Vigilance in a flock of semi-tame Greylag Geese *Anser anser* in response to approaching eagles *Haliaeetus albicilla* and *Aquila chrysaetos*

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The valley of the River Alm in the northern Alps is rich in natural wildlife. Particularly in winter, visiting birds of prey are common, including the Golden Eagle *Aquila chrysaetos* and the White-tailed Eagle *Haliaeetus albicilla*. From December to February, these eagles regularly visit the staging flock of semi-tame Greylag Geese *Anser anser* at the Konrad Lorenz-Forschungstelle, triggering alarms and flight reactions. Eagles appeared in more than 80% of the days in January and caused up to ten flights per day. Coarsely estimated, eagles may have triggered some 200 escape responses of the flock during the months December 1991 and January 1992. No goose was lost. While these disturbances may be quite a nuisance for some of our ongoing projects, their high frequency certainly provides an opportunity to highlight quantitatively some aspects of predator-prey interactions. We therefore tried to capitalise on the unique combination of a semi-tame flock and the high density of potentially dangerous aerial predators.

Predator-prey interactions in birds have frequently been studied with the background of AAM's (= sign stimuli; reviewed by Schleidt 1961) and optimal group size (cf. Bertram 1980, Kenward 1978). However, no quantitative data on the response of bird flocks to repeated visits of aerial predators are available.

From optimality theory (Krebs & Kacelnik 1991), one would predict that the escape reaction to any predator would be as effective in minimising the risk of predation as necessary and energetically as cheap as possible; flying is approximately 15 times more expensive than basic metabolic rate (BMR), alert 2.1 times more costly than BMR (Williams 1982) and should therefore be kept to a necessary minimum. It was shown that disturbances may pose considerable costs upon geese (Belanger & Bedard 1990).

The frequency of eagle visits may be used by the geese to judge the potential danger of falling victim to a predator. Therefore, geese may become increasingly wary with increasing numbers of predator visits and their behavioural response should become sensitised. This may be expressed by a positive correlation between air-times, vigilance rates and tightness of flock cohesion with disturbance frequency per day. An unlikely possibility would be the habituation of the response, as expressed by a decrease of reactivity with increasing number of predator visits.

We attempt to test these hypotheses. We also ask whether vigilance rates within the flock differ between days with many eagle visits as compared to days with only a few events.

Methods

Observations were performed in January 1992. For the general flock time budget, one spotcheck per hour on the entire flock was performed for six successive days (16 January 1992 to 21 January 1992) from dusk to dawn. The protocol considered the proportion of geese in the flock performing different behaviours as well as environmental variables. Vigilance means of matching hours were made for days with low (16, 18 and 20 January, ≤3 visits) and high frequencies (17 19 and 21 January, ≤4 visits) of bird of prey visits. Only the afternoon hours, starting with 1200 h were used, because only the second half of the day allows a judgement on the frequencies of predator visits and may therefore show any effect. During the six days of observation, 22 flight reactions of the flock were recorded. Ten of these flights were caused by White-tailed Eagles, two by Golden Eagles. In ten cases the cause for the alarm reactions remained unidentified, which was due to moderate visibility and/or geese detecting an approaching aerial predator at a greater distance than human observers.

At each alert reaction of the flock, additional observations were protocolled. Time of the day, temperature, weather conditions, the predator species causing the disturbance as well as air-time were recorded. Immediately after landing and every minute thereafter for 30 minutes, extreme head up (vigilance, Lazarus 1978, Lazarus & Inglis 1978) frequencies and flock cohesion were assessed by spotchecks. The latter was estimated by using categories from 1 (tight cohesion, average individual distance <1 m) to 4 (widely spaced flock, average individual distance >3 m).

Results

Qualitative observation: The approach of any eagle, White-tailed or Golden, caused some individuals to emit a short, low and rather specific alarm call ("fraa") and the flock took to the air within the next 1 or 2 seconds or rushed to the next pond. When the appearance of an eagle was very sudden, no alarm call was heard and the flock immediately took off. When a Golden Eagle caused the disturbance, geese usually quickly ran to the water of one of the ponds close to the research station, where they waited for the eagle to disappear. Part of the flock may also take to the air at such occasions, but land on water shortly afterwards. In the case of the larger White-tailed Eagle, all geese hectically take to the air and circle the area for several minutes. After landing again on land they form a tight aggregation.

Flock vigilance: No significant difference could be found in the percentage of flock members being vigilant when comparing the means of three afternoons of days with low (≤3 visits, mean vigilance frequency = 7.7%, sd = 3.2) with the three afternoons with high (≤4 visits, mean = 9.0%, sd = 1.5) frequencies of eagle visits. Surprisingly, there was an overall decrease in mean afternoon vigilance over the six days of observations. As eagles were already present one month before the observations started, this overall decrease in vigilance can hardly be explained by habituation (Fig. 1).

There was a significant increase in vigilance frequency with number of disturbances per day immediately after landing (from 30 to nearly 100% of all geese in the flock, Fig. 2; Spearmans, ≤<0.05). However, the decrease of vigilance frequencies did not slow down with increasing numbers of disturbances per day; decrease was always a matter of 2-4 minutes, irrespective of how many disturbances preceded (Fig. 2). There was a slight (statistically insignificant) tendency of lower basic vigilance levels (4-10 minutes after landing, Fig. 2) with number of disturbances. Air-time (av: 54.6 sec, std: 68.7 sec, min: 0 at two of 22 occa-

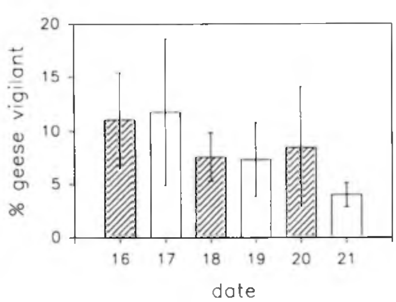

Figure 1. Greylag Goose afternoon (from five spotcheck-protocols each) mean flock vigilance frequencies on the six successive days of the observation period (16 to 21 January 1992). Each bar represents one afternoon mean ± standard deviation. Hatched bars: low frequencies of eagle appearances (≤3 per day); open bars: high frequencies of eagle appearances (4-6 per day).

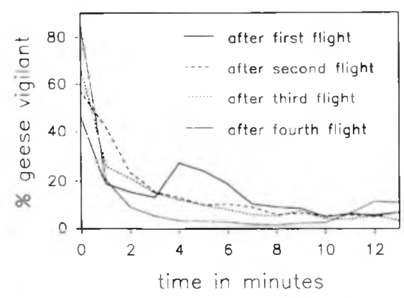

Figure 2. Minute averages of Greylag Goose flock vigilance frequencies after the first, second, third and fourth disturbance per day (based on six observations for all points), starting with the moment of landing following the disturbance.

sions, max: 272 seconds) did not increase with repeated disturbances, but rather was a function of the actual danger as perceived by the geese. This could not be quantified; however, our impression was that the closer an eagle approached before being detected, the longer the air-time. Also, the basic proportion of 7-15% of the flock members being vigilant at any time did not change with the number of disturbances (Fig. 2). Flock cohesion was always tightest immediately after landing.

The pattern as described above is valid for most observations. On two occasions eagles remained within sight of the geese (on a distant tree). Then the decrease of vigilance levels after landing was considerably slower than usual.

Discussion

The relatively minor effect of repeated eagle visits on goose vigilance supports the hypothesis that the predator avoidance response is optimised. The only significant change with repeated disturbances was initial vigilance frequency. As flock vigilance frequencies did not increase with time of the day (not shown), we are confident that this increase does not simply reflect a diurnal change in responsiveness. It even seems that 4-10 minutes after landing vigilance levels decrease with number of disturbances (Fig. 2), which could be due to an habituation effect.

A flock size of 140 is already within the optimum range with respect to predator avoidance (Lazarus 1978, Bertram 1980, Inglis & Lazarus 1981). Our own (unpubl.) observations show that vigilance levels tend to be high in temporarily split-off groups with less than 50 individuals, but show no further decrease of vigilance levels with more than 50 individuals. That group size seems more important than disturbance frequency with respect to vigilance underlines the general validity of Kenward's (1978) results that predation risk decreases drastically with increasing group size.

The drawbacks of capitalizing on such "natural experiments" are evident: time and frequencies of predator appearance as well as its actual threat to the geese cannot be influenced; indeed, geese may react very differently to the appearance of one and the same eagle; a clearly visible Golden Eagle passing the flock in the open skies of the valley rarely triggers an escape, whereas it always will when approaching out of the sun or from the cover of trees.

The functions of vigilance behaviour: Our work was based on the assumption that vigilance behaviour, as indicated by its name, directly furthers the safety of those who practice it by improving their ability to detect and monitor predators (Lazarus 1978). Alternatively, whether "on purpose" or not, the "head up" posture of vigilant geese is a conspicuous display and could well serve as a signal towards fellow flock members or even towards predators. Three alternative hypotheses will be tested with the forthcoming winter flocks:

Vigilance behaviour may indicate the approach of potential danger to neighbours, and prepare the flock for synchronized escape. Low-level warning calls as well as vigilance postures are indeed part of preflight-signalling (Black 1988), which mainly seems to serve group cohesion during departure.

Vigilance frequency may indicate social status. It is potentially expensive (particularly since birds cannot feed while vigilant) and is therefore a candidate for an honest signal (Zahavi 1977, 1991). Within the flock, family ganders, which are the most dominant individuals, also show the highest vigilance frequencies (Lazarus & Inglis 1978, Black & Owen 1989, own unpubl. observations). A few of the highest-ranking family ganders within the flock show an exaggerated version of the vigilance display, where the angle between neck and head axis exceeds 90° and therefore the beak points upwards. This posture was named "Imponiersichern" (Lorenz 1988), suggesting a function of this behaviour in dominance signalling.

Finally, the function of vigilance behaviour may be comparable to stotting in antelopes (Caro 1986). A flock with a large proportion of individuals being vigilant indeed makes a distinctive appearance and may signal to a predator that its targets are alert and may therefore deter that predator (Hasson 1991).

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Appendix: Work with the semi-tame Lorenz-flock continues.

The research station

In 1973, shortly after his retirement from the Max-Planck Institute (MPI) in Seewiesen, Bavaria, Konrad Lorenz found a new home to continue his research on semi-tame Greylag Geese in the Upper Austrian Almtal. After his death, in February 1989, this small research facility with its 140 free-roaming geese was on the brink of being closed. Due to the combined effort of scientists, politicians and the media, work at the Konrad Lorenz

Forschungsstelle für Ethologie (KLF) continues. Goals shifted from classical ethology towards eco-ethology and behavioural physiology, and scientific responsibility was assumed by one of us (JD). We are interested in developing national as well as international research connections, and work proposals are therefore cordially invited. Please contact KK.

Geese in the Almtal

The Almtal Greylags are one of the very few remaining semi-tame bird flocks in the world. Social interactions within this flock were monitored continually, starting in the 1950s at the MPI in Buldern, then in Seewiesen and since 1973 in Grünau. Records are kept for each individual flock member.

The situation of the flock in the Almtal was described by Lorenz (1988) and Lorenz *et al.* (1979). Geese live totally unrestrained, food is provided twice a day. In 1991, the flock consisted of 137 geese, organized in 46 pairs. Twenty-seven birds older than three years were singles, nine of the latter were older than ten years (mainly widowed males). There were 32 one- and two- year old adolescent, unpaired geese. In 1990 and 1991, five families fledged young, which is within the long-term average. The flock is under considerable predation pressure, mainly by red foxes *Vulpes vulpes*, eagles (see above) and Ravens *Corvus corax* (on eggs and young) and remained approximately the same size for the past ten years. During the winter, the geese stay from dusk to dawn close to the research station and spend the nights on a lake, 8 km to the south. In spring, they breed at different locations throughout the valley. After hatching, families gather at an area with ponds and meadows, where they stay to raise their young. Non-breeders moult at the lake nearby. The accessibility of our semi-tame, yet unrestrained flock, and the background of individual records makes the flock a unique model for behavioural observations and experiments.