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Feeding behaviour of the Greylag Goose *(Anser anser)*: A field study

Nahrungserwerb der Graugans *(Anser anser)*: Eine Freilandstudie

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Dedicated to the doyen of Goose Research, Prof. KONRAD LORENZ

Key words: Greylag Goose, *Anser anser*, ecology, behavioural ecology, feeding behaviour, vigilance, aggression.

Abstract

DICK, G. (1988): Feeding behaviour of the Greylag Goose *(Anser anser)*: A field study. Ecol Birds 10: 59-69. In this field study the feeding behaviour of the Greylag Goose *(Anser anser)* as well as the factors influencing this behaviour were quantitatively analysed in the Austrian Lake Neusiedl – Seewinkel area. The main objective was to find out, how the different habitats and the different group sizes of the geese influence their feeding behaviour.

The group size as such did not influence the feeding rate, but the rate varied with different habitats. In this respect winter cereal fields had the highest and the pannonic pasture, Hutweide, the lowest pecking rate. In pairs the female pecked at a higher rate whereas the male was more vigilant in the extreme head up posture. When goslings (= pulli) were present the feeding duration of the adults was significantly shorter. The feeding duration also varied between different habitats. High vegetation lowered the feeding rate and a previously unreported displacement activity was observed for the Greylag Goose. Individuals in bigger flocks were less vigilant than in smaller flocks and the time gained was devoted to feeding and comfort movements. Individuals in flocks of more than a hundred birds were more aggressive than those in smaller flocks which could be explained by the ecological situation.

Zusammenfassung

DICK, G. (1988): Nahrungserwerb der Graugans *(Anser anser)*: Eine Freilandstudie. Ökol. Vögel 10: 59-69. In dieser Freilandstudie wurde das Freßverhalten der Graugans *(Anser anser)*, sowie die dieses Verhalten beeinflussenden Faktoren im österreichischen Neusiedlersee-Seewinkel-Gebiet quantitativ analysiert. Das Hauptziel war es, die Einflußnahme der verschiedenen Habitate und der verschiedenen Truppgrößen der Gänse auf ihr Freßverhalten zu bestimmen.

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Die Truppgröße an sich beeinflußte die Freßrate nicht, aber die Freßrate war auf verschiedenen Habitaten mit verschiedener Nahrung unterschiedlich. Auf den Saatfeldern war die Pickrate am höchsten, auf der typischen pannonischen Hutweide am geringsten. Bei Paaren war die Freßrate beim Weibchen höher, wohingegen der Ganter mehr in der Sicherstellung sicherte. Bei der Anwesenheit von Gösseln (= pulli) war die Freßdauer der adulten Gänse bedeutend kürzer. Die Freßdauer variierte auch zwischen verschiedenen Habitaten. Hohe Vegetation senkte die Freßrate und eine für die Graugans bisher unbekannte Übersprungshandlung wurde beobachtet. Individuen in großen Gruppen sicherten weniger als in kleineren, wobei die gewonnene Zeit für Fressen und Komfortverhalten genutzt wurde. Individuen in Gruppen, bestehend aus mehr als hundert Gänsen, waren aggressiver als in kleineren Gruppen, was durch die ökologische Situation erklärt werden könnte.

1. Introduction

The behaviour of the Greylag Goose *(Anser anser)* has been already well studied by Konrad Lorenz and his co-workers (e.g. Lorenz 1950; Lorenz & Tinbergen 1939; Fischer 1965; Kalas 1977, 1979; Schlager 1981). The geese they have looked at were all imprinted on man, that means that the ecological dimension has been excluded. Even such essential items as food had to be provided by the researchers. One major question of interest that remains unanswered is how is the behaviour influenced by habitat and by social parameters such as group size in the natural environment? Apart from a recent study on the foraging behaviour of the western Greylag *(A. a. anser)* in the Spanish wintering area Doñana (Amat 1986), only a few field studies exist on other goose species (Drent & Eerden 1980; Inglis & Isaacson 1978; Lazarus 1978; Lazarus & Inglis 1978). The objective of this field study was to investigate the factors influencing feeding behaviour, such as habitat, vigilance and aggression. For the feeding rate the impact of habitat and vegetation height was considered. The feeding duration was measured in order to find out whether this is influenced by the presence of goslings or by habitat. The goslings' impact on their parents vigilance as well as the influence of group size on vigilance was also investigated. Finally aggressive events in feeding flocks of various sizes were analysed. The advantageous or disadvantageous influences of varying group sizes is discussed.

2. Study area and methods

This study was carried out from 1981 to 1983 in the Seewinkel area, eastern Austria, close to Lake Neusiedl (for a detailed description of the study area and habitats see Dick 1988). It also includes some supplementary data from 1985. Feeding rates were also measured in the wintering area of these Greylag Geese at Lac Ichkeul in Tunisia (Morgan 1982; Hollis 1986).

The flocks of geese were found by field glasses (10x40) and the observations were carried out with the help of a telescope (30x75). Following the ideas of Dawkins (1971) and White (1971) the data were collected by a tone producing device. Each of the six different tones encodes a certain type of behaviour (e.g. pecking, being vigilant) and is recorded on an ordinary tape recorder, ready to be computerised. Only feeding individuals of flocks on land have been recorded using this method. This was done for a total period of 33 hours and 17 minutes. Because of various disturbances (tourism, agrarian activities, hunting etc.) the length of the records vary between 5 and 20 minutes. The number of birds being vigilant was determined by the scan sampling method (Altmann 1974). The duration of one scan was half a minute and the inter-scan time one minute. One flock was observed for a quarter of an hour, if possible. Individuals in flocks were also observed for a quarter of an hour, if possible, to determine the time they were vigilant using a stop watch. Pecking rates were recorded as pecks per minute and as time for 20 pecks. This ecological pecking rate includes interrupting activities, such as looking up, but this was not measured when the interruption lasted longer than one minute. The observed individuals were selected due to their observational conditions (focal animal sampling, Altmann 1974). A goose flock is defined as two or more birds (Bertram 1978), excluding young ones as long as they are clearly distinguishable from adult birds. The flock is understood to be a unit, separated from neighbouring individuals by approximately 50 meters.

The data were analysed according to conventional statistical methods (Berthold et al. 1974; Kreyszig 1975; Clauss & Ebner 1977; Bortz 1979; Sachs 1984).

3. Results

3.1 Feeding rate

Observations of different group sizes showed, that this had no influence on the feeding rate ($r = -0{,}05$; $p > 5\%$; $n = 80$; means for various group sizes). However, the various habitats (Dick 1988) did influence the feeding rate as listed in Table 1 (normality proved, $\chi^2 = 3{,}208$; $\alpha = 5\%$). The highest value is reached on the winter cereal fields, on which the plants grow in well ordered rows. The pecking rates on the Tunisian Djoumine marsh, which is heavily grazed by cattle, was also relatively high. A similar habitat is the special pannonic pasture, Hutweide, which is not as intensively used by cattle nowadays (approximately 100 cows on 438 ha; Dick & Rauer 1982). For that reason its character has changed compared to the situation of previous decades (Festetics 1970). The feeding rates on the Hutweide were much lower than on the Tunisian grazed marshland (Table 1; $t = 7,6$; $p < 0{,}0005$; $df = 202$). On the meadow inland of the reed belt of Lake Neusiedl the goslings fed at a faster rate than the adults (Table 1).

Table 1. Habitat and feeding rate. For details see text.

Habitat	mean feeding rate pecks/min.	95%-confidence limit	n	significance
winter cereal	60,13	±2,47	248	p<0,025;df=350;t=2,04
marshland	55,46	±3,48	104	n. s.
meadow/paddock (young)	53,75	±3,87	64	p<0,0005;df=244;t=3,79
meadow/paddock (adult)	41,29	±3,56	182	n. s.
Hutweide	37,11	±3,22	100	

3.2 Feeding duration

Short feeding durations were predominant in all group size categories. Splitting the durations into periods of 10 seconds length, the duration class 0,2-10s dominates with over 50% of all durations in every group size category.

There was a statistically highly significant association between the feeding durations of adult geese on the meadow/paddock habitat and the presence or absence of goslings (contingency tabel, $\chi^2_3 = 27{,}2$; $p < 0{,}01$). Short feeding durations were more frequent (0,2-10s: observed 179; expected 158,5) than long durations (>30s:

observed 22; expected 32,7) when goslings were present. The opposite applies when goslings were absent (0,2-10s: observed 68; expected 88,5; $>$30s: observed 29; expected 18,3).
Dividing the feeding durations into bouts lasting less than 50s and more than 50s, the influence of goslings can also be demonstrated using a two by two contingency table. There is a statistically significant association between the following group size categories and the above mentioned duration classes: flocks of more than two birds with goslings, flocks of more than hundred birds ($\chi^2 = 4,45$; $p < 0,05$); pairs, flocks of 3-100 without goslings ($\chi^2 = 8,24$; $p < 0,01$). The class $<$ 50s was more frequent in the observations (420) than expected (412,2) for more than two birds with goslings while the class $<$ 50s was less frequent in the observations (927) than expected (934,7) for the group of more than a hundred birds. The same trend of short feeding durations being more frequent in the presence of goslings is found for pairs ($<$ 50s: observed 720, expected 706,9) and for flocks of 3-100 without goslings ($<$ 50s: observed 1624, expected 1637). No significant association between the two duration classes and the following group size categories could be found for: flocks of 3-100 birds without goslings and more than hundred birds ($\chi^2 = 0,09$; $p > 0,05$); pairs and more than two birds with goslings ($\chi^2 = 0,01$; $p > 0,05$). The group size as such does not have a strong influence on the feeding duration ($r = 0,187$; $p < 0,001$; $n = 1043$).
Apart from the influence of young geese the feeding duration varied with habitat. There is a highly significant association between certain habitats and particular feeding duration classes (contingency table, $\chi^2_{20} = 56, 18$; $p < 0,01$). For the sown cereals and the Hutweide the duration class »longer than 40s« was more frequent in the observations (18 and 25 respectively) than expected (11,1 and 15,2 respectively) whereas the class 0,2-10s was less frequent (89 and 107 respectively) than expected (96,0 and 131,2 respectively). In contrast to these results the duration category 0,2-10s was preferred by geese on maize fields (observed 119; expected 101,7) and rape fields (observed 50; expected 43,7) while long durations occurred less frequently ($<$ 40s: maize: obs. 5; exp. 11,8; rape: obs. 0; exp. 5,1). Similar to these two types of habitat were the stubble fields (0,2-10s: obs. 304; exp. 291,3; $>$ 40s: obs. 21, exp. 33,7). Short feeding bouts did not generally correlate with a higher pecking rate ($r = 0,039$; $p > 0,05$; $n = 168$), which suggests that short bouts are not compensated for by a higher rate.

3.3. Vegetation height and conflict behaviour

Three different categories of vegetation height can be well defined: 1. vegetation covering the feet but at the most the intertarsal joint (abbreviated as »feet«); 2. vegetation covering a goose's breast, being not higher than the base of the neck (»breast«); 3. vegetation being higher than a goose (»over head«), excluding maize fields. Measuring the time which was required for 20 pecks, the time needed increased greatly with increasing vegetation height ($r = 0,99$; $p < 0,05$; $n = 305$). There was also a highly significant association between these three vegetation heights and the time which was required for 20 pecks, when divided into periods lasting less than 30 seconds and more than 30 seconds (contingency table, $\chi^2_2 = 27{,}87$; $p < 0{,}01$). In particular periods of less than 30 seconds were preferred on »feet« vegetation (obs. 192; exp. 177,0; > 30s: obs. 39; exp. 54,0) while more time was required for 20 pecks on »breast« and »overhead« vegetation (»breast«: < 30s: obs. 28; exp. 32,2; > 30s: obs. 14; exp. 9,8; »overhead«: < 30s: obs. 13; exp. 23,8; > 30s: obs. 18; exp. 7,4). As far as the »feet« vegetation is concerned, the association between various categories of time required for 20 pecks and cereal fields and other »feet» vegetation is also significant ($\chi^2_3 = 15{,}22$; $p < 0{,}01$). Particularly the short periods were more frequent in the cereals (10,1-20s: obs. 84; exp. 70,06) compared to the other »feet« vegetations where longer periods were more frequently observed than expected (> 40s: obs. 13; exp. 8,23).

Geese can seldom be observed in high vegetation, this being a habitat with low feeding rates. Nevertheless they sometimes walk into maize fields during autumn or feed in high grass when the goslings are not yet able to fly. Considering »head shaking« (Kalas 1977) and »head on back« (Lorenz 1978) as displacement activities (Tinbergen & Van Iersel 1947) the following observations support the existence of a conflict behaviour in high grass vegetation. One adult goose in a family with four goslings in »over head« vegetation showed a sudden »head on back« movement 20 times, which was very hectically performed, in an observation period of 8 minutes and 36 seconds. This behaviour is a comfort movement under normal conditions and includes head rolling on the back to distribute the rump's secretions. In addition the same goose performed »head shaking« 29 times in the same period of time. Another goose in the same vegetation height performed »head shaking« 12 times per minute on average ($n = 10$), with a maximum of 20 times in one minute. These observations date from early June, when the goslings are still flightless. After this period of time no geese were observed in this habitat of high vegetation.

3.4 Vigilance

The identification of look up (= Aufschauen), head up (= Normalhaltung) and extreme head up (= Sichern) is as defined by Fischer (1965). The median of the proportion of time spent vigilant (extreme head up. Fig. 1) in males was significantly greater (median = 56,6; $n = 10$) than that of females (median = 16,4; $n = 10$) ($U = 6$; $p < 0{,}001$; Mann-Whitney U-test). The males, being more vigilant, spent a lower proportion of time for feeding (male, median: 20,3; female, median: 70,06; $U = 2$; $p < 0{,}05$; Mann-Whitney U-test) and also had a lower mean feeding duration (male: 6,7s; female: 15,2s; $n = 412$). A comparison was made between the time which was required for 10 pecks by males (median = 9,4s) and females (median = 8,1s), indicating that there was no significant difference ($U = 639$; $n_1 = 38$; $n_2 = 43$, n.s.; Mann-Whitney U-test). Thus ganders do not compensate their low feeding duration by a higher feeding rate. The frequencies of the extreme head up posture of males did not differ between pairs alone and pairs with goslings ($U = 5$; n.s., $n_1 = 6$; $n_2 = 4$; Mann-Whitney U-test). There was however a difference in median percentage vigilance (extreme head up) between females in pairs with (n = 6) and without (n = 4) goslings (females with goslings 26,7; females without goslings 0,9; U = 0; p = 0,005; Mann-Whitney U-test). Females in pairs are therefore more vigilant when goslings are present. There was no difference in look ups and head ups between males and females in pairs (Mann-Whitney U-test, n.s.). As more than half of the pair's time is devoted to feeding and vigilance, then inherently both parameters are expected to show a negative correlation with each other if they vary. The vigilance behaviour of the Greylag is organised so that if it is more vigilant, the duration of vigilance bouts is longer (Fig. 2; cf. McVean & Haddlesey 1980). The number of vigilance bouts and the mean vigilant duration are positively correlated ($y = 10,68 + 0,35x$; $r = 0,29$). This need not be so as an increase in vigilance could also be achieved by increasing the number of short vigilance bouts (Metcalfe 1984).

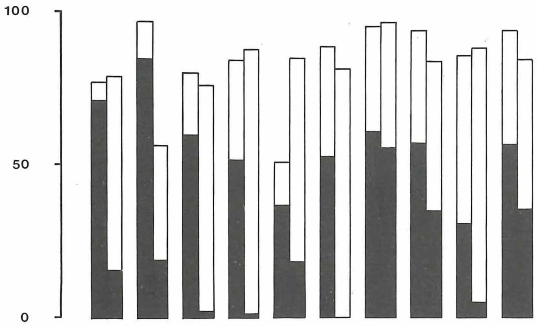
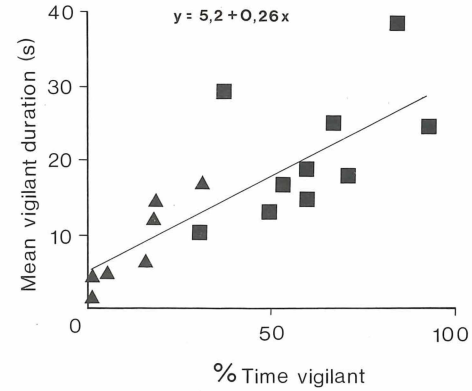


Fig. 1. Frequency distribution of extreme head up (black columns) and feeding (white columns) in ten pairs per behavioural record. The first column represents the male.

With respect to various group sizes, the proportion of individuals being vigilant becomes smaller as the group size increases (Fig. 3; Inglis & Lazarus 1981). Also individuals in larger flocks do better by spending less time being vigilant (Fig. 4) and it is quite remarkable that the variation in smaller groups is higher. The vigilance durations do not vary significantly with flock size ($r = -0,03$; $p > 0,05$; $n = 206$), but the proportion of comfort movements is higher in the observations of groups consisting of more than 100 birds than in groups of less than 100 birds (data divided by 100 and transformed after $x' = 2.\sin^{-1}.\sqrt{x}$; $\bar{x}' \geqq 100 = 35,05$; $\bar{x}' < 100 = 21,6$; $t = 2,95$; $df = 74$; $p < 0,005$). A lower proportion of vigilance (extreme head up) correlates with a higher proportion of feeding and comfort movements ($y = 74,13 . 0,97^x$; $r = 0,7$; $p < 0,001$; $n = 76$) which underlines the advantage ob bigger flocks. On the other hand no correlation between the percentage of time spent in head up posture by individuals and group size was found ($r = 0,027$; $p > 0,05$; $n = 76$) and no correlation was found either between extreme head up and head up ($r = 0,025$; $p > 0,05$; $n = 40$). Extreme head up therefore cannot be replaced by the head up posture. Another important check of the environment is the look up posture. With an interval computer programme the following possible correlations were analysed: 1. duration of look up – duration of following look up; 2. duration of look up –

duration of following pause; 3. duration of preceding pause — duration of following look up. No signifiacant correlation was found for any of these measurements. The look up durations are therefore independent of the preceding pause as well as the following pause or look up duration. The look up durations (per 20s) on two different habitats (meadow/paddock: $\overline{x} = 0{,}94$s and stubble field: $\overline{x} = 1{,}88$s) were significantly different (two-level nested analysis of variance: $F = 5{,}42$; $n_1 = 1{,}0$; $n_2 = 19{,}04$; $p = 2{,}94\%$).

Fig. 2. Correlation between per cent of time spent in extreme head up posture and mean vigilant duration. r = 0,79 (p < 0,001); n = 17. 0-values omitted. triangles: ♀; squares: ♂.



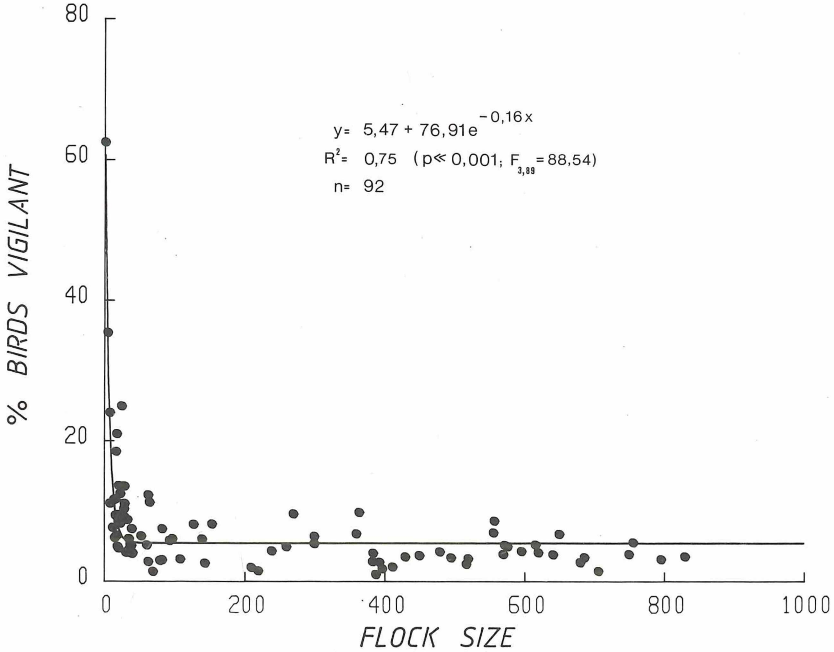


Fig. 3. Flock size and the proportion of birds vigilant (extreme head up). Data are means (0-values omitted) derived from the scanning method, two data beyond 2000 are not shown in the graph.

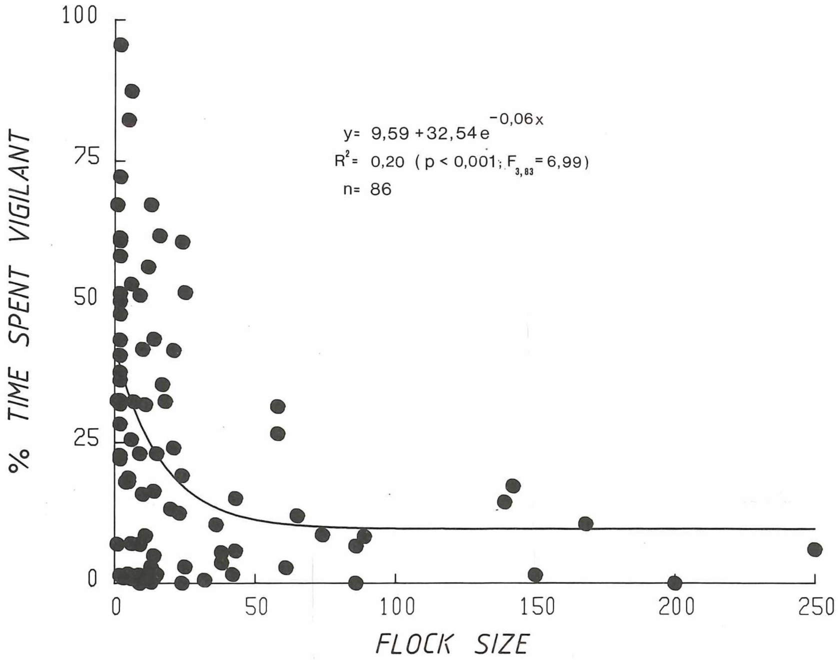


Fig. 4. Flock size and the percentage time of the individual spent vigilant (extreme head up).

3.5 Aggression

Aggressive encounters are rare events. However sudden attacks of paired geese on geese being as far as even 6 meters away (calculated by goose lengths) could be observed especially on the meadow/paddock habitat. This agrees well with Lorenz' theory on aggression (Lorenz 1963) as regards the spontaneity of these events. Nevertheless an ecological dimension to aggressiveness should also be considered (Brown & Orians 1970). There is a large difference in the frequency of threats per minute between individuals in pairs and in groups of more than 100 birds (pairs: 0,028 threats/min.; groups of more than 100 birds: 0,079 threats/min.; $z = 3{,}22$; $p <$

Table 2. Threatening events in relation to flock size. All records of individuals per group size category are added together.

Flock size	Total time of observation	Number of records	Number of threats	Threats/min.	5% confidence interval
pairs	6,4 h	38	11	0,028	0,014-0,05
3-100 without goslings	12,6 h	76	34	0,045	0,03-0,06
> 100	6,9 h	42	33	0,079	0,05-0,11

0,001; n = 800,2) as well as between individuals in groups of 3-100 birds without goslings (0,045 threats/min.) and groups of more than 100 birds ($z = 2{,}47$; $p < 0{,}01$; n = 1168). There was no difference however between the groups of 3-100 birds and pairs (z = 1,40; p = 0,08; n.s.; n = 1140,8; for details see Table 2).

4. Discussion

As vegetation structure is known to influence the pecking behaviour of geese (Owen 1978/79; Würdinger 1980) the feeding rates on various habitats (Table 1) are obviously due to vegetational differences. The grazing pressure on the Tunisian marshland apparently correlates positively with the feeding rate of the geese. On the other hand low grazing intensity by cattle on the pannonic pasture, Hutweide, correlates with the lowest feeding rate in Table 1. Most of the geese on the meadows inland of Lake Neusiedl's reed belt are found in areas of low vegetation, especially in one part which is also used as a paddock. These findings suggest that low vegetation is preferred by the geese for grazing. The ordered type of growth in the case of winter cereals may additionally be responsible for the high feeding rate as well as the supposedly higher nutritive value (cf. Owen et al. 1977).

The higher feeding rate of goslings may be due to their higher nutritive demand and to their smaller bills resulting in smaller bites (Owen 1980). Captive goslings of Barheaded Geese *(Anser indicus)* did spend more time grazing than their parents, especially during the time of maximum growth (Würdinger 1978).

As short feeding durations are not compensated by a high rate of intake (cf. 3.2.; 3.4) the influence of goslings on their parents' feeding behaviour is quite remarkable. The presence of goslings reduces the mean feeding duration of the adults by half ($\bar{x} = 22{,}09$; n = 159 versus $\bar{x} = 11{,}02$; n = 285). The gander especially spends a lot of time being vigilant (Fig. 1) which illustrates the costs of having young. After the young have hatched, the feeding duration of the female is longer than that of the gander. This has also been shown for the Barheaded Goose in addition to the influence of the hierarchial position on the feeding duration of ganders (Würdinger 1980). Also the pecking rate of female Greylags is higher than that of the gander, which agrees with the results reported for the Barheaded Goose (Lamprecht 1986b), but differs from the Pinkfooted Goose *(Anser brachyrhynchus)* (Lazarus & Inglis 1978). The energy demand of the female after the breeding period is possibly higher than that of the gander as has been reported for the period before breeding (McLandress & Raveling 1981), which could possibly explain this difference.

The habitat also influences the length of feeding durations. On the Hutweide, which is intensively used by the geese in autumn (Dick 1988), long feeding durations were measured (cf. 3.2). This may partly be due to the non-hunting status of this area. Thus the geese were less disturbed during the main hunting season in autumn.

Vegetation height influences the pecking behaviour of geese (cf. 3.3; Würdinger 1980), the feeding rate being lower in high vegetation. Short vegetation (so called »feet« vegetation) is apparently easier to be ripped off and provides a good overview for the geese. The heads of grass in high vegetation, being highly nutritious, are predominantly eaten as long as the goslings are not able to fly or shortly afterwards. Feeding in this kind of high vegetation seems to be a conflict between reduced visibility, pressure to take flight and improved feeding. In this situation the already described »head on back« movement as well as »head shaking« is easy understandable as displacement activity. The »head on back« movement has only been observed in this high vegetation and is known as a displacement activity from the Pinkfooted Goose (Lorenz 1978). Under semi-natural conditions Greylag Geese, which were imprinted on man also showed this kind of behaviour, apparently demonstrating an uneasy feeling (A. Schmitt, pers. comm.).

Although the visibility in flat areas, such as Seewinkel is normally no problem for the geese (cf. Metcalfe 1984) high grass and straw after harvest may restrict visibility. On a harvested cereal field I could observe one goose out of 21 running on a heap of straw (approx. as high as a goose) being vigilant (extreme head up) five times in 20 minutes. As the geese can completely disappear between the rows of straw, such heaps provide a good view.

The vigilance behaviour of males and females with goslings is different (Heinroth 1941; Fischer 1967). As found for the Pinkfooted Goose (Lazarus & Inglis 1978) and the ostrich (Bertram 1980) the male is more vigilant (extreme head up) than the female (Fig. 1). This is due to the principle of the division of labour (Klopfer 1973) according to which the gander is more concerned with the defence. There is a decreasing tendency to vigilance which correlates with the increasing age of the goslings (Lorenz 1950; Lamprecht 1986a). The female is more concerned with the goslings due to filial imprinting. Either the male is in fact feeding less during that time or he compensates by feeding during night time.

In larger flocks there are relatively fewer individuals vigilant (Fig. 3) and the individuals use less time for vigilance (Fig. 4). This supports the general theory about the advantage of bigger groups for the vigilant behaviour of various animals and man (e.g. Inglis & Lazarus 1981, Barnard & Thompson 1985; Underwood 1982; Alados 1985; Hoogland 1979; Wirtz & Wawra 1986). The time thus gained is then used for comfort movements and feeding (cf. Drent & van Eerden 1980).

The look up posture is another vigilant behaviour which proved to be unpredictable. Its duration is independent of the pause preceding or following as well as of the following look up duration. This look up pattern seems to be highly useful to detect any disturbance or predator (cf. Lendrem 1986). The longer look up durations on the stubble field compared to the meadow may be explained by a higher level of disturbance, but also by the neccessity of detecting grain. These remainders of the harvest represent locally concentrated food items and are possibly easier detected by looking up more frequently.

The dispersion of food items on maize and stubble fields may also be responsible for a higher amount of aggressiveness (Table 2). Bigger flocks occur on these habitats and the search paths of the geese may cross more often. However, a continuation of feeding on the place of encounter has been observed on several occasions (cf. Vines 1980). This supports the hypothesis that aggressiveness is due to competition for these food items. A similar hypothesis has been put forward by Black & Owen

(1984) for large brood juveniles of Barnacle Geese *(Branta leucopsis)* utilizing patchily distributed food sources. This ecological dimension to aggression could easily be proved with semi-captive geese, as various parameters such as group size or dispersion of food items can be varied experimentally.
As the structure of hierarchy could not be considered in this study, a field study on geese of known social status would be required to unravel the whole complex problem of feeding behaviour. The general benefits and costs of flocking could then be defined in detail for various subunits.

5. Acknowledgements

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