# Territoriality and habitat-use of wintering Common Buzzards (*Buteo buteo*) in Schleswig-Holstein, Germany.

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# Territorialität und Habitatnutzung überwinternder Mäusebussarde (*Buteo buteo*) in Schleswig – Holstein, Deutschland.

## ZUSAMMENFASSUNG

In Herbst und Winter 2000/2001 wurden verschiedene Aspekte bezüglich Raumnutzung, Verteilung und sozialer Dominanz von Mäusebussarden (*Buteo buteo*) in Schleswig–Holstein untersucht, um Erkenntnisse über die Territorialität der Bussarde zu erlangen. Die relative Häufigkeit von Wühlmauslöchern, die Anzahl der Ansitzwarten sowie die Nähe zu vorjährigen Bussardhorsten beeinflussten direkt die Antreffwahrscheinlichkeit der Greifvögel. Signifikant weniger Bussarde wurden in Horstnähe beobachtet als auch in Gebieten mit besseren Ansitzmöglichkeiten. Daraus ist zu schließen, dass Nichtbrüter, durchziehende und überwinternde Vögel, bedingt durch die Territorialität der dominanten Standvögel, in suboptimale Habitate abgedrängt werden. In diesen Habitaten waren die höchsten Dichten der Vögel zu finden. Auch außerhalb der Territorien der Standvögel waren in Gebieten mit einer höheren Anzahl an Ansitzwarten weniger Bussarde zu beobachten. Deshalb ist anzunehmen, dass auch Nichtbrüter und Überwinterer exklusive Nahrungsterritorien ausbilden.

# Territoriality and habitat-use of wintering Common Buzzards (*Buteo buteo*) in Schleswig-Holstein, Germany.

## ABSTRACT

In autumn and winter 2000/2001 we studied various aspects of habitat-use, spatial distribution, and social dominance of Common Buzzards (*Buteo buteo*) in Schleswig–Holstein, Germany, to obtain information about the territoriality of the birds. The relative availability of voles, the amount of perching sites, but also proximate nests of buzzards of the previous breeding period directly affected the encounter probability of the raptors. Significantly less buzzards were found in areas close to nesting sites and in areas with better perching possibilities: consequently, we conclude that territoriality of sedentary pairs force non-breeders and wintering birds to feed in suboptimal habitats. Also outside from Common Buzzards territories, considerably less birds were observed in areas of better perching possibilities: this leads us to the conclusion that also non-breeders and wintering birds show territoriality.

# INTRODUCTION

The Common Buzzard (*Buteo buteo*) is widespread throughout Europe and is one of the most frequent birds of prey in the western palaearctis (Cramp & Simmons, 1980). Consequently, many seminal works on raptor ecology as published recently are conducted on the Common Buzzard concerning demography, habitat-use, territoriality, dispersal, social factors, home-range sizes, and reproductive success (Walls & Kenward 1995, Hodder et al. 1998, Tyack et al. 1998, Walls & Kenward 1998, Walls et al. 1999, Kenward et al. 2000, Kenward et al. 2001a, 2001b, 2001c, Krüger & Lindström 2001, Walls & Kenward 2001).

As many other birds of prey, the Common Buzzard is known to be territorial during the breeding time (Glutz et al. 1989). In addition, this species does not only defend the immediate vicinity of the nest, but also shows territoriality in regards to its feeding areas, which lie, in general, closely to the nesting-sites (Newton 1990). Occasionally non-breeders or wintering birds show territoriality, but these birds are scarcely examined for methodical difficulties (see Brown 1976, Kostrzewa 1985, Newton 1990). Ultimately, improvement in radio-tagging technology enabled detailed researches of individual movements, allowing to study differently non-breeders and wintering birds of prey (e. g. Kenward et al. 2001c).

We attempted to validate the territoriality of Common Buzzards during winter time by comparing the bird numbers from outside versus inside the territories of sedentary breeding pairs. Due to the fact, that monocausal relations are not expected in animal ecology, it is essential to analyse simultaneously various aspects of the complex system of relationships between the environment and the raptors (Newton 1986, Kostrzewa & Kostrzewa 1993, Kostrzewa & Kostrzewa 1995) Thus, to be able to testify the territoriality of the birds, we examined habitat parameters, relative prey availability, the number of perching possibilities, and the potential interspecific competition with the Rough-legged Buzzard (*Buteo lagopus*).

In the present paper, we want to describe the effects of habitat and social parameters on

the spatial distribution of the Common Buzzard as measured by encounter probabilities: we will show how that distribution depends on prey availability and habitat parameters such as perching possibilities, wetness of the ground, and the amount of grassland. We postulate that the winter distribution of the Common Buzzard is strongly affected by the territoriality of the birds and try to validate this hypothesis. Furthermore, we want to analyse the effects presumably caused by sympatrically wintering Rough-legged Buzzards. We try to detect the direct and indirect interrelations among all those factors as well as between the factors and the distribution of the Common Buzzard. Finally, we will demonstrate which conclusions can be made on the territorial behaviour of the Common Buzzard during winter season.

# METHODS

## Study area

Our studies were conducted near Bergenhusen (54° 22 N and 9° 19 W), Schleswig–Holstein, Germany, during November and December 2000. The 20 $km^2$ large study area is divided into two sites, Börmerkoog and Meggerkoog, formerly dried lakes ("Köge"). Both sites are similar in size and have a distance of only 1 km between each other. This lowland, typical of the western parts of Schleswig–Holstein, is dominated by grassland and bordered by small woods and villages (Figure 1). Permanent pumping formed the open landscape, which is interrupted by bush rows ("Knicks") and has an elevation about sea level (-1 to +10 m).

The study area in the lowlands of Schleswig-Holstein was chosen for being homogeneous and because of the many studies on Common Buzzards that have been completed there previously (Looft 1968, Looft 1981, Hohmann 1992, Hohmann 1994, Hohmann 1995, Grünkorn 1998, Grünkorn 1999, Grünkorn 2000). Studies about autumn migration (Looft 1981, Kjellen 1994, 1999) indicate that Common Buzzards move from southern Scandinavia to northern Germany. Therefore, in autumn and winter, concentrations of Buzzards are frequent, providing optimal conditions to investigate territorial behaviour.

## Census techniques

From 23rd of November to 12th of December 2000, Common Buzzards *(Buteo buteo)* were counted by distribution mapping. We divided the study area into several parts, of which each could be observed from one landmark point without difficulties. These points were easily accessible by car and the observed buzzards within the certain parts were plotted onto a map (Scale 1 : 25,000). Maps were superimposed with a 250 x 250 meter grid and buzzards classed into the corresponding grid units. This was only possible for perched or hovering birds and for birds at ground level, but not for passing ones, which were consequently excluded. Each part of the study area was observed once a day and all buzzards observed from the fixed observation point within this part were recorded, whereas buzzards noticed in a neighbouring part were excluded as data for the currently observed part. Furthermore, buzzards were counted once for each part and if they moved, only the first location was taken.

Due to the open landscape all birds could easily be detected with binoculars (Minolta 10 x 50). Normally we distinguished without any trouble between the Common Buzzards and the sympatrically wintering Rough-legged Buzzards (*Buteo lagopus*), but under certain conditions such as bad light and further distances small errors were possible. The relation of Common Buzzards to Rough-legged Buzzards was about 14 : 1. Interspecific territoriality between the two buzzard species is demonstrated in southern Sweden (Sylven 1978), and, therefore, Rough-legged Buzzards were also plotted in the grid units using the same method as for Common Buzzards.

To avoid bias by visiting same points at same time every day, we alternated the order of the visitation of the two sites each day and the direction in which we travelled every second day. Thus, we had four possibilities to cover the route and every fourth day we took the same course. Censuses done by Deán (1996, 1998) in Spain indicate a uniform encounter probability for buzzards during the day, although activity patterns are changing (e. g. Rockenbauch 1975, Glutz et al. 1989).

It was not possible to analyse voles *(Microtus sp.)* in detail. To obtain a component of

relative distribution of voles in the study area, a total amount of 775 transects of approximately 200 steps were placed in the parcels of land (one in each) and holes of voles were counted within a 1.5 meter range of the transect. Holes with visible water inside were excluded from the analysis. Due to the short winter days, this method was of advantage, because it enabled a large area to be examined within a short amount of time. Likewise, it was necessary to investigate the abundance of prey at the same time as the predator. However, it has to be considered that it was impossible to distinguish between holes in use and abandoned ones.

The transects were also used to identify land-use and to classify wetness, thereby the parcels of land were firstly categorised into woodland, moor land, arable land and grassland. Secondly the degree of wetness was evaluated and categorised into five levels, as a function of the percentage of superficial water and the moisture of the ground. The grass was similarly short in length in all fields.

In February 2001 we registered all possible structures in the study area, which could function as a perch for buzzards. We differentiated into punctual (such as pickets, lattice doors, bushes, trees), linear (like picket-rows, bush-rows, tree-rows), and areal structures, such as tree or bush groups and recorded lengths of linear and numbers of punctual perches. Altitude and type of each perch were noted (unpublished data). Buzzards use natural perches like trees and bushes, as well as artificial perches like pickets, telegraph poles, lattice doors (Glutz et al. 1989, Kitowski 2000, Mülner 2000, Meunier et al. 2001). Therefore we mapped more than 2100 of these structures found in the study area. Punctual perches, which formed common structures such as branches of one tree or bush, and pickets situated closely to each other (< 5 m) were counted as only one punctual perch.

Territories of sedentary breeding pairs of the season 2000, defined as the surrounding 60 ha open ground from the nest and overlaps between these constructed territories and grid units were calculated. Nest sites of Common Buzzards are known, due to a study made by Grünkorn (2000) in spring 2000.

The amount of 60 ha was chosen, because of similar sizes of 50 ha and 56 ha (Walls & Kenward 2001) described for individual exclusive territories. Walls & Kenward (2001) estimated 56 ha for exclusive territories by 90% cluster polygon method for individual buzzards in Dorset, UK, and Kenward et al. (2000) 50 – 51 ha for the same region. Winter territories should be smaller than breeding territories, because of less need of food in non-breeding time (Sylvén 1978, Weir & Picozzi 1983). Also Walls & Kenward (2001) found that non-breeders space themselves further from active nests in summer than in winter. We also have chosen this small amount for the constructed territories to get only parts inside, which are strongly affected by territorial buzzards. However, by working with overlap categories it is not necessary to choose the exact amount for the area of territory, because results of buzzard abundance for the different categories will indicate the size of the area, where buzzard territoriality affects their abundance.

We classified the grid units into six categories (Overlap categories of grid units, here after OCGU), depending on the percentage of overlap with the buzzard territories (see Table 1).

**Data analysis and statistical treatment**

To be able to correlate parcel and grid unit parameters, parcels of land were drawn with GIS (ARC View) and geo-referenced. Following that, the fishnet was superimposed and the percentage of parcel area per grid unit was calculated. This process was necessary to shift parameters related to parcels in relation with grid units.

Only grid units that could be totally examined for the presence of buzzards and that contained observed parcels of land of more than 80 % of the total grid area were used for further analysis. The remaining 290 grid unit equalled to an area of 18.125 $km^2$. This area contains 95 % grassland, the remaining 5 % being principally arable land. In 20 days at this area 1537 encounters of Common Buzzards were recorded. Likewise 109 encounters occurred regarding Rough-legged Buzzards.

Relative Common Buzzard (*Buteo buteo*) encounter probability (COB) was given by the number of observed Common Buzzards per grid unit during the 20 day period of investigation. The parameter ROB, the presence of sympatrically wintering Rough-legged Buzzard (*Buteo lagopus*), was defined as 1 or 0 dependent on whether or not we recorded birds of this species inside a grid unit during the study time.

Vole-hole index (here after VHI) was formed by relating the number of counted holes to the distance of 200 steps for each field. Of these vole-hole densities the VHI of the grid units was ascertained by calculating the weighted arithmetic middle of the vole-hole densities of the parcels of land, which overlap with the certain grid unit.

$$VHI_j = 200 * \Sigma (F_{ij} * Vh_i * / St_i)$$

$VHI_j$ = vole-hole index of grid unit j.
$F_{ij}$ = proportion of parcel of land i in the grid unit j.
$Vh_i$ = Holes of voles counted in the transect of parcel i.
$St_i$ = Longitude of transect of parcel i in steps.

Wetness of the ground and density of the holes were related for each transect, resulting in the first 3 wetness categories (very dry to middle) being similar in the vole-hole density. Therefore, we pooled the five categories of wetness to generate only two – wet (former categories 4 and 5) and dry (former categories 1 to 3). This enabled us to calculate the percentage of dry area (DLA) for each grid unit.

Dividing the area covered with grass through the totally investigated area of each grid unit, we calculated the proportion of meadow coverage (GLA). Most grid units had a percentage of meadows of 100%.

In order to compute the parameter PUP, the number of punctual perches was counted for each grid unit. Furthermore, the sum of the lengths of "linear perches" within a grid unit was calculated and the half of the circumferences of areal perches was added to these lengths (because the length of a linear structure is equivalent to the half of its circumference). This way we computed the parameter LIP (length of linear perches). Picket rows were excluded from LIP as a consequence of the large numbers of these structures separating nearly each parcel, and because of their regular distribution in the study area. It is considered impossible for them to be a limiting factor for buzzards in our study area, and therefore, they should have no impact on distribution and habitat-use of the birds.

We related the OCGUs with the relative encounter probability of the buzzards (COB) to obtain a limit, where influence of territories was noted or not. Therefore, a multivariate poisson regression was applied including orthogonal contrast-Dummy-Coding (Bortz et al. 1990) for the overlap categories to estimate COB (Table 1). The remaining six parameters, (i.e. PUP, LIP, ROB, VHI, GLA and DLA) were also integrated in this analysis.

The limit was revealed between overlap categories 1 and 2. We detected exclusively one significant change in COB between OCGU 1 and all the following categories (Table 1). In order to indicate whether or not a grid unit lies inside the Common Buzzard territories, a new parameter (i.e. TER) was constructed. Consequently the grid units of the categories 0 and 1 were classified now as "out of buzzard territory" in the subsequent analyses and recoded with "0", whereas the remaining categories were classified as "inside of buzzard territories" and recoded with "1".

**Table 1.** OCGUs based on the percentage of overlap between grid units and constructed Common Buzzard territories. In order to detect an overlap limit, where Buzzard exclusive territoriality would still affect the densities of cospecific birds, the multiple poisson regression analysis was calculated to estimate COB from the dummy-coded (by orthogonal contrast method, Bortz et al. 1990) categories and the remaining parameters (i.e. PUP, LIP, VHI, ROB, GLA, DLA). N = 290. OCGU = Overlap category of grid unit, DV = Dummy-Variables, for remaining abbreviations see Table 2. 10,000 random permutations, P-values for log-likelihood-function (observed model). The bold values mark significant results after Bonferroni correction.

| OCGU | % overlap | N | DV1 | DV2 | DV3 | DV4 | DV5 |
|---|---|---|---|---|---|---|---|
| 0 | 0 | 171 | -5 | 0 | 0 | 0 | 0 |
| 1 | 0 < x < 25 | 32 | 1 | -4 | 0 | 0 | 0 |
| 2 | 25 < x < 50 | 17 | 1 | 1 | -3 | 0 | 0 |
| 3 | 50 < x < 75 | 8 | 1 | 1 | 1 | -2 | 0 |
| 4 | 75 < x < 100 | 31 | 1 | 1 | 1 | 1 | -1 |
| 5 | 100 | 31 | 1 | 1 | 1 | 1 | 1 |

| | PUP | LIP | VHI | ROB | GLA | DLA | DV1 | DV2 | DV3 | DV4 | DV5 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| coefficient | -2.71E-02 | -9.98E-04 | 1.35E-02 | -8.09E-02 | +8.35E-01 | -4.62E-01 | -3.1E-02 | -8.29E-02 | –1.35E-02 | +5.78E-02 | –9.75E-03 |
| P-Value | **0.0068** | **0.0012** | **0.0002** | 0.4764 | 0.0388 | 0.0902 | 0.1070 | **0.0228** | 0.8280 | 0.6042 | 0.9238 |

A multivariate poisson regression combined with randomisation tests (for the theoretical background see Edgington 1987, Agresti 1996, Flury 1997; the computations were done by a computer intensive statistical package, written by Nemeschkal 1999) was applied to analyse the dependences between relative Common Buzzard encounter probability (COB) and the 7 parameters, which are:

- the number of punctual perches (PUP),
- the length of linear perches (LIP),
- the presence of Rough-legged Buzzards (ROB),
- the vole-hole index (VHI),
- the location of the grid unit in respect to Common Buzzard territories (TER),
- the percentage of grassland (GLA), and
- the percentage of dry land (DLA).

$$_{COB}\mu_i = \exp\,[b_0 + b_1 * PUP_i + b_2 * LIP_i + b_3 * ROB_i + b_4 * TER_i + b_5 * VHI_i + + b_6 * DLA_i + b7 * GLA_i] + resid_i$$

i…number of grid unit, i = 1 to n
resid = residual
n = 290 grid units

Two additional approaches analysed the dependences between COB and the remaining 6 parameters for:

- grid units with influences of Common Buzzard territories and for
- grid units without influences of territories.

$$_{COB}\mu_i = \exp\,[b_0 + b_1 * PUP_i + b_2 * LIP_i + b_3 * ROB_i + b_4 * VHI_i + b_5 * DLA_i + + b_6 * GLA_i] + resid_i$$

i…number of grid unit, i = 1 to n
resid = residual
n = 203 for grid units from outside the Common Buzzard territories and n = 87 for grid units from inside the territories.

Note that there only remain 6 parameters because one parameter, i. e. TER, is obsolete here.

Additionally, pair-wise bivariate relations between the 6 or 7 parameters were calculated, for each model employing simple linear regression analysis (Statgraphics package), and are expressed simultaneously with the results from Poisson-regression analyses by path diagrams.

To estimate the significance levels of the dependent parameters, 10,000 random permutations were computed for each parameter and design revealing P-values. Single P-values were only taken as significant after a correction with respect to Bonferroni inequality (the cumulative $P \leq 0.05$).

# RESULTS

The multiple poisson regression analysis indicates a complicated network of significant relationships between the various parameters and the relative encounter probability of Common Buzzards (COB), resulting in the frequency of the birds to be above all related with vole-hole index (VHI). Additionally, it depends on the number of punctual perches (PUP) as well as on the length of linear perches (LIP; Table 2).

Furthermore, as postulated, COB is affected by the location of the grid unit concerning the Common Buzzard territories (TER). We observed significantly more buzzards in grid units outside the territories (Table 2).

Significant relations of the different parameters to each other and to the dependent variable are represented in the path diagrams (Figure 2 to Figure 4). P-Values and coefficients are shown in Table 3 and Table 4. For the observed grid units the result is that PUP, LIP, TER and VHI are directly related to COB. VHI is also related to the presence of Rough-legged Buzzards (ROB), to the proportion of grassland (GLA) and to the proportion of dry land (DLA). We also found a relation between PUP and LIP, LIP and DLA as well as among LIP and TER. Moreover, GLA is related with DLA and TER.

**Table 2.** Results of the multivariate poisson regression analyses estimating the relative encounter probability of Common Buzzard (COB). ALL = all grid units without specification, OUT = grid units from outside the Common Buzzard territories only, IN = grid units from inside the Common Buzzard territories only; PUP = number of punctual perches, LIP = length of linear perches, TER = location of the grid unit with respect to Common Buzzard territories, VHI = vole-hole index, GLA = proportion of grassland, DLA = proportion of dry land, ROB = presence of Rough-legged Buzzards (*Buteo lagopus*). The standard error (S.E.) is not calculated here, P-values were calculated instead by random permutational testing (see "Data analysis and statistical treatment"). 10,000 random permutations. The bold values mark significant results after Bonferroni correction.

| | ALL, n = 290<br>full model: P < 0.0001 | | OUT, n = 203<br>full model: P < 0.0001 | | IN, n = 87<br>full model: P < 0.0193 | |
|---|---|---|---|---|---|---|
| Predictor | coefficient (b) | P-value | coefficient (b) | P-value | Coefficient (b) | P-value |
| Constant | + 1.3203 | 0.5202 | + 1.6953 | 0.9710 | + 7.9538E-01 | 0.6872 |
| PUP | – 2.7346E-02 | **0.0052** | – 3.5269E-02 | **0.0026** | – 1.3852E-02 | 0.4356 |
| LIP | – 9.9785E-04 | **0.0028** | – 1.1010E-03 | **0.0050** | – 5.4141E-04 | 0.3752 |
| ROB | – 6.6171E-02 | 0.5848 | – 7.8686E-02 | 0.5240 | – 7.0799E-02 | 0.8226 |
| TER | – 2.6559E-01 | **0.0188** | | | | |
| VHI | + 1.3634E-02 | **<0.0001** | + 1.3317E-02 | **<0.0001** | + 1.5068E-02 | 0.0674 |
| GLA | + 8.5163E-01 | 0.0338 | – 3.8630E-01 | 0.4278 | + 1.3304 | **0.0440** |
| DLA | – 4.8073E-01 | 0.0788 | + 4.4195E-01 | 0.1854 | – 8.7286E-01 | 0.1620 |

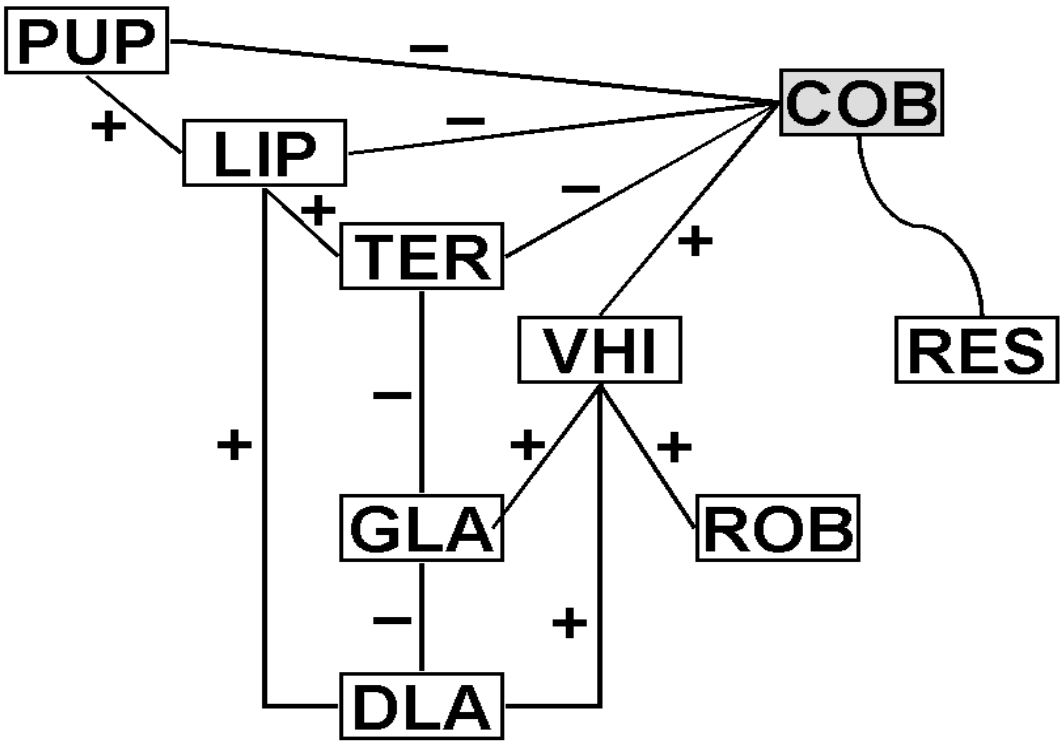


**Figure 2.** Direct and indirect influences of different parameters on the probability of encounter of Common Buzzards (COB). **All** grid units included (n = 290). Only significant relations are shown. PUP = number of punctual perches, LIP = length of linear perches, TER = location of the grid unit in respect to Common Buzzard territories, VHI = Vole-hole index, GLA = proportion of grassland, DLA = proportion of dry land. COB = relative encounter probability of Common Buzzards (*Buteo buteo*), ROB = presence of Rough-legged Buzzards (*Buteo lagopus*), RES = residual.

In the grid units from outside the buzzard territories, COB depends on VHI, including PUP and LIP (Table 2). In addition, there is a relation between VHI and GLA as well as among VHI and DLA. There also exists a relation between LIP and PUP and between LIP and DLA. ROB is neither related with any other predictor nor with the dependent variable (Figure 3).

In both multiple regression analyses – for grid units without specification , as well as for the units from outside the Common Buzzard territories only – VHI show positive, but PUP and LIP show negative correlation, with COB. As contrasted to the other parameters, neither ROB and DLA nor GLA are directly affecting COB (Table 2).

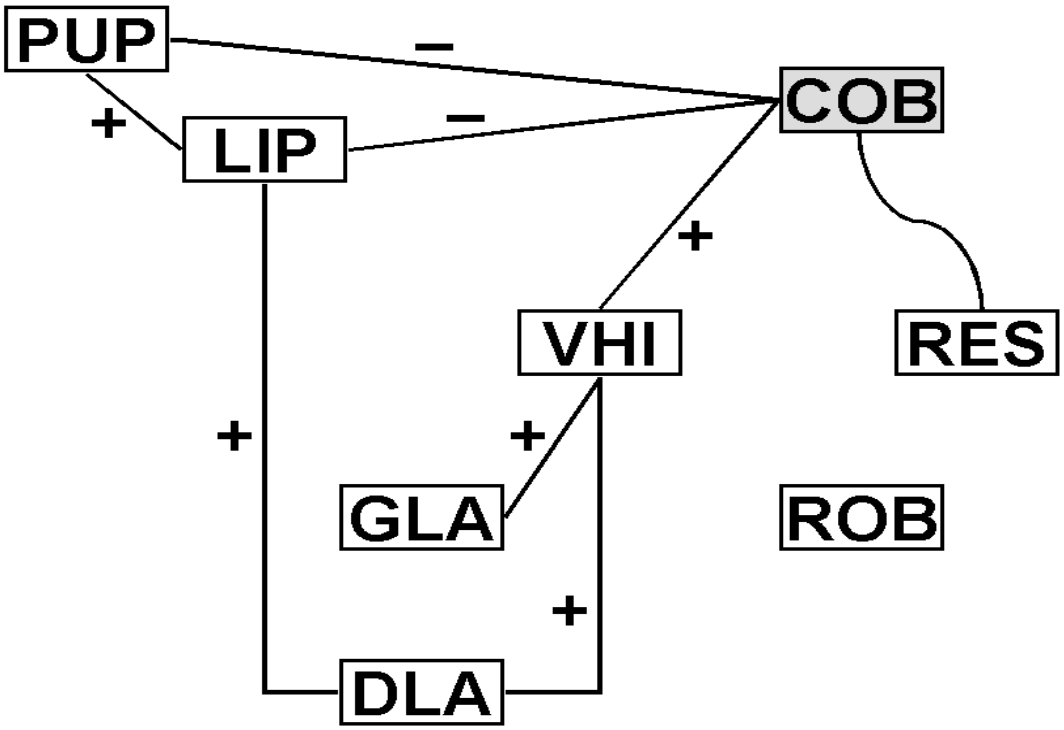


**Figure 3.** Direct and indirect influences of different parameters on the probability of encounter of Common Buzzards (COB). Grid units from **outside** the Common Buzzard territories only (n = 203). Only significant relations are shown. For abbreviations see Figure 2.

The result of the multivariate regression analysis for the grid units from inside the Common Buzzard territories is that COB exclusively is significantly related with GLA. All the other predictors do not show any direct relation to the buzzard frequency (Table 2), although GLA is also significantly related with ROB, VHI and LIP. Moreover VHI is related to DLA and to ROB (Figure 4).

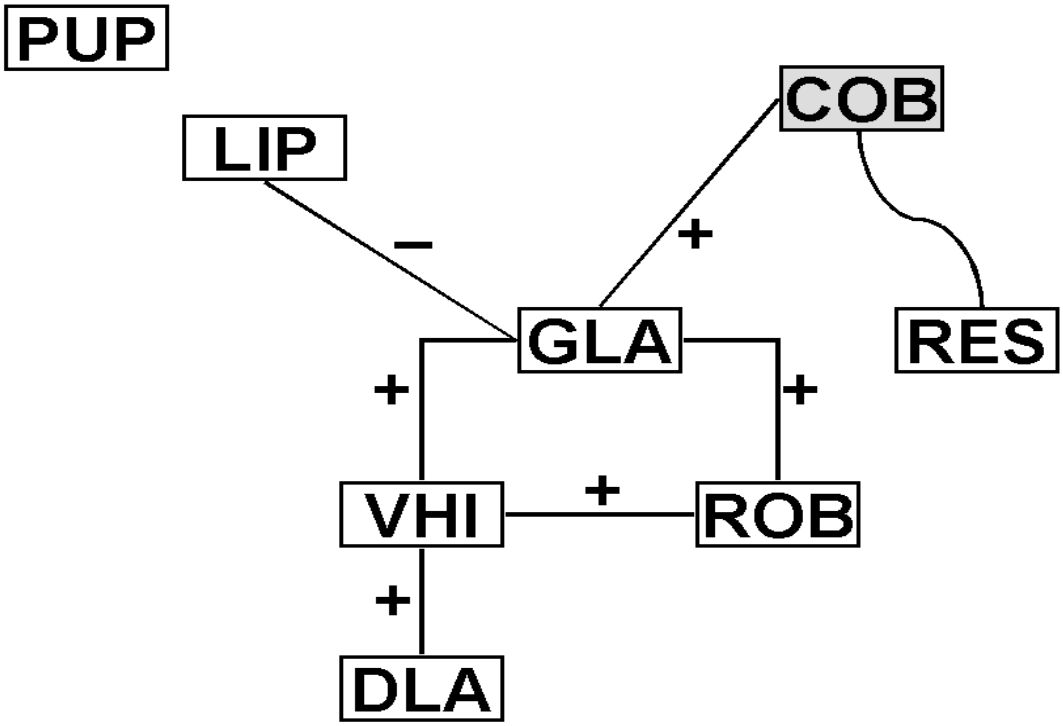


**Figure 4.** Direct and indirect influences of different parameters on the probability of encounter of Common Buzzards (COB). Grid units from **inside** the Common Buzzard territories only (n = 87). Only significant relations are shown. For abbreviations see Figure 2.

# DISCUSSION

## Habitat parameters

Winter densities of raptors seem to be even more strongly related to prey availability than summer densities (Newton, 1990). We were able to show that the encounter probability of Common Buzzard is directly and positively affected by the density of holes of voles as an aspect of availability of prey (Table 2), and therefore, indirectly by the moistness of the ground and the percentage of grassland (Figure 2).

Buzzards are mainly preying on voles, demonstrated for the study area by Looft (1981), Hohmann (1992, 1995) and Grünkorn (1999) as well as for other regions, e. g. by Mebs (1964), Rockenbauch (1975), Sylven (1978), Cramp & Simmons (1980), Glutz et al. (1989), Spidsø & Selås (1988), and Melde (1995). In Poland 85 % of prey biomass of Common and Rough-legged Buzzards during the three winters 1987/88 until 1989/90 is contributed by the field vole (*Microtus arvalis,* Kowalski & Rzepala 1997). Field voles are also the most frequent micromammals of the study area. In September 2000, 32 of 33 micromammals (97 %) captured by Bruns (pers. comment) in Meggerkoog were *M. arvalis* and in September 1999, 59 out of 62 or 95 %.

The number of punctual perches as well as the length of linear structures, which can be used as perches, shows a negative effect on COB. Thus, we have to assume that they more frequently use open landscape with few perches or that territorial buzzards displaced most of the birds from good hunting areas with plenty of perches. Common Buzzards mainly prey from perches (e. g. Glutz et al. 1989) furthermore, the poor situation of prey in the study area in autumn 2000 (Bruns, pers. comment) makes it more likely that they show strong territoriality. Therefore, we assume that the negative correlation between encounter probability of buzzards and the amount of perching possibilities is caused by the strong territoriality of the birds, and not because they prefer areas without perches.

**Social relations**

Due to Buzzard exclusive territoriality we found significantly less buzzards in territories next to their nests than outside (Table 2). This leads us to the assumption that non-breeders and wintering buzzards are displaced to suboptimal habitats, where the highest densities are found.

In southern Sweden the proportion of juveniles is low (20 %) in wintering but significantly higher (60 %) in migrating buzzards (Kjellen 1994), indicating that subordinate individuals are forced to migrate from breeding grounds or the best (nearest) wintering areas due to competition from more dominant buzzards. This, moreover, is predicted for partial migrants by the social-dominance hypothesis (Cox 1968, Mueller et al. 1977, Gauthreaux 1978, 1982).

The fact that fewer buzzards were found in areas with more perches, even if grid units inside the exclusive territories of breeders were excluded from analysis, indicates that also non-breeders or wintering birds show territoriality. This was also demonstrated by another study done in the same study area by radio-tracking (Hohmann 1995). Southern Sweden demonstrated that Common Buzzards, which bred northwards, as well as individuals of wintering Rough-legged Buzzard, annually returned to the same winter territories (Sylven 1978). For wintering Steppe Buzzard (*B. buteo vulpinus*) in South Africa such “Ortstreue” was found during one season (Whitelaw 1995, Moreau 1972) as well as for many following years (Moreau 1972). Fidelity to previous wintering areas of these three taxa is also described by Glutz et al. (1989) and Newton (1990).

Interspecific relations and interspecific territoriality between Rough-legged and Common Buzzards is already shown for southern Sweden (Sylven 1978). Therefore, we included in our studies the observation of the frequency of Rough-legged Buzzards, which population dynamics is analysed in detail by Potapov (1997). Although we found out that ROB, the presence of sympatric wintering Rough-legged Buzzards, is related to habitat parameters such as VHI, there was no significant relation between their presence and Common Buzzard frequency (COB). We suppose that these differences to southern

Sweden in interspecific territorial behaviour are caused by the low abundance of Rough-legged Buzzards or because of other habitat (Looft 1981).

**Indirect influences on Common Buzzard encounter probability**

Relations between parameters as shown in path diagram (Figure 2) indicate that even parameters, which do not show any direct effect on relative encounter probability of Common Buzzards (COB) can also cause changes, because of significant relation with parameters, which show direct influence. GLA, the proportion of grassland, shows positive correlation with VHI and negative correlation with the location of the grid unit in respect to Common Buzzard territories (TER). Therefore, a higher percentage of grassland increases COB by these two paths.

The proportion of dry land, DLA, shows a positive correlation with VHI, but also with the length of linear perching structures, LIP. Hence, a higher percentage of dry land reduces COB by raising LIP and raises COB by augmenting VHI.

Following on, we found a positive correlation between ROB and VHI, but it seems more likely that VHI affects the presence of Rough-legged Buzzards than the reverse. Thus, we have to suppose that ROB, the presence of Rough-legged Buzzards, does not even have an indirect effect on Common Buzzard encountering probability in the researched area.

Additionally, the parameters which show direct significant relation with the frequency of Common Buzzards (VHI, PUP, LIP and TER) show significant correlations to each other, which completes the complex relationship of the system of habitat-use and social factors of these birds of prey for the study area in winter 2000.

This situation is valid, when we include all grid units of the study area. If we exclude the grid units where exclusive territoriality of Common Buzzards is demonstrated, the relationship between the parameters is almost maintaining, but TER drops out of analysis. Additionally the relation between VHI and ROB as well as the relation between GLA and DLA is not significant any more (Figure 3).

On the contrary, if we only take into consideration the grid units inside Common Buzzard territories the system changes strongly – in this case only the proportion of grassland, GLA, shows a significant relation with the encounter probability of the birds. Furthermore, we have to suppose that the parameters which show significant relation with GLA (i.e. LIP, VHI and ROB) do not affect the percentage of grassland – the reverse way seems to be more likely – so that they neither can have any indirect influence on COB (Figure 4).

It is necessary to state that there remain unanalysed factors, which could affect the distribution of Common Buzzards like disturbance by human activities (e.g. Tubbs 1974, Looft 1981, Selås 1988, Melde 1995) and remaining aspects of availability of prey. Leaving out the Rough-legged Buzzards there are also other species of bird, feeding on the same prey like the Common Buzzard, such as Hen Harriers (*Circus cyaneus*), Kestrels (*Falco tinnunculus*), and Grey Herons (*Ardea cinerea*). Furthermore, flocks of Carrion Crows (*Corvus corone*) were observed in some parts of the study area, and buzzards often were attacked or disturbed by the corvids (unpublished data). Also direct predation by Eagle Owls (*Bubo bubo*) could be an important factor for buzzards (Suchy 1990, Foerstel 1995, Sergio et al. 1999). Especially in western Schleswig-Holstein the Common Buzzard is the second important prey of the owl with 16 % of biomass (Grünkorn, 2000), however, Grünkorn's study as well as Dalbeck (1994) indicates that eagle owls above all prey on buzzards in the breeding season and only in a smaller scale in autumn and winter. Nonetheless, all these factors could influence the relative encounter probability of the Common Buzzard, and therefore, they could make a valuable contribution to complete the analysis of the system of wintering Common Buzzards in the lowlands of Western Schleswig-Holstein.

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# SUPPLEMENT

**Table 3.** Pair-wise bivariate linear relations between the independent variables. For abbreviations see Table 2. P-Values were estimated by computing 10,000 random permutations. Bold P-Values mark significant results after Bonferroni correction. a) grid units without specification, b) separated regression analyses for grid units from outside and from inside the Common Buzzard territories. For corresponding coefficients see Table 4.

a) P-Values for ALL

| | PUP | LIP | ROB | TER | VHI | DLA | GLA |
|---|---|---|---|---|---|---|---|
| PUP | | | | | | | |
| LIP | **0.0046** | | | | | | |
| ROB | 0.3982 | 0.179 | | | | | |
| TER | 0.3234 | **0.0106** | 0.1932 | | | | |
| VHI | 0.7686 | 0.2404 | **0.0030** | 0.9896 | | | |
| DLA | 0.1358 | < **0.0001** | 0.6442 | 0.0382 | < **0.0001** | | |
| GLA | 0.8880 | 0.0314 | 0.2462 | **0.0022** | < **0.0001** | **0.003** | |

b) P-Values for OUT and for IN.

| | | IN | | | | | |
|---|---|---|---|---|---|---|---|
| | | PUP | LIP | ROB | VHI | DLA | GLA |
| OUT | PUP | | 0.7668 | 0.9980 | 0.0424 | 0.6084 | 0.0592 |
| | LIP | **0.0002** | | 0.4066 | 0.2466 | 0.0514 | **0.0322** |
| | ROB | 0.3632 | 0.4716 | | **0.0034** | 0.2252 | **0.0026** |
| | VHI | 0.2518 | 0.5470 | 0.0990 | | **0.0094** | < **0.0001** |
| | DLA | 0.0448 | < **0.0001** | 0.8436 | **0.0038** | | 0.0920 |
| | GLA | 0.1242 | 0.9708 | 0.3896 | **0.0008** | 0.0468 | |

**Table 4.** Pair-wise bivariate linear relations between the independent variables. For abbreviations see Table 2. Coefficients were calculated by simple linear regression analysis and are only specified for significant relations. a) the grid units without specification, b) grid units from outside the territories only and c) grid units from inside the territories only. For the corresponding P-Values see Table 3.

a) Regression coefficients for ALL

| | | independent variable | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | PUP | LIP | ROB | TER | VHI | DLA | GLA |
| dependent variable | PUP | 1 | 5.71E-03 | n.s. | n.s. | n.s. | n.s. | n.s. |
| | LIP | 5.24E+00 | 1 | n.s. | 5.29E+01 | n.s. | 1.96E+02 | n.s. |
| | ROB | n.s. | n.s. | 1 | n.s. | 5.42E-03 | n.s. | n.s. |
| | TER | n.s. | 4.43E-04 | n.s. | 1 | n.s. | n.s. | -5.78E-01 |
| | VHI | n.s. | n.s. | 5.83E+00 | n.s. | 1 | 1.61E+01 | 2.43E+01 |
| | DLA | n.s. | 2.32E-04 | n.s. | n.s. | 2.36E-03 | 1 | -1.40E-01 |
| | GLA | n.s. | n.s. | n.s. | -6.07E-02 | 2.65E-03 | -1.04E-01 | 1 |

b) Regression coefficients for OUT

| | | independent variable | | | | | |
|---|---|---|---|---|---|---|---|
| | | PUP | LIP | ROB | VHI | DLA | GLA |
| dependent variable | PUP | 1 | 9.68E-03 | n.s. | n.s. | n.s. | n.s. |
| | LIP | 8.23E+00 | 1 | n.s. | n.s. | 1.72E+02 | n.s. |
| | ROB | n.s. | n.s. | 1 | n.s. | n.s. | n.s. |
| | VHI | n.s. | n.s. | n.s. | 1 | 1.49E+01 | 2.24E+01 |
| | DLA | n.s. | 2.66E-04 | n.s. | 2.36E-03 | 1 | n.s. |
| | GLA | n.s. | n.s. | n.s. | 1.41E-03 | n.s. | 1 |

c) Regression coefficients for IN

| | | independent variable | | | | | |
|---|---|---|---|---|---|---|---|
| | | PUP | LIP | ROB | VHI | DLA | GLA |
| dependent variable | PUP | 1 | n.s. | n.s. | n.s. | n.s. | n.s. |
| | LIP | n.s. | 1 | n.s. | n.s. | n.s. | -2.26E+02 |
| | ROB | n.s. | n.s. | 1 | 9.98E-03 | n.s. | 4.56E-01 |
| | VHI | n.s. | n.s. | 1.16E+01 | 1 | 2.23E+01 | 2.73E+01 |
| | DLA | n.s. | n.s. | n.s. | 2.37E-03 | 1 | n.s. |
| | GLA | n.s. | -2.89E-04 | 1.16E-01 | 5.95E-03 | n.s. | 1 |

## Abbreviations

**OCGU** Overlap categories of the grid units with the constructed territories of the Common Buzzards.

**DV1 – DV5** Dummy variables for dummy coded overlap categories.

Approaches for multivariate regression analyses:

**ALL** all grid units are included in analysis, without specification (n= 290),

**IN** only grid units inside Common Buzzard territories are included in analysis (n=87),

**OUT** only grid units outside Common Buzzard territories are included in analysis (n=203).

Dependent variable:

**COB** the number of observed Common Buzzards per grid unit during the study period.

Independent variables:

**DLA** the percentage of dry land,

**GLA** the percentage of grassland,

**LIP** the length of linear perches,

**PUP** the number of punctual perches,

**ROB** the presence of Rough-legged Buzzards,

**TER** the location of the grid unit in respect to Common Buzzard territories,

**VHI** the vole-hole index.