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Influence of Abiotic Factors on Preroosting Behavior of Greylag Geese (*Anser anser*)

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In socially living birds like Greylag Geese (*Anser anser*), one of the most impressive behavioral propensities of the individual is its effort to keep in contact with the group (Lorenz 1988), that is, keeping track of its partner, family, and flock. This is particularly obvious in the evening, before birds fly to their roosts. In many birds roosting time is strongly influenced by abiotic factors (Eiserer 1984) and follows the rules of endogenous, light-entrained rhythmicity (Gwinner 1975).

Social interactions also have been shown to have entraining (review with bird examples by Mrosovsky et al. 1989) and disruptive effects (Regal and Conolly 1980) on circadian-rhythmic activity. This also may be the case in the timing of the departure to the roost. However, the delaying of the take-off because of social activity could be disadvantageous (e.g. starting or landing late at low visibility may lead to crashes; pers. obs., Schmitt 1991). Thus, one may predict that time of departure should not be affected by social interactions leading to group cohesion (synchronization and coordination caused by head shaking or tossing, vocalizations and adjusting movements; Rav-

eling 1969, Black and Barrow 1985, Black 1988, Lorenz 1988, Schmitt 1988, 1991).

Data necessary to quantify the association between group cohesion and departure time are difficult to collect in wild populations because both abiotic factors and group structure vary daily (e.g. number and identity of individuals). This problem did not exist in the tame flock of Greylag Geese I studied, the very same individuals living together for months at a time. Moreover, the social structure of the flock was stable and known during the summer. Actually, during each of both summers of my study, only three wild immigrants lived for some weeks within the flock and, altogether, only six adult individuals disappeared. Thus, this unique field situation provided an opportunity to determine if abiotic factors influenced both flock synchronization (which was used as a measure of group cohesion) and departure time to the roost, and/or if flock synchronization affected departure time.

Materials and methods.—I observed preroosting behavior in a free-living, but tame flock of about 150 Greylag Geese (mixed population of *Anser anser anser* and *A. a. rubirostris*) in Grünau/Almtal, Austria (47°48'N, 13°57'E) during two summers (22 July to 7 October 1986; 25 July to 11 September 1987). During daily moves between feeding and sleeping areas, the distances covered by the flock roughly corresponded

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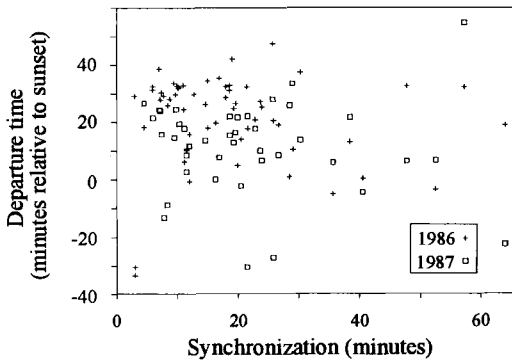


Fig. 1. Relation between departure time to roost (average between departure of first goose and flock) and synchronization of flock. Positive values on Y-axis indicate that departure was after sunset.

to those of wild-living populations (Rutschke 1982, 1987, Wright and Boyd 1983). In the evening, about 2.5 h before sunset, the geese were fed in Ganslbach, a manmade area of about 10,000 m² with a pond and meadows, the amount of food being the same each day. From Ganslbach, the geese flew each evening to their roost (Lake Alm, which is 6 km away).

Observations began about 2 h before take off. I recorded the time the first goose took off and the time when 90% of the geese in the flock had left for the roost ("first" refers to groups of 1 to 65 geese [median 12] that took off together within seconds). The difference between these two times was a measure of flock synchronization. Behavioral measures were evaluated relative to weather, temperature, and light conditions, as well as sunset and day length (extrapolated from *Astronomical Almanac*; Anonymous 1986, 1987; day length decreases regularly by about 3 min per day during summer).

Weather data were provided by the weather station "Almsee" of the Hydrographic Service Austria located about 1 km south of the study site. They were grouped into three categories, separately for evening weather and average daytime weather: sunny (0–50% of sky covered by clouds, estimated to nearest 10%), cloudy (60–100%, no rain) and rainy (100%, rain). It was possible to determine average daytime weather since, during summers, weather typically did not change from morning to late afternoon.

In 1987, I additionally measured illumination level (photocell directed toward zenith, Panlux electronic 2, Gossen, Hamburg, Federal Republic of Germany) and temperature (°C, Hg-thermometer) on the spot at intervals of 2 to 10 min, starting 2 h before the expected take off.

Statistical data analysis was performed by using departure times relative to sunset (with the obvious exception of correlations between take-off time, sunset, and civil twilight). All data presented hereafter

TABLE 1. Summary table of stepwise multiple-regression analysis (criteria for entry 0.05, removal 0.10) on departure time of the flock (1987, $n = 46$).

Variable	R ² change ^a	Partial correlation	P
Illumination ^b decrease ^c	0.915	0.96	0.000
Day length	0.008	-0.32	0.024
Day-length change	0.012	0.20	0.109
Illumination ^b at sunset	—	0.55	0.000
Illumination ^b at take off	—	-0.74	0.000
Temperature decrease ^c	—	0.03	0.440
Temperature at sunset	—	0.21	0.098
Temperature at take off	—	0.22	0.092
Synchronization of flock	—	0.12	0.226

^a — indicates variable did not enter analysis. Total for R² change was 0.935.

^b LOG(lux).

^c Decrease indicates difference between values at sunset and take off of flock.

were normally distributed as checked by the Kolmogorov-Smirnov test, all levels of significance were two-tailed, and all correlations were Pearson's product-moment coefficients. Since variances were not always homogenous (checked by *F*-test), distribution-free tests were used to compare take-off data between the three weather conditions (*H*-test or one-way analysis of variance by ranks after Kruskal-Wallis, Dunn's *a posteriori* test for pairwise comparison of means). Both years were assumed to be independent and weather data were combined using the *z*-values obtained by the Dunn tests (for details of combination method, see Rosenthal and Rosnow 1984). Time is Central European Time (CET).

Results.—Correlations between departure time and flock synchronization were not significant (Fig. 1 and Table 1; 1986, $r = -0.05$, $n = 58$, ns; 1987, $r = 0.23$, $n = 43$, ns). Thus, neither early nor late take off results in low synchronization.

There were no significant differences in average take-off data for sunny, cloudy, and rainy daytime weather in 1986 or in 1987 (*H*-tests for departure time of first goose, for that of flock, and for flock synchronization; all six $H < 2.9$, all $P > 0.19$, n in Fig. 2). In contrast, there were significant differences in average take-off data for sunny, cloudy and rainy evenings for both 1986 and 1987 (Fig. 2). The combination of both years showed that both the first goose and the flock took off earlier on rainy evenings (r) than on cloudy evenings (c ; $P < 0.001$), and earlier on cloudy evenings than on sunny evenings (s ; $P < 0.05$; departure time summed up: $r < c < s$). Synchronization was lower on rainy than on cloudy and sunny evenings (both $P < 0.001$), but cloudy and sunny evenings did not differ ($P > 0.50$; synchronization: $r < c = s$). Rainy evenings were colder and darker than cloudy evenings and those were colder and darker than sunny evenings (temperature, $r < c < s$, *H*-test,

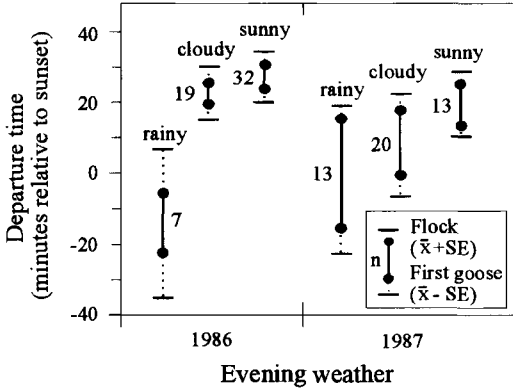


Fig. 2. Departure time to roost and flock synchronization relative to evening weather conditions. Positive values on Y-axis indicate that departures were after sunset. Length of vertical line represents flock synchronization. *H*-tests for differences among the three weather conditions (1986, first goose, $H = 13.9$, $P = 0.003$; flock, $H = 13.7$, $P = 0.003$; synchronization $H = 10.5$, $P = 0.015$; 1987, first goose, $H = 19.3$, $P = 0.0002$; flock, $H = 6.7$, $P = 0.079$; synchronization, $H = 7.4$, $P = 0.059$).

$H = 6.8$, $P = 0.04$; illumination level, $r < c < s$, statistics below). Thus, departure time changed with temperature and illumination level; the colder and darker the evening, the earlier the geese took off. In contrast, no analogous approximate association could be established for synchronization; on cloudy and sunny evenings, the flock was equally well synchronized, whereas temperature and illumination level were significantly different.

Temperature and illumination level not only are important physical variables describing weather conditions, but also change with sunset. Thus, as expected, sunset and departure time were highly correlated (Fig. 3).

The above associations confound influences of light and temperature. In order to better describe the relative importance of both variables in the timing of roosting behavior, illumination level and temperature were measured on site in 1987. Average illumination levels at sunset differed among the three weather conditions (*H*-test, $H = 19.2$, $P < 0.001$; sunny evenings, $\bar{x} = 447$ lux; cloudy, $\bar{x} = 284$ lux; rainy, $\bar{x} = 248$ lux; *n* in Fig. 2), but illumination levels at take off were not significantly different among the three weather conditions (first goose and flock, both $H <$

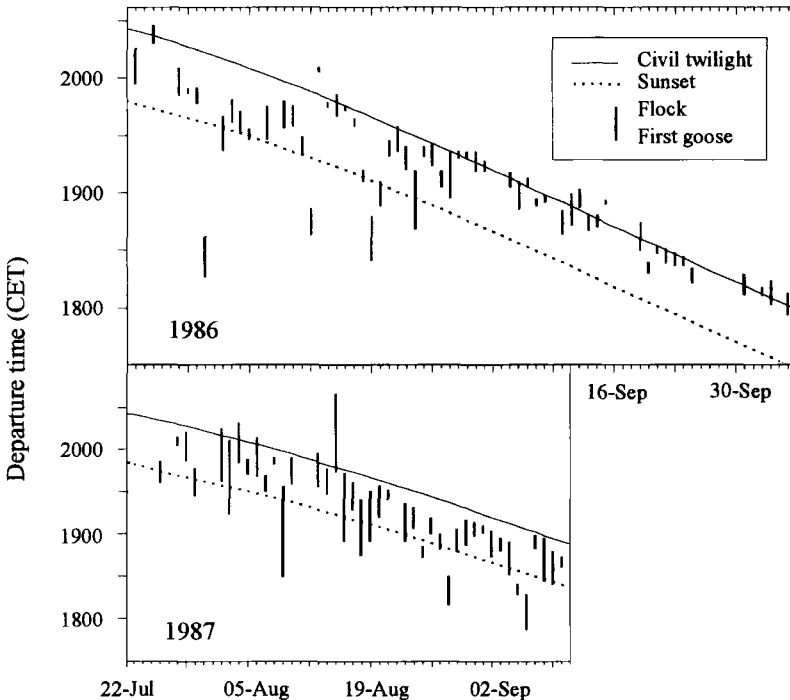


Fig. 3. Departure time, flock synchronization, sunset, and civil twilight. Beginning and end of vertical line indicate departure time of first goose and time when 90% of geese in flock have flown to roost. Length of vertical line represents flock synchronization. Correlations (Pearson's r) between time of sunset and departure time: 1986, first goose, $r = 0.84$, $n = 59$, $P < 0.001$, flock, $r = 0.91$, $n = 59$, $P < 0.001$; 1987, first goose, $r = 0.78$, $n = 45$, $P < 0.001$, flock, $r = 0.83$, $n = 45$, $P < 0.001$.

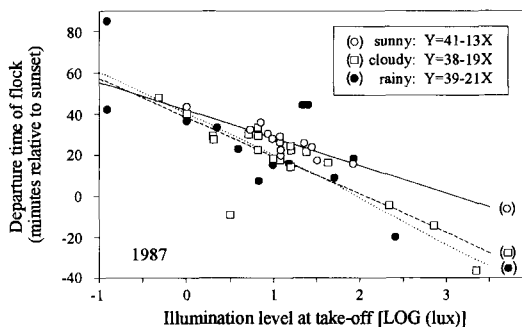


Fig. 4. Relation between illumination level (X) and departure time of the flock (Y). Note that X -axis is logarithmic. Positive values on Y -axis indicate that departure was after sunset (loglinear regression lines for rainy evenings, $r = -0.86$, $n = 13$, $P < 0.0003$; cloudy $r = -0.85$, $n = 20$, $P < 0.0001$; sunny $r = -0.97$, $n = 13$, $P < 0.0001$; linear-regression analyses yielded much lower r of -0.60 , -0.66 and -0.80 , respectively).

1.4, both $P > 0.40$), and varied considerably ($\bar{x} \pm SE$; first goose, 215 ± 31 lux, $CV = 92\%$, $n = 44$; flock, 40 ± 16 lux, $CV = 267\%$, $n = 46$).

Departure time of the flock changed with the logarithm (LOG) of the illumination level (Fig. 4). The regression lines in Figure 4 indicate that geese departed to the roost later at lower illumination levels and earlier at higher levels (e.g. on sunny evening with level of 50 lux, flock would be expected to depart about 4 min earlier than with level of 25 lux).

Multiple-regression analysis explained 93.5% of the variance in departure time (Table 1). The decrease in evening illumination level contributed nearly all of that total, with day length and day-length change being responsible for the remaining small part (in 1986, correlations of day length and day-length change with departure time of flock were $r = -0.45$ and 0.31 ; both $n = 58$, $P < 0.001$ and < 0.02). Thus, change of evening illumination was much more important than illumination per se. Moreover, in contrast to correlations of illumination level with departure time of the flock (Fig. 4), correlations of light decrease with departure time were nearly the same in all weather conditions (rainy evenings, $r = 0.94$, $n = 13$, $P < 0.0003$; cloudy, $r = 0.97$, $n = 20$, $P < 0.0001$; sunny, $r = 0.98$, $n = 13$, $P < 0.0001$). Partial correlations (Table 1) indicate that geese tended to take off to the roost relatively early when light decreased quickly, on long days, and on dark evenings. Temperature variables and flock synchronization failed to predict departure time.

The same multiple-regression analysis on synchronization showed that none of the variables reached the entry limit of 0.05 (0% explained variance; partial correlations were between -0.18 and 0.24 , all ns).

Discussion.—The mutual independence of departure time and flock synchronization, and the results of the multiple-regression analysis strongly suggest that almost none of the variation in departure time is due to variation in social interactions leading to flock synchronization. That is, most of the variation in departure time is due to factors external to the flock (e.g. weather and temperature, and sunset and light, as well as possibly biotic factors like intensity of songs by birds, human disturbances, etc.).

Whereas the influence of the daily amount of solar radiation or of day length and day-length change on departure time have been demonstrated in some birds (Krantz and Gauthreaux 1975, Reeb 1986); in my summer study, departure time of Greylag Geese did not change with weather conditions during the day and was only weakly predicted by day length and day-length change, (e.g. by total amount of sunshine). It has often been demonstrated that birds depart to the roost earlier in rainy or cloudy evening weather and at low temperatures (e.g. Raveling 1969, Davis and Lussenhop 1970, Raveling et al. 1972, Swingland 1976, Clergeau 1983, Reeb 1986 and references therein). My findings show that this is also the case for Greylag Geese for weather conditions, but that temperature conditions (when analyzed together with other variables) fail to predict departure time. The latter may be due to the relatively high summer evening temperatures ($\bar{x} = 14^\circ\text{C}$ at take off, range $7\text{--}22^\circ\text{C}$), which are unlikely to elicit much thermoregulatory behavior.

Evening light conditions strongly influenced departure time. Prerosting behavior might be triggered when a fixed illumination level (threshold) is reached, or light might act continuously, its effects cumulating. Since the former implies that departure time is not correlated with the (invariable) light intensity at take off, the data corroborate the latter. Actually, (i) illumination level varied considerably at take off and was correlated with departure time, the negative slopes of the regression lines in Figure 4 indicating that departure time was a (logarithmic) function of illumination level and time. This last point has also been demonstrated for European Starlings (*Sturnus vulgaris*; Davis and Lussenhop 1970), Rooks (*Corvus frugilegus*; Swingland 1976), Black-billed Magpies (*Pica pica*; Reeb 1986), and Bean or Pinkfooted Geese (*Anser fabalis*; Van Impe 1980; these authors used linear-regression analysis). (ii) Decrease in illumination level, which has not been tested in any other study, explained nearly all of the variance in departure time. Note that action of light seems not to be cumulated over the whole day since there is only a weak influence of day length and day-length change on departure time and none of daytime weather (e.g. sunny vs. cloudy days); exactly when the influence of light starts is an important issue.

As expected, flock synchronization and departure time were mutually independent. Moreover, none of

tested abiotic factors influenced flock synchronization. This raises the question of how synchronization is achieved. At first look, preroosting behavior seems to be a simultaneous interplay of many elements: restless walking around; a decrease in interindividual distances; a menotaxis that induces geese to stand or walk parallel to each other (Schmitt 1991); an increase in the rate of vocalizations and head movements (for details and quantification, see Raveling 1969, Black and Barrow 1985, Schmitt 1988). If all of these behavioral elements are influenced directly and each separately by abiotic factors, these factors must act continuously and consistently on each individual goose in order to synchronize and coordinate the group. Even a slight deviation from continuity (e.g. abrupt changes from dark to bright due to cloud movements) or consistency (e.g. temperatures remain stable, but light varies during thunderstorms; one goose waits for departure while swimming in cold water, while another waits in a grassy area) could disrupt the interplay of social mechanisms. However, if interactions of geese were independent of abiotic factors, efficient flock cohesion would be ensured, but the Zeitgeber function of the environment would be lost. The above theoretical difficulties are removed if only one behavioral element is dependent on abiotic factors and if this element in turn triggers social interactions leading to flock cohesion.

There is circumstantial evidence that locomotor activity is such a behavioral element in Greylag Geese. Actually it is the first behavioral element to change during preroosting (geese get restless about 30 min before take off, Schmitt 1988). Moreover, increased locomotion is associated with an increase in the number of go-away calls and of head movements, which are essential in the self-organizing process leading to group cohesion (Black and Barrow 1985, Black 1988, Schmitt 1988). Restlessness is typical in the preroosting behavior of many other birds and always precedes other behavioral elements (Van Impe 1980, Eiserer 1981, 1984). My results and the above arguments suggest that abiotic factors affect only one behavioral element (probably locomotor activity), which in turn triggers social dynamics. This ensures that abiotic factors determine departure time but do not disturb flock cohesion.

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Does the Early Common Raven Get (and Show) the Meat?

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In the forests of western Maine, Common Ravens (*Corvus corax*) aggregate in large crowds at feeding bonanzas such as carcasses (Heinrich 1988a). A variety of evidence from field observations (Heinrich 1988b, 1989, Marzluff et al. 1994) indicates that the large crowds are primarily the result of recruitment from nocturnal communal roosts, although local enhancement by vocalizations also plays a role in short-range recruitment (Heinrich 1988b, 1989, Marzluff and Heinrich 1991, Heinrich and Marzluff 1991).

While build-up of large numbers is associated with recruitment from roosts, the mechanism whereby this occurs is unknown. There is no obvious vocal signal that birds give when leaving their roosts (Marzluff and Heinrich unpubl. data), so it seems unlikely that knowledgeable birds draw the rest of the roost behind them by way of a vocal display. One hypothesis is that, given a roost containing many hungry individuals that have no knowledge of food, the birds knowledgeable of a bonanza will leave first and the rest follow (Ward and Zahavi 1973). This hypothesis predicts that at new food bonanzas the birds (such as ravens, which can go many days without food; Heinrich 1994a) that have not previously fed should arrive early and in a crowd. Subsequently, after most of the birds are knowledgeable concerning the food source and have become satiated, they no longer have need to follow the early bird, and they should then arrive later and in smaller groups. I here test these predictions.

Methods.—My studies on group numbers and recruitment were conducted in the two winters (November–March) of 1991–1993 in western Maine (see Heinrich 1988b, 1989). Feeding stations of primarily cattle carcasses were provided in the forest. Throughout most of the study, night temperatures were below -15°C and the meat was “rock” hard. Although ravens cache much food when they can tear off chunks (Heinrich 1989), at subzero temperatures the birds can only remove the meat in small chips, and no caching occurred. Flights of birds to the meat were observed every morning from approximately 30 min prior to sunrise until an hour after. Observations of arrivals were made from the tops of spruce trees located at

least 200 m away from the bait. Observations of crowd composition were conducted from blinds constructed of conifer branches within 5 to 10 m of the bait. Additional data on flock sizes from 1987 are also included.

The raven groups were often diffuse and “strung out” at the later stages of a feeding cycle at a bait. This leaves room for interpretation as to what constitutes a group or a “flock.” To be conservative, I defined as a group those birds that arrived approximately within no more than 10 s of each other. In level flight, ravens fly at approximately 50 km/h (as determined by car odometer of birds patrolling along roadsides). Thus, birds as far apart as 150 m were considered to arrive together because they were potentially (and likely) in visual contact of each other. Generally, however, most groups were separated by at least a minute (nearly 1 km).

Known individuals were observed at food patches to determine residence times for estimating the total numbers of birds that may arrive at a bait, as well as the effect of dominance on residence times. The individuals were identified primarily by patagial wing tags (see Heinrich 1988b), although previously unmarked birds were also identified by obvious physical features (e.g. a white wing feather, an unusual bill shape). Twelve of the patagial-marked birds that were observed at the bait came from a pool of 419 released near the site over the previous six years. Seventeen other individuals that earlier had been marked and released near the bait in the current studies were sited at the feeding stations. These birds came from two groups, A and B. All of the birds of group B were first-year birds (for method of identification, see Heinrich 1994a), and all of the birds in group A had molted to adult plumage. Birds of groups A and B were released on 17 January 1993, after having been held in an aviary complex within 1 km of the release site for 12 and 3 months, respectively. The dominance status of these birds had been determined (as described by Marzluff and Heinrich 1991) prior to release and assigned as D (dominant), S (subordinate), or M (intermediate) through a total of 517 dominance interactions. Dominance of the previously uncaged