

Population Limitation in Buzzards *Buteo buteo* and Kestrels *Falco tinnunculus*: the different roles of habitat, food and weather

Achim Kostrzewa and Renate Kostrzewa

ABSTRACT

627 Buzzard nests were studied over 12 years (1980-1991) in a 690km² area and 128 Kestrel nests over 10 years (1982-1991) in a 100km² area near Cologne and Bonn. Vole availability during the breeding season was also monitored.

Habitat use - Both species showed a wide overlap in hunting habitat deriving from the same food preference - mainly voles. Kestrels nest in open farmland or suburban habitats. Buzzards nest in woodland. Thus both species' breeding habitat differs markedly.

Density - Both populations were sedentary. Buzzards were limited by territorial behaviour only during the breeding cycle. Their territories were regularly spaced. Kestrels were mainly limited by winter temperature via reduction of food availability and resulting starvation. Their territories were irregularly spaced.

Reproductive Success - In total 629 young Buzzards fledged from 627 occupied territories (reproductive success = 1.0; fledged young per clutch = 1.33; fledged young per successful pair = 1.7).

Buzzards' reproductive success was mainly influenced by rainfall in May ($r = -0.80$; $P < 0.001$) but not by vole-rank ($r = 0.36$; N.S.). Two more factors of minor importance were identified a) interference by Goshawks and b) grade of territory as a measure for territory quality.

In total 378 young Kestrels fledged from 128 occupied territories (reproductive success = 2.95; fledged young per clutch = 3.6; fledged young per successful pair = 4.2).

Kestrels' reproductive output was affected by two main factors: vole-rank ($r = 0.89$; $P < 0.001$) and temperature in May-June ($r = 0.64$; $P < 0.05$). Vole-rank was also clearly associated with laying date ($r = -0.82$; $P < 0.01$).

It was interesting to see how differently two sympatric raptors reacted to vole availability: the Buzzard obviously did not react in its production of young but the Kestrel's success was strongly affected by vole availability.

INTRODUCTION

Food has been an outstanding limiting factor in the ecology of birds for a long time (Lack 1954), but during the last 20 years ecologists found increasing evidence that raptors' density and breeding success are also affected by other factors than food, as reviewed by Newton (1979). The objective of raptor studies changed over the years as ecologists tried to find out which factors are responsible and how they apply in each case. Most papers deal with multifactorial analyses for single species as for example Sparrowhawks (Newton 1986, 1991), Goshawks (Sulkava *et al.* this volume) or Kestrels (Village 1990). Some researchers try to quantify the amount of each significant limiting factor (e.g. Newton & Marquiss 1986), covering food, weather, intra- and interspecific competition, nest-sites, nesting- and hunting habitat. These factors can be easily studied with relatively large sample sizes. In contrast, others working on the level of individual birds are much more time-consuming and will not be discussed here.

We had the unique opportunity to do research on a raptor community of nine different species (Kostrzewa & Kostrzewa 1988), four of which provided a large enough sample to address ecological questions. Out of these two, the Buzzard and Kestrel used mainly voles as their prey base. In this paper, therefore, we compare the ecology of these two species, which react differently to changes in prey.

STUDY AREA AND METHODS

627 Buzzard nests were studied (by AK and co-workers) over 12 years from 1980 to 1991 in a 690km² area and 128 Kestrel nests (by RK) in a smaller area of 100km² over 10 years, from 1982 to 1991.

The study area is situated near Cologne and Bonn on the west side of the River Rhine (Germany). The Kestrel area is located within the Buzzard study area. Both populations were sedentary. More information about the area and our methods of study have been given in previous papers (see below). For this paper we have updated all information to 1991 which adds three more years (=20-25% of total). To stress the overall success of each species, we use "fledged young per territorial pair" instead of "fledged young per successful pair" (as in Kostrzewa & Kostrzewa 1990, 1991) in all correlations dealing with success.

Methods of nest-habitat evaluation or assessment of competition were given in Kostrzewa (1986, 1989, 1991, in prep.)

RESULTS

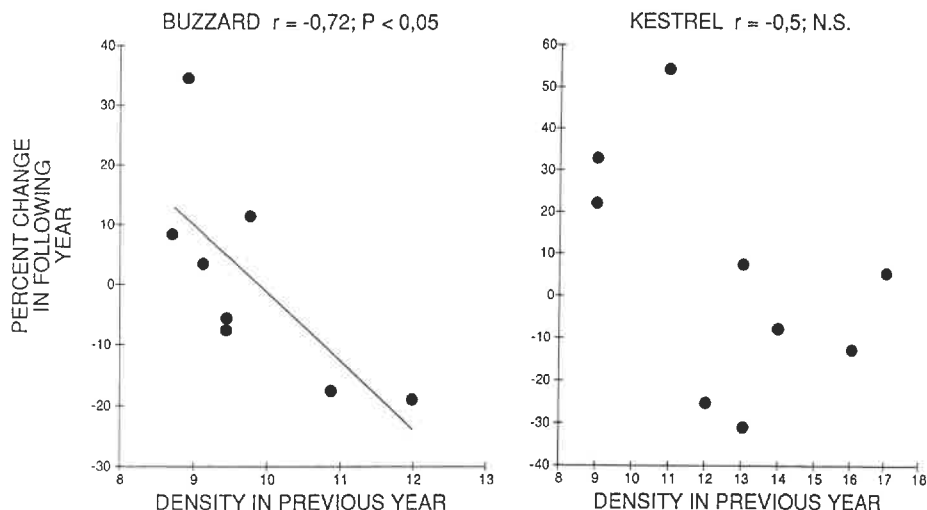
The nesting habitat

Buzzards bred in self-constructed stick nests within woodland, whereas Kestrels bred mostly in nest boxes or cavities in buildings like farmhouses or churches in open farmland or suburban habitat. Thus both species' nesting habitat differs strictly in our area. The overlap is in hunting habitat, where both species mainly catch voles.

Spacing and regulation of density

Within woodland Buzzards are regularly spaced out as the G-test according to Brown and Rothery (1978) shows ($G=0.77$), whereas Kestrels are irregularly scattered over their suitable nesting habitat because they depend on manmade structures which are spaced by chance ($G=0.47$). We also considered density-dependent-regulation in both species. Buzzards do regulate themselves significantly (Fig. 1), testing density in the previous year versus percent change in the following year (according to Newton & Marquiss 1986). We interpret both findings in Buzzards as a manifestation of territorial behaviour, which can also be observed in the field. In contrast we found neither evidence from observations nor from correlations that Kestrels regulate themselves spatially or temporally by territorial behaviour (Fig. 1).

Figure 1. Comparison of density-dependence in the population fluctuations of Buzzards ($r = -0.72$; $P < 0.05$) and Kestrels ($r = -0.50$; N.S.).



Kestrel

If there is no density-dependent-regulation in Kestrels, what does limit their numbers?

The numbers of territorial and laying pairs (Fig. 2) fluctuate more or less in parallel. There are years with greatly reduced density, such as 1985 and 1987. From observations of starved Kestrels we focussed our interest on two factors: (a) winter temperature and (b) vole numbers during spring and early summer (given here as 1=low, 2=medium and 3=high vole density). Winter temperature is highly significantly correlated with the number of territorial pairs in the following spring ($r=0.84$; $P < 0.001$), whereas vole rank is not correlated with Kestrel density ($r=0.07$; N.S.). This does not mean that food could be unimportant for survival, but low winter temperatures mean also more snow cover, which prevents Kestrels from hunting (Kostrzewa 1989).

Therefore we concluded that Kestrel territory numbers were mostly limited by winter temperature.

The next question was: what limits Kestrel's breeding success? Most observers have found voles to be most important, and this was also true in our population. Vole-rank and reproductive success were highly significantly correlated (Fig. 3a). This correlation implicates the finding that most early clutches were observed during years with high vole levels (Fig. 3b)

Findings in other raptors - including Buzzards - indicate that weather could also influence breeding success. The correlation between success and temperature in May and June (i.e. during incubation and the early stages of hatching) was significant (Fig. 4a). The correlation of success versus precipitation during the same period was not significant. This seems easy to explain because more than 95% of our Kestrel pairs breed in sheltered boxes or buildings (Fig. 4b).

Another factor which is now known to affect raptors' breeding success is territory quality. In Kestrels we found frequently used territories being more successful (Fig. 5). At this stage we cannot say exactly why, but habitat analysis is still in progress. Previous results showed contrasting pictures: success was significantly correlated positively with built-up areas and negatively with areas of mixed farmland in 50ha plots around the nest site (Kostrzewa 1989). But we would have expected an opposite result since mixed farmland provides the most vole habitat in the measured plots. Focussing more sharply on meadows and other good vole habitat, correlations were more scattered but still different from those expected. Two explanations seemed to be possible: (a) the Kestrels did not hunt over the measured plots or (b) the nest-habitat analysis itself was inappropriate. From our own observations and the literature (Village 1990) we think that the first hypothesis is correct and that most of the hunting success is outside the measured plot which has a diameter of just 800m. Therefore the plot fits with the description of nesting habitat, but not with hunting habitat and cannot be used to describe territory quality, which is dependent on both. Breeding success itself is closely correlated to vole-rank assessed in the whole study area (Fig. 3).

Figure 2. (a & b) Kestrel population data, (c) vole-rank and (d) winter-temperature for the study area during 1982-1991.

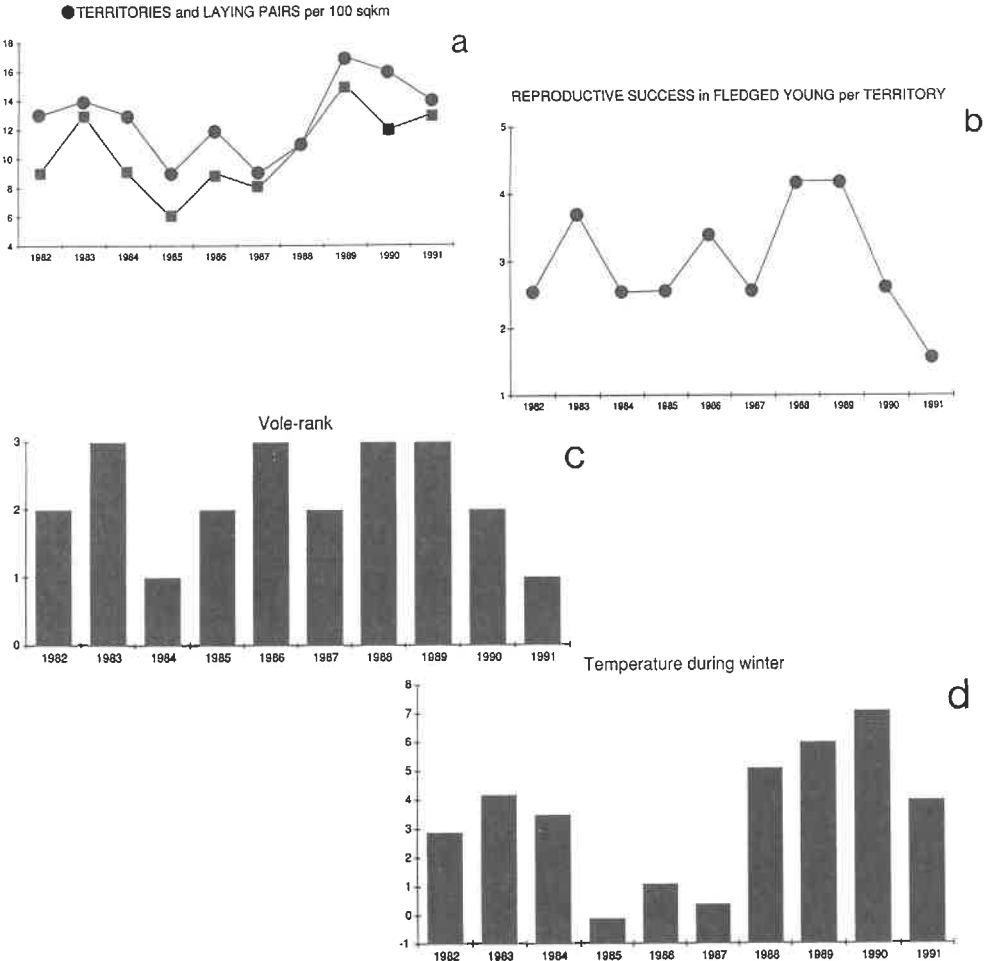


Figure 3. (a) Vole-rank and reproductive success ($r = 0.89$; $P, 0.001$) and (b) vole-rank and laying date ($r = -0.82$; $P < 0.01$) in Kestrels are highly significantly correlated.

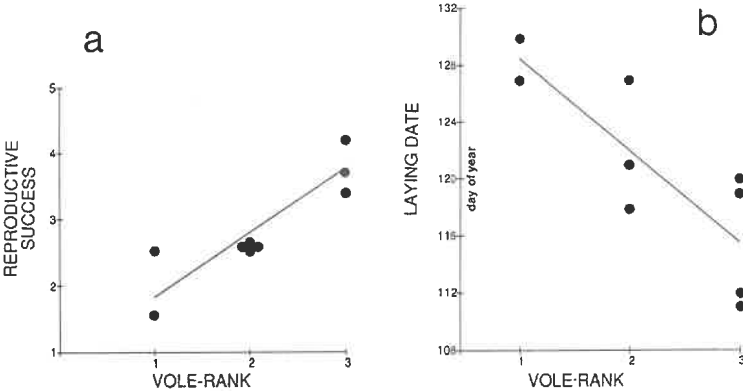


Figure 4. Reproductive success (a) versus temperature in May and June ($r = 0.64$; $P < 0.05$) is significantly correlated and (b) versus precipitation in May and June ($r = -0.21$; N.S.) is not correlated in Kestrels.

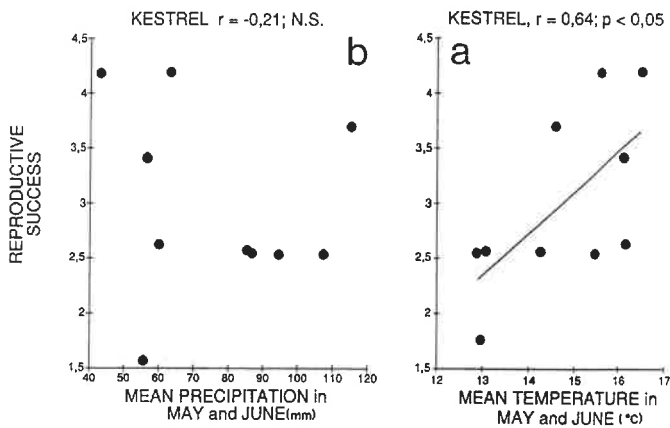
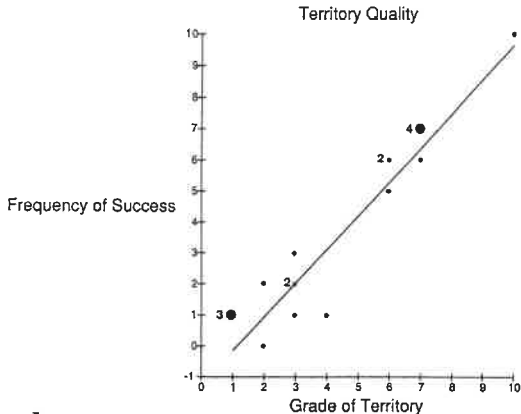


Figure 5. Relationships between frequency of nest success and grade of territory (measured as frequency of occupancy) in Kestrel territories ($r = 0.95$; $P < 0.001$; $N = 19$).



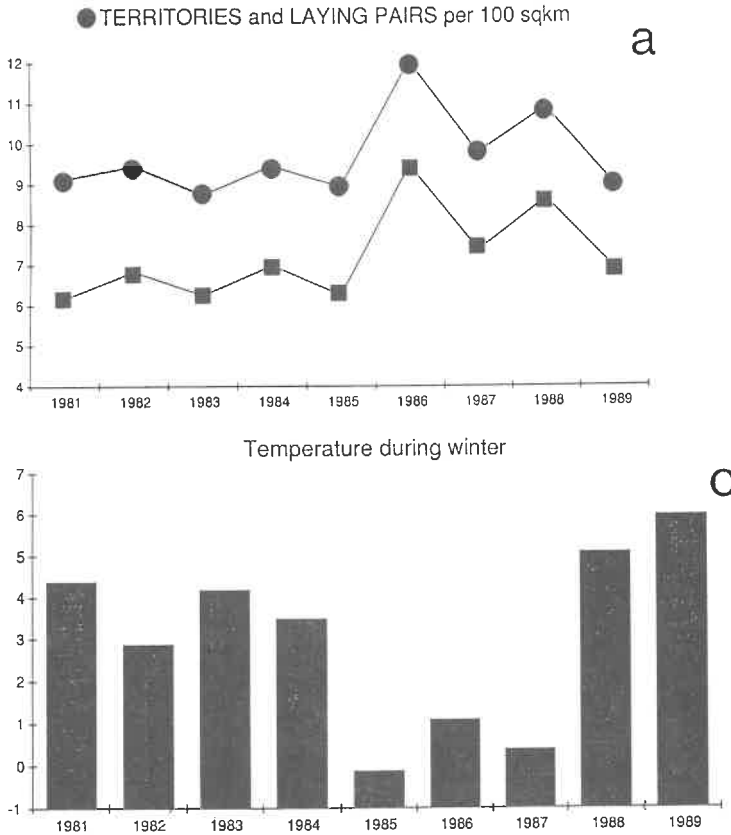
Buzzard

We found no evidence that Buzzard numbers were affected by changes in vole availability (Fig. 6). A high vole rank in 1983 was not accompanied by a change in the number of territories; in 1986 density rose but in 1989 it dropped despite a good vole year ($r=0.20$; N.S.). Also in winter temperature the correlation to Buzzard territory numbers is nearly nil ($r= -0.01$, N.S.).

We have therefore concluded that spacing by territorial behaviour is the most important factor for limiting Buzzard numbers in our area. Territory size itself seemed to be adjusted to food supply, because we found different mean nearest-neighbour-distances in two parts of the study area (cf. Kostrzewa 1991, Table 3 for Buzzards).

Buzzards' breeding success should be regulated similarly to that of the Kestrel, because both species depend on the same food resources. But when comparing success to vole rank (Fig. 7) both factors seemed to be not correlated. From observations we concluded that rainfall in May (the stage of incubation and early hatching) was the most important factor as the significant correlation showed (Fig. 8a). To illustrate this very interesting result more clearly we marked the dots in the rainfall correlation with its vole rank and found that a high vole rank is outweighed by high rainfall in May and that a mean breeding success can also be achieved during a dry May with a low vole level (see arrows in Fig. 8a). The same process can be shown between success and vole-rank (Fig. 8b) which gave no significant correlation. Dry years showed generally better success than wet ones.

Figure 6. (a) Density, (b) vole-rank (shown in Fig. 7b: 1981-89) and (c) winter-temperature for the Buzzard over nine years.



We concluded therefore that the main factor in Buzzards' breeding success was not voles but weather, which can suppress the benefits of a good vole year almost totally for the Buzzards, because they live in unsheltered stick-nests.

The question of territory quality in Buzzards was investigated from the early stages of this study, beginning with 1983 when I started my PhD-work and found evidence for two other factors affecting Buzzards' breeding success in our study population.

One factor was interspecific competition: Buzzard territories close to a Goshawk site were less successful. From 282 nesting records we found a clear correlation between distance to next Goshawk site and the breeding success of individual Buzzard pairs (see Kostrzewa 1991: Fig. 1). Secondly the nest-site itself had influence on the breeding success of its occupant. Sites which were only used once failed more often than sites with a higher degree of use (Fig. 9).

Comparing grade of territory with the frequency of its success, we found a clear positive correlation: sites used more often do have greater success. This was not only true for frequency (Fig. 10) but also for the number of young raised ($r=0.69$; $P<0.001$; $N=119$) which is not shown here. Some habitat features such as the area of open farmland (=hunting habitat) around the nest site were strongly positively correlated with its success (further data on 30 habitat parameters were given in Kostrzewa 1989). The results were consistent with my hypothesis that nest-habitat choice and nest-habitat quality should be positively correlated (Kostrzewa in prep.).

Thus we can conclude that some territories and nest-sites gave a better success than others, but we do not know why. It could be habitat alone, but I believe the quality of individual pairs might also be involved, with the most competent pairs occupying the best territories (Newton 1991).

Figure 7. (a) Reproductive success, (b) vole rank and (c) May rainfall in Buzzards over 12 years.

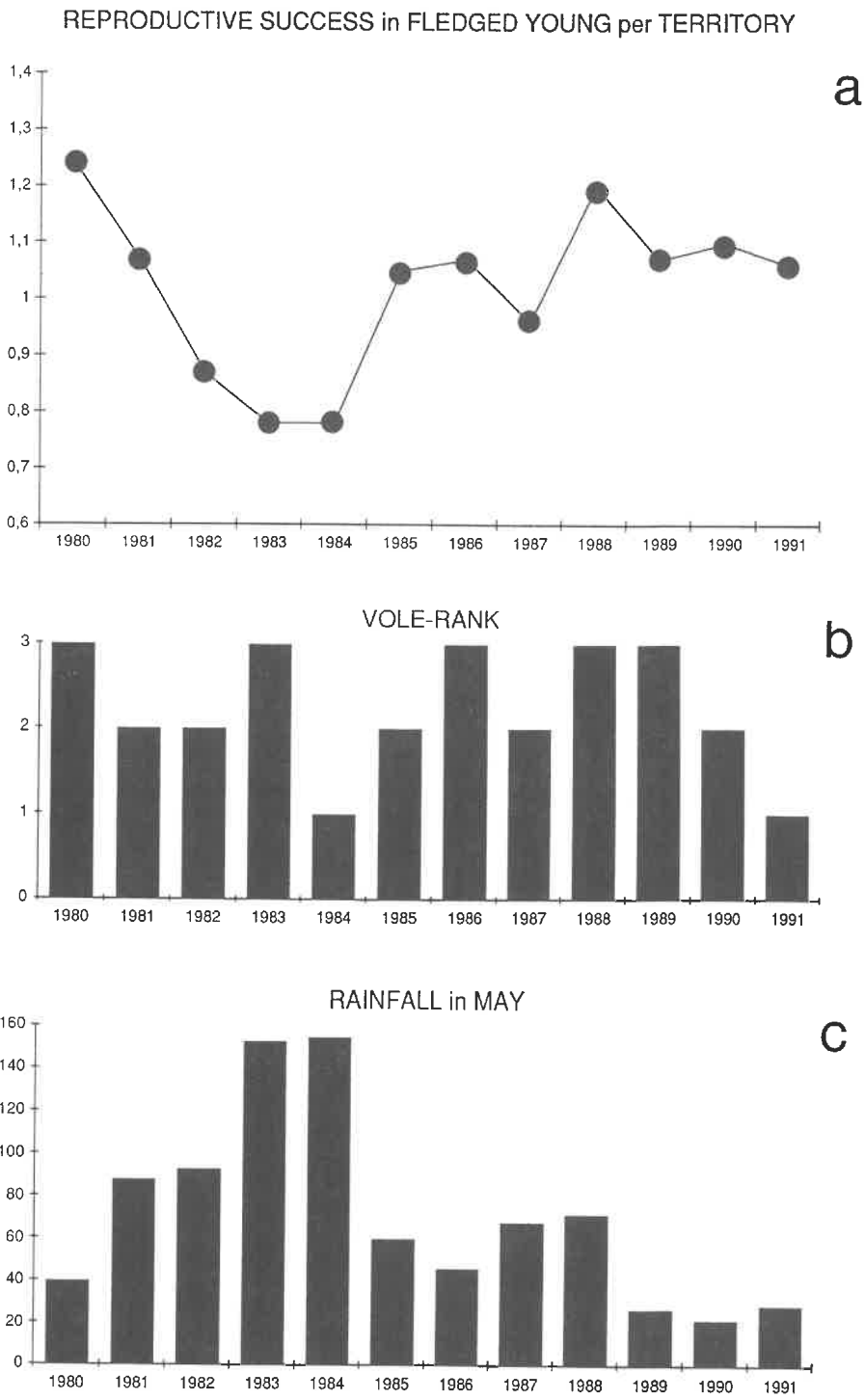


Figure 8. Reproductive success is (a) highly correlated with rainfall in May ($r = -0.80$; $P < 0.001$) but (b) not with vole-rank ($r = 0.36$; N.S.) in Buzzard.

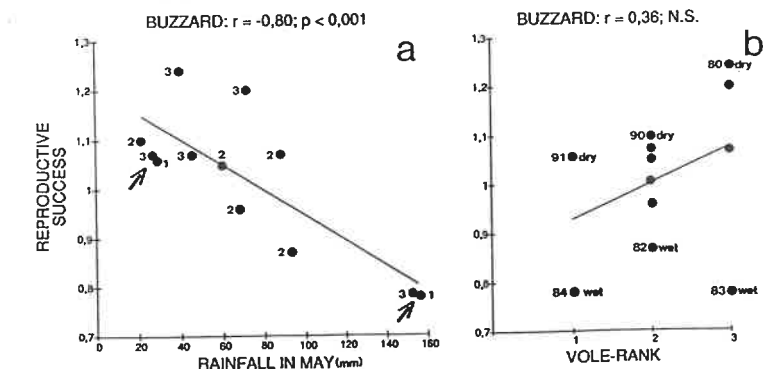


Figure 9. Low grade territories failed more often totally in the Buzzard.

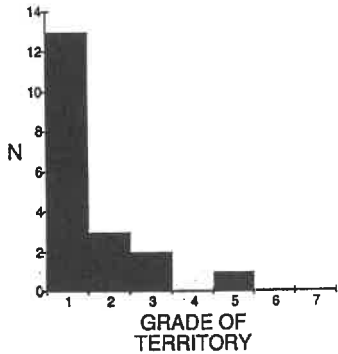
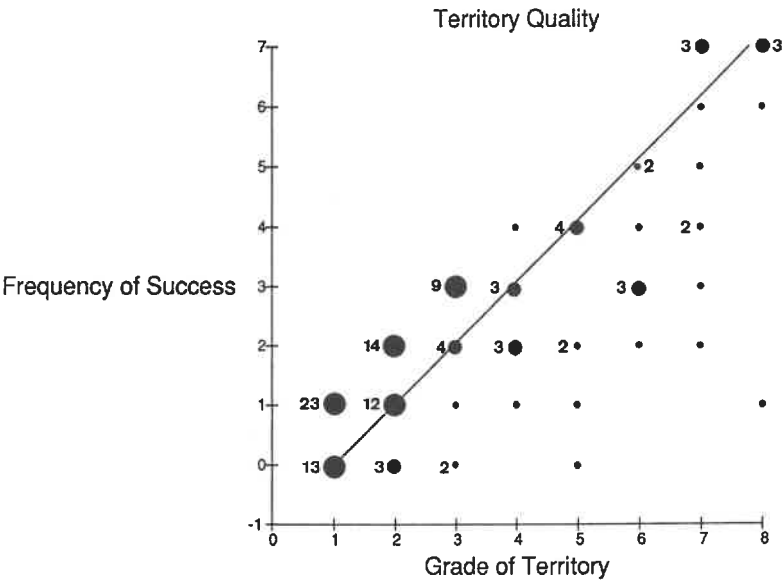


Figure 10. Relationships between frequency of nest success and grade of territory (measured as frequency of occupancy) in Buzzard territories ($r = 0.81$; $P < 0.001$; $N = 119$).



DISCUSSION

In both cases density is not directly dependent on food resources. Buzzards regulate themselves by spacing behaviour. Suitable territories and nest-sites limit the number of pairs in our area (cf. Kostrzewa 1991). A constant number of ca. 30% of all territories were non-laying over the years (Fig. 6; cf. Hohmann this volume). These were mostly low grade territories (unpubl. data). This would also highlight the importance of limited nest-sites for Buzzards. Kestrel numbers were mostly limited by starvation because of low winter temperatures causing prolonged snowcover, which prevented Kestrels from hunting efficiently. Buzzards (c. 1000g) weigh up to four times more than Kestrels (c. 250g), so it was to be expected that Kestrels were more affected by food shortage. The population bottleneck for both sedentary species is therefore during winter for the small Kestrels and during spring - while spacing themselves - for Buzzards.

Breeding success in the open nesting Buzzards was affected mainly by weather, especially by rain during the time of hatching in May, which had more effect on the annual variations than voles. Nest habitat also had a significant influence on breeding success (Kostrzewa in prep.) as did interspecific competition (Kostrzewa 1991).

For Kestrels breeding in boxes or cavities, voles were the main factor influencing annual variations in success, but also temperature during hatching had a minor influence. With three more years of data weather has lost its central position in affecting breeding success in Kestrels (cf. Kostrzewa & Kostrzewa 1990). The influence of nest-habitat on success in Kestrels seems to be not measurable, because in most cases hunting-habitat and nesting-habitat were spatially separated (Kostrzewa & Kostrzewa 1993; Village 1990).

We do not know whether our findings on the importance of food availability were typical for Central Europe, since some other studies have found Buzzard density and success more affected by voles (cf. Mebs 1964; Looft & Busche 1981; or Rockenbach 1975). But these workers never considered factors other than voles and the relationship between voles and abundance or breeding was often not so clear as they thought (see Rockenbach 1975). Under Central European conditions food and nest-sites might be of equal importance for species density and a Buzzard population, having reached the ceiling of available nesting territories, may cease to fluctuate with vole numbers. Our Kestrels should do the same, but we have good evidence that there are more nest-sites available (Kostrzewa 1989) than the maximum of 17 territorial pairs can occupy. If we have some warm winters during the coming years this population would probably also reach its density limit.

Future studies should therefore take different limiting factors for density and breeding success into consideration. Food should not always be the ultimate factor (as in Lack 1954). It can also act as a proximate factor, especially when prey and predator are more regulated by weather as the real ultimate factor governing animal populations and their behaviour over wide areas.

ACKNOWLEDGEMENTS

The Buzzard study was partly funded by the Graduiertenförderung des Landes Nordrhein-Westfalen (during 1985-86) and by a post-doctoral fellowship and grant from the Deutsche Forschungsgemeinschaft (Ko 943, 1986-89). The Kestrel study has been partly funded by the Deutsche Ornithologen Gesellschaft since 1992. We obtained several smaller grants from the Freunde und Förderer der Universität Köln. We are grateful to all of these.

The field study on Buzzards was performed by F. & R. Borger, W.v. Dewitz, A. & R. Kostrzewa and G. Speer. During more than 10 years of field work at the Department of Zoology, University of Cologne, we were supported by Profs. A. Egelhaaf, H. Engländer and especially by the late U. Lehmann. Dr Ian Newton considerably improved our manuscript.

REFERENCES

- BROWN, D. & P. ROTHERY 1978. Randomness and local regularity of points in a plane. *Biometrika* 65: 115-122.

- HOHMANN, U. (this volume): Statusspecific habitat use in the Common Buzzard *Buteo buteo*.
- KOSTRZEWA, A. 1986. Quantitative Untersuchungen zur Ökologie, Habitatnutzung und Habitattrennung von Mäusebussard *Buteo buteo*, Habicht *Accipiter gentilis* und Wespenbussard *Pernis apivorus* unter Berücksichtigung von Naturschutzmanagement und Landschaftsplanung. Dissertation, Univ. K+In.
- KOSTRZEWA, A. 1989. Nest habitat separation in three European raptors *Accipiter gentilis*, *Buteo buteo* and *Pernis apivorus* - a multivariate analysis. In: B.U. Meyburg & R.D. Chancellor (Eds.) *Raptors in the Modern World*. Proceedings of III World Conference on Birds of Prey: pp. 553-559.
- KOSTRZEWA, A. 1991. Interspecific interference competition in three European raptor species. *Ethology, Ecology & Evolution* 3: 127-143.
- KOSTRZEWA, A. (in prep.): Nest-site occupancy and breeding performance as indicators for nest-habitat quality in three European raptor species.
- KOSTRZEWA, A. & R. KOSTRZEWA 1988. Bestandstrends der Greifvögel *Falconiformes* in der Niederrheinischen Bucht. *J. Orn.* 129: 457-461.
- KOSTRZEWA, A. & R. KOSTRZEWA 1990. The relationship of spring and summer weather with density and breeding performance of the Buzzard *Buteo buteo*, Goshawk *Accipiter gentilis* and Kestrel *Falco tinnunculus*. *Ibis* 132: 550-559.
- KOSTRZEWA, R. 1989. The biology of the Kestrel *Falco tinnunculus* in different areas in the Federal Republic of Germany and West-Berlin. (in German with summary). Doctoral Thesis, Univ. Cologne.
- KOSTRZEWA, R. & 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.
- KOSTRZEWA, R. & A. KOSTRZEWA 1993. *Der Turmfalke (Falco tinnunculus)*. Aula-Verlag, Wiesbaden.
- LACK, D. 1954. *The Natural Regulation of Animal Numbers*. Univ. Press, Oxford.
- LOOFT, V. & G. BUSCHE 1981. *Greifvögel*. Vogelwelt Schleswig-Holsteins. Band 2. Neumünster.
- MEBS, T. 1964. Zur Biologie und Populationsdynamik des Mäusebussards *Buteo buteo*. *J. Orn.* 105: 247-306.
- NEWTON, I. 1979. *Population Ecology of Raptors*. Poyser, Berkhamsted.
- NEWTON, I. 1986. *The Sparrowhawk*. Poyser, Calton.
- NEWTON, I. 1991. Habitat variation and population regulation in Sparrowhawks. *Ibis*. 133 suppl. 1: 76-88.
- NEWTON, I. & M. MARQUISS 1986. Population regulation in Sparrowhawks. *J. Anim. Ecol* 55: 463-480.
- ROCKENBAUCH, D. 1975. Zwölfjährige Untersuchung zur Ökologie des Mäusebussards *Buteo buteo* auf der Schwäbischen Alb. *J. Orn.* 116: 39-54.
- SULKAVA, S., S. HUHTALA & R. TORNBERG (this volume): Regulation of Goshawks *Accipiter gentilis* breeding in Western Finland over the last 30 years.
- VILLAGE, A. 1990. *The Kestrel*. Poyser, London.

Drs. A. & R. Kostrzewa
Bonnstr. 63
D-50321 Brühl
Fed. Rep. of Germany