht. Das Verhältnis der aktiven Rehe in der Population wurde für jedes 2-Std-Tagesintervall geschätzt, und Daten über Umweltsfaktoren, die die Aktivität beeinflussen könnten, wurden aufgenommen. Die über 16 Monate gesammelten Daten der Dämmerungsintervalle wurden getrennt von den Tageszeitdaten (von Morgen- bis Abenddämmerung zwischen Mai und August gesammelt) analysiert. Die ANOVA aller Dämmerungsintervalldaten zeigte eine höhere Populationsaktivität in der Morgendämmerung, tiefere Niveaus im Frühling und höhere Aktivität während der Brunft. Der Einfluss des Mondzyklus auf das Aktivitätsniveau war nicht signifikant. Die ANOVA der Tageszeitdaten zeigte höhere Aktivität während der Morgen- und Abenddämmerungsintervalle als während der anderen Tageszeitintervalle. Wenn 2-weg-Interaktionen zwischen Variablen ignoriert wurden, waren Windgeschwindigkeit und Lufttemperatur mit den Aktivitätsniveaus negativ korreliert. Wurden jedoch solche Interaktionen in das Varianzmodell eingeschlossen, so traten Tageszeit und Windgeschwindigkeit nicht mehr als signifikante Faktoren auf; Lufttemperatur blieb eine signifikante negative Covariable. Weder die Anzahl potentieller menschlicher Störungen noch Regen während eines Intervalls hatten einen signifikanten Einfluss auf die Populationsaktivität. Diese Resultate werden mit Bezug auf Futtereinnahme und energetischen Constraints in Futtersuchstrategie-Modellen für Herbivore diskutiert.



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*Author's address:*

Ethology and Wildlife Research
Zoology Institute
University of Zurich
Birchstrasse 95
CH-8050 Zurich
Switzerland