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TERRITORIALITY AND HABITAT USE OF COMMON BUZZARDS (*BUTEO BUTEO*) DURING LATE AUTUMN IN NORTHERN GERMANY

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ABSTRACT.—We studied habitat use and spatial distribution of Common Buzzards (*Buteo buteo*) in Schleswig–Holstein, northern Germany during the autumn of 2000, to assess the raptors' territoriality and its consequences for their use of space. For this purpose, we performed point counts covering an area of 20 km^2 during each of 20 continuous days and recorded 1537 observations of Common Buzzards and 109 of Rough-legged Hawks (*Buteo lagopus*). Applying multivariate Poisson regression combined with randomization tests, we detected that Common Buzzards showed a preference for areas with a larger distance from nesting sites of the previous spring ($P = 0.019$; $n = 290$ grid units of 250 × 250 m in all three cases), a high density of vole holes ($P < 0.001$), and a low density of perch-sites ($P = 0.005$). These preferences regarding vole holes and perches were also valid when only grid units far from the nesting sites were considered. Indirectly, the buzzards were also affected by the amount of grassland and by the amount of dry land, as these parameters were strongly related to vole-hole density. The distributions of the sympatric wintering species Rough-legged Hawk and Common Buzzard did not affect each other. Our study indicated that territorial sedentary breeding pairs displaced nonbreeders and wintering birds into suboptimal habitats, and it offers valuable clues on the constraints for Common Buzzards in areas where they occur in high abundance during late autumn and winter.

KEY WORDS: *Common Buzzard*; Buteo buteo; *nonbreeding*; *season*; *spatial distribution*; *survey*; *wintering*.

TERRITORIALIDAD Y USO DE HÁBITAT DE *BUTEO BUTEO* A FINES DEL OTOÑO EN EL NORTE DE ALEMANIA

RESUMEN.—Estudiamos el uso de hábitat y la distribución espacial de *Buteo buteo* en Schleswig—Holstein, norte de Alemania, durante el otoño del año 2000, para evaluar la territorialidad de la especie y sus consecuencias en el uso que la rapaz hace del espacio. Para este propósito llevamos a cabo conteos en

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puntos cubriendo un área de 20 km² durante 20 días consecutivos y registramos 1537 observaciones de *B. buteo* y 109 de *B. lagopus*. Al aplicar la regresión multivariada de Poisson combinada con pruebas de aleatorización, detectamos que *B. buteo* evidenció una preferencia por áreas ubicadas una mayor distancia a los sitios de nidada de la primavera anterior ($P = 0.019$; $n = 290$ unidades de grilla de 250 × 250 m en cada uno de los tres casos), con una alta densidad de madrigueras de campañol ($P < 0.001$), y una baja densidad de sitios de percha ($P = 0.005$). Estas preferencias con respecto de las madrigueras de campañol y de perchas también fueron válidas cuando sólo se consideraron las unidades de grilla lejanas a los sitios de nidada. Indirectamente, *B. buteo* también se vio afectado por la cantidad de pastizales y por la cantidad de suelo seco, al estar estos parámetros fuertemente relacionados con la densidad de madrigueras de campañol. Las distribuciones de las especies de invernada simpátricas como *B. buteo* y *B. lagopus* no se vieron mutuamente afectadas. Nuestro estudio indicó que las parejas reproductivas territorialmente sedentarias desplazaron a las aves no reproductivas e invernantes hacia hábitats menos óptimos. Además, ofrece pistas valiosas sobre las limitaciones que afectan a *B. buteo* en áreas donde se encuentra en elevadas abundancias a fines de otoño y en invierno.

[Traducción del equipo editorial]

The Common Buzzard (*Buteo buteo*) is widespread throughout Europe and is one of the most common raptors in the western palearctic (Cramp and Simmons 1980). It is a commonly used model organism for raptor ecology studies regarding population demography, habitat use, territoriality, dispersal, social behavior, home range sizes, and reproductive success (Walls and Kenward 1995, 1998, 2001, Hodder et al. 1998, Walls et al. 1999, Kenward et al. 2000, 2001a, 2001b, Krüger and Lindström 2001, Krüger 2002, Prytherch 2009). Like most other raptors, Common Buzzards are territorial during the breeding season (e.g., Poirazidis et al. 2009, Prytherch 2009), with exceptions due primarily to individuals being related (Walls and Kenward 1995, 1998, 2001, Prytherch 2009). Common Buzzards defend both the immediate vicinity of the nest and feeding areas, which generally lie in close proximity to the nesting sites (Newton 1990, Kenward et al. 2001a, 2001b).

Due to limited resource availability and increased energetic costs, the winter season is a crucial period in a raptor's life cycle (Warkentin and West 1990, Krüger and Lindström 2001, Fairhurst and Bechard 2005, Wikar et al. 2008, Moser and Garton 2009, Kasprzykowski and Ciesluk 2011). However, most studies on the Common Buzzard focus on the breeding season. Thus, despite some local case studies (Kowalski and Rzepala 1997, Probst 2002, Wuczyński 2005, Nikolov et al. 2006, Wikar et al. 2008), the ecological constraints of wintering Common Buzzards are not well investigated, and little is known about their winter territoriality (Newton 1990, Prytherch 2009).

The goal of the present study was to determine the factors affecting the distribution of Common Buzzards at a local scale during late autumn, in an area where, for a short period of time, local sedentary birds are confronted with many partial migrants from further north. We postulated that the distribution of Common Buzzards would be strongly affected by the territoriality of the birds. We also examined the influence of prey availability, habitat variables, and the potential interspecific competition with Rough-legged Hawks (*B. lagopus*), because the raptor's local distribution is likely influenced by these factors (Sylvén 1978, Kostrzewa and Kostrzewa 1991, Kenward et al. 2001b, Krüger 2002, Wuczyński 2005).

METHODS

Study Area. We conducted our study near Bergenhusen (54°22′N, 9°19′W), Schleswig–Holstein, northern Germany, during November and December 2000 (Fig. 1). The 20 km² study area consisted of two dry lake beds (''Börmerkoog'' and ''Meggerkoog''), 1 km apart, which were similar in size and formed part of the lowland of the three rivers Eider, Treene, and Sorge, representing the largest contiguous wetland area in Schleswig–Holstein (Weiers et al. 2003, Busche and Kostrzewa 2007). The study area consisted of 775 parcels of land, which were divided mostly by channels, hedgerows, and fences. It was dominated by grassland (meadows and pastures), interspersed with arable land and small riverine woodlands, and surrounded by small woodlots, marshland, and villages. This landscape, with elevations between −1 and +10 m asl, was created and is maintained by water extraction.

The study site was chosen because studies on autumn migration indicated that a portion of the Scandinavian Common Buzzard population migrates into northern Germany (Looft and Busche 1981, Kjellen 1994, 1999). Further advantages were that the region is known for high densities of wintering Common Buzzards (Busche and Berndt 1994, Berndt 1998), that the landscape is relatively homogeneous, representative of the traditional extensive land use of the

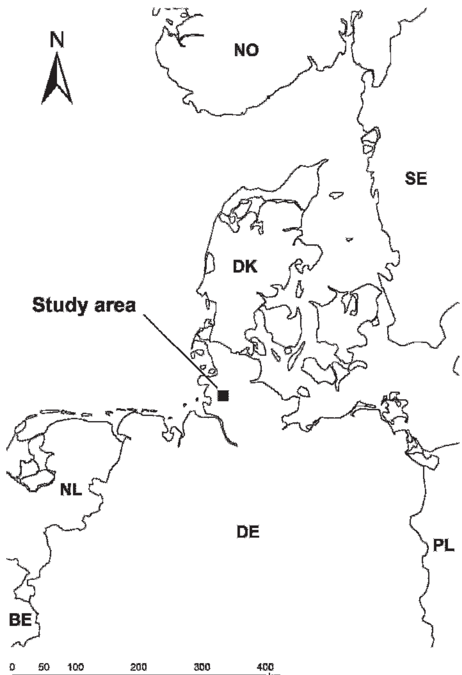

Figure 1. The study area in Schleswig–Holstein, northern Germany.

area, and that other studies on habitat use by Common Buzzards had been conducted here (Hohmann 1994, 1995).

Census Techniques. We conducted point-count surveys of Common Buzzards. To cover the study area entirely, we divided it into 25 subareas, each of which was fully visible from a single vantage point. We scanned the field of view with binoculars from each vantage point once per day and plotted observations of perched or hovering Common Buzzards (but not those merely passing through our field of view) onto a 1:25 000 map overlaid with a 250 × 250 m grid. We repeated this survey 20 times during the 20 consecutive days from 23 November to 12 December 2000. We also mapped locations of Rough-legged Hawks, because interspecific territoriality between this species and Common Buzzards has been demonstrated during winter in southern Sweden (Sylvén 1978). The time spent per vantage point varied between 5 and 12 min and depended on visibility as well as on the time needed to determine the exact buzzard locations and to discriminate between the two species. We made every effort to avoid double-counting and recorded birds that moved during the observation period only at the location where they were first observed. The surveys lasted—depending on visibility and weather—approximately from 0900 H until 1400–1500 H, which was nearly the entire daylight period. To avoid any bias that might be generated by visiting the same points at the same time of day, we alternated the order we visited the two dry lake beds each day and the direction in which we traveled every second day. Thus, every fourth day the vantage points were visited in the same order.

It was not possible to analyze vole availability (*Microtus* spp.) in detail, but to obtain a relative distribution of voles in the study area, we walked single transects of approximately 150 m diagonally across all parcels of land (n = 775) and counted the number of unflooded and therefore potentially active vole holes within 1.5 m of the transect line. Due to the spatial compactness of the study area, the homogeneous habitat and the short vegetation in all grassland patches, this method seemed an appropriate way to obtain information about the relative availability of voles. Similar methods, based on potentially active vole holes, have been applied for the same purpose (Mülner 2000, Krüger 2002, Steiner et al. 2007). (Sign surveys are generally known to be very cost-efficient [Barea-Azcón et al. 2007], but see also Gervais [2010] for a critical assessment of the performance of vole abundance indices based on signs of presence.) We did not walk transects in woodland or marshland parcels because vole holes would not be found in these habitats due to the higher vegetation. While walking the transects, we grouped the parcels into one of five wetness categories depending on the percentage of surface water and the moisture of the ground. Furthermore, we evaluated land use of the parcels by categorizing them as woodland, marshland, arable land, or grassland.

As buzzards use several kinds of natural and artificial perches (Glutz et al. 1989, Mülner 2000, Probst 2002), we mapped all potential buzzard perching sites in the study area (>2100 perches), distinguishing between punctual perches (e.g., trees, bushes, gates, specific fence posts), and linear perches (e.g., mainly rows of bushes and trees). We did not map rows of fence posts because they are of subordinate importance as perches (Hohmann 1994, Wuczyński 2005, Nikolov et al. 2006) and could not have been a limiting factor for buzzards in the study area, as they separated nearly all field parcels and thus were regularly distributed. Punctual perches that formed common structures, such as branches of one tree or bush, and posts situated very close to each other (<5 m) were counted as a single punctual perch.

Data Analysis and Statistical Treatment. For data analysis, we used only grid units that were entirely within the Common Buzzard survey area and for which we had collected data on the predictor variables (see below) for at least 80% of the grid area. Thus, 290 grids remained, covering an area of 18.13 km^2 and comprising 95% grassland and 5% arable land.

We calculated eight variables for each grid unit (see Schindler 2002 for detailed explanations): the encounter probability for Common Buzzards and seven predictor variables. (1) Relative Common Buzzard encounter probability was the sum of Common Buzzard encounters in each grid unit during the 20-d period of investigation. (2) We defined presence and absence of Rough-legged Hawks for each grid square, with presence implying at least one observation of Rough-legged Hawk during the 20 point counts. (3) Vole-hole index (VHI) equaled the number of unflooded holes per transect m in each parcel. We assigned these densities to grid units by creating a map of the parcel boundaries in GIS (ArcView, ESRI, Redlands, California, U.S.A.), overlaying it with the 250 × 250 m grid, and calculating for each grid unit the area-weighted arithmetic mean of the vole-hole densities of the parcels. (4) Very dry, dry, and medium dry wetness assessment categories contained similar vole hole densities, so we aggregated the five categories of wetness into two, ''wet'' and ''dry'' and calculated the percentage of dry area for each grid unit. (5) We calculated the proportion of grassland. (6) We evaluated the number of punctual perches for each grid unit and (7) the length of linear perches. To account for the edges of small patches of woodland, we added half of their patch circumference to the length of linear perches.

(8) Our last variable was a dummy code to classify the grids into those which were located inside and those which were located outside territories of sedentary buzzard pairs. To estimate territories, we defined Thiessen polygons of 60 ha of open ground (Walls and Kenward 2001), centered on the active nest sites of the previous breeding season of the year 2000 (Grünkorn 2000). Then, we classified the grid units into six categories (0%; 0–<25%; 25–<50%; 50–<75%; 75–<100%; 100%), depending on the percentage of overlap with the estimated buzzard territories. We related these overlap categories of the grid units to the relative encounter probability of buzzards to obtain a threshold of overlap, where influence of territories was noted or not. For this purpose, we applied a multivariate Poisson regression including orthogonal contrast-dummy-coding (Bortz et al. 1990) and integrated in this analysis the remaining six parameters to avoid pseudo-correlations. We detected a threshold between the overlap categories 0% < x < 25% and 25% < x < 50% (Schindler 2002) and considered for subsequent analyses the grid units with <25% overlap as being outside of buzzard territories (recoded with '0') and those with >25% overlap as being inside of buzzard territories (recoded with '1').

Finally, we performed a multivariate Poisson regression combined with randomization tests (Edgington 1987, Agresti 1996) to analyze the relationships between relative Common Buzzard encounter probability and the seven predictors for all 290 grid units. Randomization tests have several advantages, including flexibility, the support of significance testing without distributional assumptions, and the possibility for testing specific hypotheses with complex, ecological dependent data (Cheverud et al. 1989, Manly 1997, Fortin and Jacquez 2000, Ricotta 2007). Using the software 'computer intensive statistics' written by Nemeschkal (1999), we estimated the significance levels (*P*-values) of the dependent parameters by computing 10 000 random permutations for each parameter, and only regarded them as significant (cumulative $P \leq 0.05$) after combining the several events of hypothesis testing on the ground of basic probability theory (Sachs 1991). Additionally, we calculated pair-wise bivariate relations between the parameters employing simple linear regression analysis (Statgraphics Plus 4.0, Manugistics, Rockville, Maryland, U.S.A.), and expressed them simultaneously with the results from Poisson-regression analysis in path diagrams. We also repeated these analyses two further times, separately for the grid units within and for the grid units outside buzzard territories.

RESULTS

During the 20 d of this study, we recorded 1537 observations of Common Buzzards and 109 of Rough-legged Hawks. Thus, the average density of Common Buzzards was 4.2 individuals per km^2 and its ratio to the Rough-legged Hawk was about 14:1. As postulated, the location of the grid unit relative to buzzard breeding territories influenced the number of observations of Common Buzzards, as

Table 1. Results of the multivariate Poisson regression estimating the relative encounter probability of Common Buzzards. ALL: all grid units without specification (n = 290; full model: $P < 0.001$), OUT: grid units outside the Common Buzzard territories only (n = 203; full model: $P < 0.001$), IN: grid units inside the Common Buzzard territories only (n = 87; full model: $P < 0.019$), 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 Hawks. The standard error (SE) is not calculated here; P-values were calculated instead by random permutational testing (10 000 random permutations). The bold values indicate significant results with a cumulative $P \leq 0.05$.

	ALL		OUT		IN	
PREDICTOR	COEFFICIENT (b)	P-VALUE	COEFFICIENT (b)	P-VALUE	COEFFICIENT (b)	P-VALUE
Constant	+1.32	0.520	+1.70	0.971	+7.95 E-01	0.687
PUP	−2.73 E-02	**0.005**	−3.53 E-02	**0.003**	−1.39 E-02	0.436
LIP	−9.98 E-04	**0.003**	−1.10 E-03	**0.005**	−5.41 E-04	0.375
ROB	−6.62 E-02	0.585	−7.87 E-02	0.524	−7.08 E-02	0.823
TER	−2.66 E-01	**0.019**				
VHI	+2.04	**<0.001**	+2.00	**<0.001**	+2.27	0.067
GLA	+8.52 E-01	0.034	−3.86 E-01	0.428	+1.33	**0.044**
DLA	−4.81 E-01	0.079	+4.42 E-01	0.185	−8.73 E-01	0.162

we observed significantly more buzzards in grid units outside territories (Table 1). The multiple Poisson regression analysis further indicated that the relative encounter probability of Common Buzzards was positively related to the vole-hole index (VHI), but inversely proportional to the number of punctual perches and the length of linear perches (Table 1). The presence of Rough-legged Hawks was not significantly related to Common Buzzard encounter probability, but was directly proportional to VHI, which in turn was positively related to the proportion of grassland and the proportion of dry land (Fig. 2a).

Considering only the grid units outside buzzard territories, the number of encountered Common Buzzards was also positively related to VHI and inversely proportional to the amount of perches (Table 1), whereas no variable was significantly related to the presence of Rough-legged Hawks (Fig. 2b). The multivariate regression analysis for the grid units within buzzard territories showed that Common Buzzard occurrence was significantly related only to the proportion of grassland cover (Table 1), which also determined the presence of Rough-legged Hawks (Fig. 2c).

DISCUSSION

Territoriality. The study area held a very dense population of Common Buzzards during late autumn, with densities higher than almost all others reported for this species for the winter season (Mülner 2000, Boano and Toffoli 2002, Nikolov et al. 2006 and references therein; but see Helbig et al. 1992, Busche and Berndt 1994, and Berndt 1998 for exceptional high winter densities under particular circumstances). Applying multivariate Poisson regression analyses, we detected significant constraints for the wintering raptors, demonstrated the effects of territoriality on their distribution pattern, and were thus able to provide evidence for some preliminary conclusions of Hohmann (1994, 1995), who observed interactions of paired, unpaired, and transient Common Buzzards in the same study area. We detected significantly fewer buzzards in areas near nests of the previous spring, suggesting that breeding buzzards excluded nonbreeders and wintering birds, perhaps pushing them to the lowest parts of the study area, which were also the most remote from the small woodlots. This displacement to potentially suboptimal habitat may have been encouraged by increased territoriality related to the low vole density in the study area during autumn 2000 (H. Bruns pers. comm.). Covering a larger study area in the same region, Busche and Kostrzewa (2007) concluded that the wet lowlands were sink habitats for Common Buzzards, whereas the areas surrounding the woodlands were source habitats.

In addition, Müller et al. (1979) found an abundance of wintering immature Common Buzzards in the wetter and lower parts of their study area, and Prytherch (2009) stated that in winter intruders are normally chased out promptly by residents. Territorial behavior of Common Buzzards during the winter season is also described by Weir and Picozzi

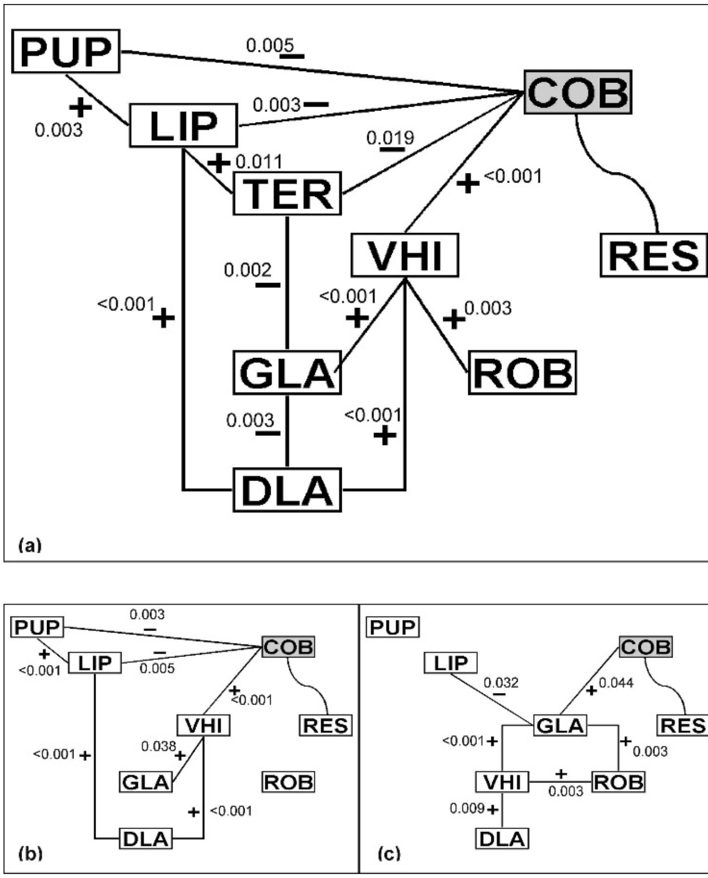

Figure 2. Direct and indirect influences of different parameters on the probability of encounter of Common Buzzards (COB). Only significant relations are shown, numbers represent *P*-values for pair-wise linear regressions between the variables. PUP = number of punctual perches, LIP = length of linear 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 Hawks, RES = residual. (a) **All** grid units included (n = 290), (b) Grid units **outside** the Common Buzzard territories only (n = 203), (c) Grid units **inside** the Common Buzzard territories only (n = 87).

(1975), and fidelity to winter territories is described for the Common Buzzard, the subspecies Steppe Buzzard (*B. b. vulpinus*) and the Rough-legged Hawk by several authors (Mebs 1964, Moreau 1972, Sylvén 1978, Glutz et al. 1989, Newton 1990, Whitelaw 1995). Kjellen (1994) revealed that in southern Sweden the proportion of juvenile buzzards is low in winter, but significantly higher among migrants and birds wintering in marginal coastal areas, suggesting that subordinate individuals were more motivated to migrate from breeding grounds or the nearest wintering areas due to competition from more dominant (adult) buzzards. This situation is predicted for partial migrants by the social-dominance hypothesis (Cox 1968, Gauthreaux 1978, 1982, Kjellen 1994, Gyllenberg et al. 2008).

In our study, the number of punctual perches and the length of linear structures that could be used as perches were inversely proportional to Common Buzzard encounter probability. As buzzards mainly hunt from perches (e.g., Wuczyński 2005), we assume that this negative correlation was also related to the strong territoriality of the birds. The fact that it was significant, even if grid units inside the territories of breeders were excluded from analysis, may indicate that unpaired birds, which are resident for some weeks to several months might establish temporary territories in these parts of the study area (Hohmann 1994). Hunting from the ground can be a rather effective alternative hunting strategy during the winter season (Wikar et al. 2008), in particular for young and inexperienced Common Buzzards (Müller et al. 1979, Wuczyński 2005, Prytherch, 2009). Hohmann (1994) observed that territories of paired, but not of unpaired Common Buzzards, contained high perches, while transient buzzards, probably to avoid aggression, were frequently located next to high perches without using them. Weir and Picozzi (1975) and Prytherch (2009) also described the use of high perches by territorial pairs and the use of low ones by immature Common Buzzards trying to defray aggression. Similarly, in an alpine valley of open landscape, first-winter buzzards perched significantly lower than did adults, and concentrated in areas with lower perches or without any perches (Probst 2002).

In our study area, there was no significant relation between the presence of wintering Rough-legged Hawks and Common Buzzard frequency, although interspecific territoriality between Rough-legged Hawk and Common Buzzards was detected in southern Sweden (Sylvén 1978). This difference was possibly caused by habitat differences between the two study areas or by the relatively low abundance of Rough-legged Hawks in Schleswig–Holstein (Looft and Busche 1981).

Habitat Use and Prey Availability. We found differences in the Common Buzzards' habitat use depending on the distance to active nests of the previous spring. Within the territories of sedentary buzzards, non-grassland areas were avoided, and the other predictor variables had a weaker influence on the raptor's distribution, whereas in the heavily used areas outside of territories of sedentary buzzards, the number of Common Buzzards was related primarily to prey availability. This difference may have been caused by the shorter resident time of the transient buzzards, as they presumably tried to obtain food without investing much energy in territoriality (Hohmann 1994, Prytherch 2009).

According to Newton (1990), winter densities of raptors seem to be even more strongly related to prey availability than do summer densities. We showed that the occurrence of Common Buzzards at a local scale was directly and positively correlated to the density of vole holes. In our study area, buzzards prey mostly on voles (Looft and Busche 1981, Hohmann 1995, Grünkorn 1999), as has been documented for other areas (Mebs 1964, Sylvén 1978, Gamauf 1987, Spidsø and Selås 1988, Mülner 2000, Šotnár and Obuch 2009). In Poland, up to 85% of prey biomass consumed by Common Buzzards and Rough-legged Hawks during the winters 1987/88 to 1989/90 was field voles (*Microtus arvalis*; Kowalski and Rzepala 1997). Field voles are also the most frequently occurring microtine rodents in the study area. In September 2000, 32 of 33 microtines (97%) captured in Meggerkoog were *M. arvalis* and in September 1999, 59 out of 62 or 95% (H. Bruns pers. comm.). Despite skepticism regarding the use of burrows and other vole sign as indices of vole abundance (Gervais 2010), we suggest that the highly significant relationship of the VHI to the occurrence of Common Buzzards indicated that the VHI was a good indicator of prey availability for our study area. This might be caused by the spatial compactness of the study area and the homogeneous habitat, which should result in a limited influence of habitat on the vole hole occupancy.

Some habitat parameters that did not show a direct effect on spatial use of Common Buzzards may have indirect effects. The proportion of grassland, which proved important for Common Buzzards' space use elsewhere (Kenward et al. 2001b), showed in our study a positive correlation with VHI and a negative correlation with the location of the grid unit relative to Common Buzzard territories. Therefore, a higher percentage of grassland increased the likelihood of observing buzzards in late autumn indirectly via these two paths, whereas within the Common Buzzard territories, the proportion of grassland was directly related to the Common Buzzard encounter probability.

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Literature Cited

Agresti, A. 1996. An introduction to categorical data analysis. John Wiley and Sons, New York, NY U.S.A.

Barea-Azcón, J.M., E. Virgós, E. Ballesteros-Duperón, M. Moleón, and M. Chirosa. 2007. Surveying carnivores at large spatial scales: a comparison of four broad-applied methods. *Biodiversity and Conservation* 16:1213–1230.

BERNDT, R.K. 1998. Ornithologischer Jahresbericht für Schleswig-Holstein 1996. *Corax* 17:146–168.

BOANO, G. AND R. TOFFOLI. 2002. A line transect survey of wintering raptors in the western Po Plain of northern Italy. *Journal of Raptor Research* 36:128–135.

BORTZ, J., G.A. LIENERT, AND K. BOEHNKE. 1990. Verteilungsfreie Methoden in der Biostatistik. Springer-Verlag, Heidelberg, Germany.

BUSCHE, G. AND R.K. BERNDT. 1994. Ornithologischer Jahresbericht für Schleswig-Holstein 1992. *Corax* 15:317–343.

——— AND A. KOSTRZEWA. 2007. Zunehmende Brutbestände des Mäusebussards *Buteo buteo* im westlichen Schleswig-Holstein im Zeitraum 1966–2006: Bestandswachstum durch sequentielle Habitatbesetzung. *Vogelwarte* 45:209–217.

CHEVERUD, J.M., G.P. WAGNER, AND M.M. DOW. 1989. Methods for comparative analysis of variation patterns. *Systematic Zoology* 38:201–213.

COX, G.W. 1968. The role of competition on the evolution of migration. *Evolution* 22:180–192.

CRAMP, S. AND K.E.L. SIMMONS. 1980. The birds of the western palearctic, Vol. II. Oxford University Press, London, U.K.

EDGINGTON, E.S. 1987. Randomization tests. Marcel Dekker, New York, NY U.S.A. and Basel, Switzerland.

FAIRHURST, G.D. AND M.J. BECHARD. 2005. Relationships between winter and spring weather and Northern Goshawk (*Accipiter gentilis*) reproduction in northern Nevada. *Journal of Raptor Research* 39:229–236.

FORTIN, M.-J. AND G.M. JACQUEZ. 2000. Randomization tests and spatially auto-correlated data. *Bulletin of the Ecological Society of America* 81:201–205.

GAMAUF, A. 1987. Dreijährige Untersuchung an einer Greifvogelwinterpopulation im südlichen Burgenland. *Egretta* 30:24–37.

GAUTHREAUX, S.A. 1978. The ecological significance of social dominance. Pages 17–54 *in* P.P.G. Bateson and P.H. Klopfer [EDS.], Perspectives in ethology. Plenum Press, New York, NY U.S.A.

———. 1982. The ecology and evolution of avian migration systems. Pages 93–168 *in* J.R. King, D.S. Farner, and K. Parkes [EDS.], Avian biology. Academic Press, New York, NY U.S.A.

GERVAIS, J.A. 2010. Testing sign indices to monitor voles in grasslands and agriculture. *Northwest Science* 84:281–288.

GLUTZ VON BLOTZHEIM, U.N., K.M. BAUER, AND E. BEZZEL. 1989. Handbuch der Vögel Mitteleuropas, Bd. 9: Falconiformes. Aula-Verlag, Wiesbaden, Germany.

GRÜNKORN, T. 1999. Brutbestand und Bruterfolg des Mäusebussards (*Buteo buteo*) auf einer Probefläche bei Schleswig 1999. Jahresbericht im Auftrag der Obersten Jagdbehörde im Ministerium für Umwelt, Natur und Forsten Schleswig-Holstein, Kiel, Germany.

———. 2000. Brutbestand und Bruterfolg des Mäusebussards (*Buteo buteo*) auf einer Probefläche bei Schleswig 2000. Jahresbericht im Auftrag der Obersten Jagdbehörde im Ministerium für Umwelt, Natur und Forsten Schleswig-Holstein, Kiel, Germany.

GYLLENBERG, M., E. KISDI, AND M. UTZ. 2008. Evolution of condition-dependent dispersal under kin competition. *Journal of Mathematical Biology* 57:258–307.

HELBIG, A.J., A. RUSCHENDORF, H. BELTING, AND J. LUDWIG. 1992. High densities of wintering hen harriers *Circus cyaneus* and buzzards *Buteo buteo* in the Lake Dummer area, NW Germany. *Vogelwarte* 36:196–202.

HODDER, K.H., R.E. KENWARD, S.S. WALLS, AND R.T. CLARKE. 1998. Estimating core ranges: a comparison of techniques using the Common Buzzard (*Buteo buteo*). *Journal of Raptor Research* 32:82–89.

HOHMANN, U. 1994. Status specific habitat-use in the Common Buzzard *Buteo buteo*. Pages 359–366 *in* B.-U. Meyburg and R.D. Chancellor [EDS.], Raptor conservation today: Proceedings of the IV World Conference on Birds of Prey and Owls. World Working Group on Birds of Prey and Owls, Berlin, Germany.

———. 1995. Untersuchungen zur Raumnutzung und zur Brutbiologie des Mäusebussards (*Buteo buteo*) im Westen Schleswig-Holsteins. *Corax* 16:94–104.

KASPRZYKOWSKI, Z. AND P. CIESLUK. 2011. Rough-legged Buzzard *Buteo lagopus* wintering in central eastern Poland: population structure by age and sex, and the effect of weather conditions. *Ornis Fennica* 88:98–103.

KENWARD, R.E., R.T. CLARKE, K.H. HODDER, AND S.S. WALLS. 2001a. Density and linkage estimators of home range: nearest-neighbor clustering defines multinuclear cores. *Ecology* 82:1905–1920.

———, S.S. WALLS, AND K.H. HODDER. 2001b. Life path analysis: scaling indicates priming effects of social and habitat factors on dispersal distances. *Journal of Animal Ecology* 70:1–13.

———, ———, ———, M. PAHKALA, S.N. FREEMAN, AND V.R. SIMPSON. 2000. The prevalence of non-breeders in raptor populations: evidence from rings, radio-tags and transect surveys. *Oikos* 91:271–279.

KJELLEN, N. 1994. Differences in age and sex ratio among migrating and wintering raptors in southern Sweden. *Auk* 111:274–284.

———. 1999. Different migration strategies among Swedish Common Buzzards *Buteo buteo* revealed by the proportion of white birds. *Ornis Svecica* 9:11–18.

KOSTRZEWA, R. AND A. KOSTRZEWA. 1991. Winter weather, spring and summer density, and subsequent breeding success of Eurasian Kestrels, Common Buzzards, and Northern Goshawks. *Auk* 108:342–347.

KOWALSKI, M. AND M. RZEPALA. 1997. Diet of the Common Buzzard *Buteo buteo* and Rough-legged Buzzard *Buteo lagopus* in the autumn-winter season. *Notatki Ornitologiczne* 38:121–130.

KRÜGER, O. 2002. Dissecting Common Buzzard lifespan and lifetime reproductive success: the relative importance of food, competition, weather, habitat and individual attributes. *Oecologia* 133:474–482.

——— AND J. LINDSTRÖM. 2001. Lifetime reproductive success in Common Buzzard, *Buteo buteo*: from individual variation to population demography. *Oikos* 93:260–273.

Looft, V. and G. Busche. 1981. Vogelwelt Schleswig-Holsteins, Greifvögel. Karl Wachholtz Verlag, Neumünster, Germany.

Manly, B.F.J. 1997. Randomization, bootstrap and Monte Carlo methods in biology. Second Ed. Chapman and Hall, Boca Raton, FL U.S.A.

Mebs, T. 1964. Zur Biologie und Populationsdynamik des Mäusebussards (*Buteo buteo*) unter besonderer Berücksichtigung der Abhängigkeit vom Massenwechsel der Feldmaus (*Microtus avalis*). *Journal für Ornithologie* 105:247–306.

Moreau, R.E. 1972. The palaearctic-African bird migration systems. Academic Press, London, U.K.

Moser, B.W. and E.O. Garton. 2009. Short-term effects of timber harvest and weather on Northern Goshawk reproduction in northern Idaho. *Journal of Raptor Research* 43:1–10.

Müller, K., S. Schuster, and F. Spittler. 1979. Zehn Jahre Greifvogel-Winterzählungen auf Probeflächen im Bodenseegebiet. *Journal für Ornithologie* 120:174–187.

Mülner, B. 2000. Winterliche Bestandsdichten, Habitatspräferenzen und Ansitzwartenwahl von Mäusebussard (*Buteo buteo*) und Turmfalke (*Falco tinnunculus*) im oberen Murtal (Steiermark). *Egretta* 43:20–36.

Nemeschkal, H.L. 1999. Morphometric correlation patterns of adult birds (Fringillidae: Passeriformes and Columbiformes) mirror the expression of developmental control genes. *Evolution* 53:899–918.

Newton, I. 1990. Population ecology of raptors, Second Ed. T. and A.D. Poyser, Berkhamsted, U.K.

Nikolov, S., S. Spasov, and N. Kambourova. 2006. Density, number and habitat use of Common Buzzard (*Buteo buteo*) wintering in the lowlands of Bulgaria. *Buteo* 15:39–47.

Poirazidis, K., S. Schindler, C. Ruiz, and C. Scandolara. 2009. Monitoring breeding raptor populations - a proposed methodology using repeatable methods and GIS. *Avocetta* 33:5969.

Probst, R. 2002. Greifvogelüberwinterung 1998 bis 2002 im Bleistätter Moos, Kärnten. *Carinthia II* 114:509–516.

Prytherch, R.J. 2009. The social behaviour of the Common Buzzard. *British Birds* 102:247–273.

Ricotta, C. 2007. Random sampling does not exclude spatial dependence: The importance of neutral models for ecological hypothesis testing. *Folia Geobotanica* 42:153–160.

Sachs, L. 1991. Angewandte Statistik, Seventh Ed. Springer Verlag, Berlin, Germany and New York, NY U.S.A.

Schindler, S. 2002. Territoriality and habitat-use of wintering Common Buzzards (*Buteo buteo*) in Schleswig-Holstein, Germany. M.S. thesis, University of Vienna, Austria. http://othes.univie.ac.at/12690/1/Diploma_thesis_S_Schindler_2002.pdf (last accessed 04 August 2011).

Šotnár, K. and J. Obuch. 2009. Feeding ecology of a nesting population of the Common Buzzard (*Buteo buteo*) in the Upper Nitra region, central Slovakia. *Slovak Raptor Journal* 3:13–20.

Spidsø, T.K. and V. Selås. 1988. Prey selection and breeding success in the Common Buzzard *Buteo buteo* in relation to small rodent cycles in southern Norway. *Fauna Norvegica Serie C Cinclus* 11:61–66.

Steiner, J.J., W.E. Gavin, G.W. Mueller-Warrant, S.M. Griffith, G.W. Whittaker, and G.M. Banowetz. 2007. Conservation practices in western Oregon perennial grass seed systems. III. Impacts on gray-tailed vole activity. *Agronomy Journal* 99:537–542.

Sylvén, M. 1978. Interspecific relations between sympatrically wintering Common Buzzards (*Buteo buteo*) and Rough-legged Buzzards (*Buteo lagopus*). *Ornis Scandinavia* 9:197–206.

Walls, S.S. and R.E. Kenward. 1995. Movements of radio-tagged buzzards *Buteo buteo* in their first year. *Ibis* 137:177–182.

——— and ———. 1998. Movements of radio-tagged buzzards *Buteo buteo* in early life. *Ibis* 140:561–568.

——— and ———. 2001. Spatial consequences of relatedness and age in buzzards. *Animal Behavior* 61:1069–1078.

———, S. Mañosa, R.M. Fuller, K.H. Hodder, and R.E. Kenward. 1999. Is early dispersal enterprise or exile? Evidence from radio-tagged buzzards. *Journal of Avian Biology* 30:407–415.

Warkentin, I.G. and N.H. West. 1990. Ecological energetics of wintering Merlins *Falco columbarius. Physiological Zoology* 63:308–333.

Weiers, S., M. Bock, M. Wissen, and G. Rossner. 2003. Mapping and indicator approaches for the assessment of habitats at different scales using remote sensing and GIS methods. *Landscape and Urban Planning* 67:43–65.

Weir, D. and N. Picozzi. 1975. Aspects of social behavior in the buzzard. *British Birds* 68:125–141.

Whitelaw, D.A. 1995. Home range behaviour of the Steppe Buzzard *Buteo buteo vulpinus* in the non-breeding season. *Ostrich* 66:94–96.

Wikar, D., M. Ciach, M. Bylicka, and M. Bylicka. 2008. Changes in habitat use by Common Buzzards (*Buteo buteo*) during non-breeding season in relation to winter conditions. *Polish Journal of Ecology* 56:119–125.

Wuczyński, A. 2005. Habitat use and hunting behaviour of Common Buzzards *Buteo buteo* wintering in south-western Poland. *Acta Ornithologica* 40:147–154.

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