

# WINTER WEATHER, SPRING AND SUMMER DENSITY, AND SUBSEQUENT BREEDING SUCCESS OF EURASIAN KESTRELS, COMMON BUZZARDS, AND NORTHERN GOSHAWKS

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**ABSTRACT.**—We examined territory density, percent laying, and breeding success in Eurasian Kestrel (*Falco tinnunculus*), Common Buzzard (*Buteo buteo*), and Northern Goshawk (*Accipiter gentilis*) pairs in relation to weather conditions during the preceding winters. In kestrels, density and percentage of laying pairs were related mostly to winter temperature and snow cover. The percentage of laying pairs also depended on vole availability in the spring. Density and percentage of laying pairs in buzzard and goshawk were unaffected by winter weather. Weather conditions of the preceding winter did not affect the production of young in any of the species. We attributed different reactions to severe winters in these species to different feeding ecology as well as different body mass and its consequences for thermoregulation. Received 11 October 1989, accepted 22 October 1990.

WINTER weather affects the subsequent breeding density of many bird species (Elkins 1983). Examples include the Gray Heron (*Ardea cinerea*; Knief and Drenckhahn 1984), the Song Thrush (*Turdus philomelos*; Lack 1966), and the Peregrine Falcon in Australia (*Falco peregrinus*; Olsen and Olsen 1988). Survival rates of Eurasian Coots (*Fulica atra*) (Cavé and Visser 1985) and Great and Blue tits (*Parus major* and *P. caeruleus*; Lack 1966) depend partly on winter severity.

Energetic studies show that body mass, ambient temperature, and food availability are vital for winter survival (cf. Drent and Daan 1980). To cope with winter weather, birds use different strategies (for raptors, see Newton 1979). Some species migrate, but others that live in temperate climates stay in their home area and may hold winter territories as do some birds of prey. Philopatry in winter can enhance survival and breeding success in the next year (cf. Davies 1978). Several species show both patterns: in temperate regions they are sedentary, and under more severe conditions they become migratory (cf. Newton 1979, Cramp and Simmons 1980, Village 1990). The populations we studied are sedentary.

Winter survival can be achieved by appropriate behavioral changes. Snow cover denies vole-hunting species, like the Common Buzzard (*Buteo buteo*) or Eurasian Kestrel (*Falco tinnunculus*), their main prey, and they shift to

more available prey, such as carrion or birds. Bird-hunting species, such as the Northern Goshawk (*Accipiter gentilis*) and Eurasian Sparrowhawk (*A. nisus*), need not change their food sources (Newton 1986) and should be better able to survive hard winters. Both food preferences and body mass (approximately 800–1,200 g in Common Buzzard and Northern Goshawk, and 150–300 g in Eurasian Kestrel and Eurasian Sparrowhawk) may influence winter survival as body mass influences energy turnover.

We examined the density of territorial and laying kestrel pairs during 1982–1989 and the density of buzzards and goshawks during 1981–1988 in relation to weather conditions during the preceding winters. We considered the potential influence of winter weather on the density of territorial pairs, laying pairs, and breeding success. The kestrel data were compared with rather similar data in Eurasian Sparrowhawks obtained by Newton (1986).

In Germany, the density of territorial kestrels in the breeding season decreased significantly after severe winters in 1985 and 1987 (Kostrze-wa 1988). Anecdotal reports from other parts of Europe (e.g. Cramp and Simmons 1980) also suggested that kestrel numbers decline during and after hard winters. We observed no such effects for buzzards and goshawks in our area (Kostrze-wa and Kostrze-wa 1988).

## STUDY AREA AND METHODS

The study area (called "Niederrheinische Bucht," 50°48'N, 6°50'E) was 100 km<sup>2</sup> of mixed farmland for

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TABLE 1. Winter weather data (January through March) for the study area.

Year	Days of snow cover	Mean temperature (°C)
1981	18	4.4
1982	17	2.9
1983	13	4.2
1984	3	3.5
1985	38	-0.1
1986	36	1.1
1987	33	0.4
1988	4	5.1
1989	0	6.0

kestrels and 690 km<sup>2</sup> of mixed area (woodland = 11.5%, farmland = 72.5%, and built-up area = 16.0%) for buzzards and goshawks situated on the west side of the River Rhine between Cologne and Bonn. Winters are relatively warm and dry with a mean temperature of 3.0°C.

We defined *density* as the number of territorial pairs per 100 km<sup>2</sup> and included all pairs found in their territory from March to late June (i.e. holding a long-term territory). *Laying pairs* (LP; given here as a percentage of territorial pairs) were those pairs that laid at least one egg. Laying was sometimes confirmed by direct observation, but more commonly from behavioral observations like brooding, manipulating the eggs, and findings of eggshell remains. All other pairs, which were not proved to have laid, were considered *nonlaying pairs* (given as percentage of all TP). Most territorial raptors were resident in the area during winter (unpubl. data). Methods are described elsewhere (Kostrzewa and Kostrzewa 1990; and more broadly in A. Kostrzewa 1985, R. Kostrzewa 1985).

We acquired data from a weather station situated within the study area (Table 1). To estimate vole numbers in the area we used different sources: (1) vole counts made by the Institute for Pest Control of the "Landwirtschaftskammer des Rheinlandes" at Bonn (H. Greib), given as ranked values for three different counting areas during March and April; (2) the breeding performance of the Tawny Owl (*Strix aluco*) and the Long-eared Owl (*Asio otus*), which eat voles; and (3) food analyses at kestrel nest sites during May and June. These sources gave a clear picture of relative vole numbers, which were then ranked as: 1 = low, 2 = intermediate, and 3 = peak years (Fig. 1).

Statistical procedures were similar to Kostrzewa and Kostrzewa (1990). Means are given  $\pm$ SD.

## RESULTS

*Eurasian Kestrel*.—The density of territorial kestrels varied considerably from 9 to 17 pairs per 100 km<sup>2</sup> ( $\bar{x}$  = 12.3  $\pm$  2.66; coefficient of variation = 12.25). Laying pairs varied from 6 to 15

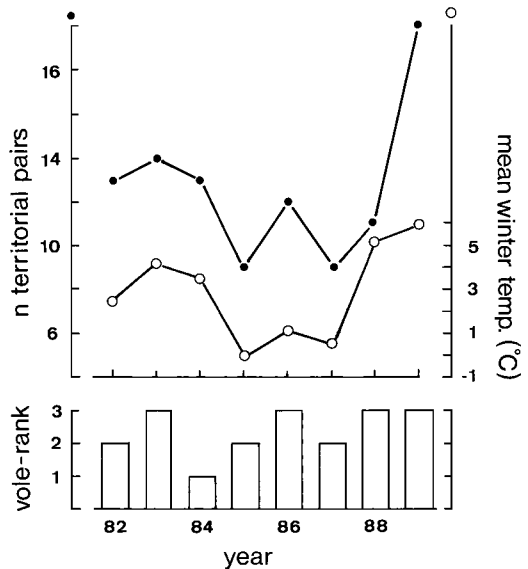


Fig. 1. Winter temperature (○) and number of territorial kestrels (●). Bar graph shows vole rank data, deriving from spring counts and food analyses at kestrel nesting sites during early summer.

per 100 km<sup>2</sup> (Fig. 1). The density of territorial kestrels was highly positively correlated with winter temperature and negatively with days of snow cover (Table 2).

Winter temperature and kestrel density (Figs. 1 and 2) change in parallel. The exception in 1988 (Fig. 2) probably occurred because there were not enough recruits to form new pairs. This was the only year when all territorial pairs bred successfully (R. Kostrzewa 1989). We omitted 1988 data from the regression and recalculated the correlation, which was highly significant ( $r_s$  = 0.98;  $P$  < 0.001; see Fig. 2, Table 2). In 1989, after the second warm winter, kestrel density rose dramatically with temperature (Fig. 1).

The percentage of laying pairs was also highly positively correlated with winter temperature and negatively dependent on days with snow cover (Table 2). The number of fledged young per successful pair was independent of winter weather (Table 2), but it was highly correlated with temperature in May and June (Kostrzewa and Kostrzewa 1990).

Data from band recoveries in the northern part of West Germany (Fig. 3) demonstrated that most kestrels found dead were found during

TABLE 2. Relationship of winter weather and breeding biology of three raptor species according to Spearman's rank correlations. Levels of significance: \* =  $P < 0.05$ , \*\* =  $P < 0.02$ , \*\*\* =  $P < 0.01$ , \*\*\*\* =  $P < 0.001$ .

Variable	No. of territ. pairs	% laying pairs	Fledged young/pair
<b>Eurasian Kestrel</b>			
Winter temp.	0.75**a	0.95****	0.26
Snow cover	-0.66*	-0.70*	0.20
<b>Common Buzzard</b>			
Winter temp.	-0.01	-0.24	0.62*
Snow cover	0.24	0.12	-0.23
<b>Northern Goshawk</b>			
Winter temp.	0.09	0.13	0.32
Snow cover	0.44	-0.52	0.04

<sup>a</sup>Omitting 1988; see Fig. 1 and 2,  $r_s = 0.98****$ .

January and February. Deaths classified by the national band-scheme as due to cold or starvation were pooled, and they peaked in these months (Fig. 3). Therefore both temperature and food availability (i.e. vole numbers) have consequences on kestrel winter survival. The density of territorial pairs and vole rank were not significantly correlated ( $r_s = 0.32$ ), but the percentage of laying pairs and vole rank were significantly correlated ( $r_s = 0.68$ ;  $P < 0.05$ ). We used multiple regression analyses to check for interrelations between winter temperature, snow cover, and vole rank (Table 3). Winter temperature was much more important than snow cover, and voles were least important, for the density of territorial pairs (Table 3: eqs. a-c). For laying pairs, winter temperature was highly significant and voles were the second factor. Snow cover was unimportant (Table 3: eqs. d-f).

*Common Buzzard*.—Density of territorial buzzards ranged from 8.7 to 12.0 pairs per 100 km<sup>2</sup>

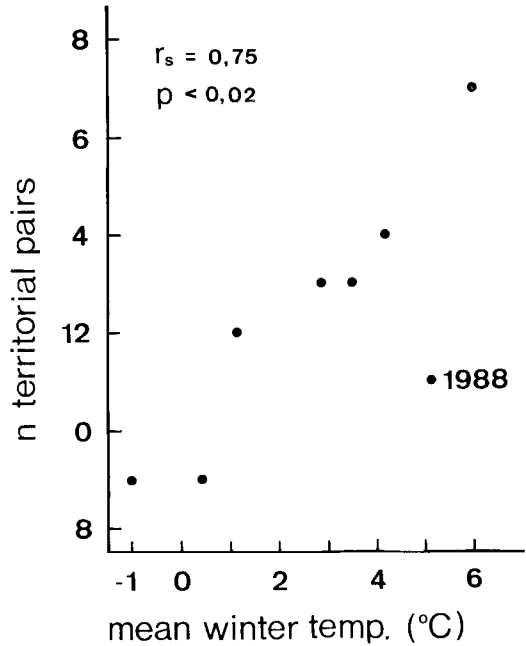


Fig. 2. Correlation between winter temperature and density of territorial kestrels. 1988 was omitted (see Fig. 1 and Table 2),  $r_s = 0.98****$ .

( $\bar{x} = 9.6 \pm 1.11$ ; coefficient of variation = 1.06; cf. Kostrzeva and Kostrzeva 1990) and laying pairs from 6.2 to 9.4 per 100 km<sup>2</sup>.

The population was more stable than that of kestrels, and there was no apparent effect of severe winters. In fact density of territorial pairs was independent of both winter temperature and snow cover (Table 2). The only significant correlation was between young fledged per successful pair and winter temperature (Table 2). Because neither territorial nor laying pairs were influenced, we interpret this result cautiously. It may be simply due to chance, especially because April and May precipitation appeared as

TABLE 3. Stepwise multiple regression analyses: number of territorial (TP) or laying (LP) pairs of kestrels in relation to winter temperature (WT), days with snow cover (SC), and vole rank (VR) ( $n = 8$ , 1982–1989; \*\* =  $P < 0.01$ , \* =  $P < 0.05$ ).

	P	r <sup>2</sup>
a. TP = 9.52 + 0.94WT*	0.02	0.63
b. TP = 9.37 + 0.93WT* + 0.07VR	NS	0.63
c. TP = 6.91 + 1.71WT + 0.09SC - 0.68VR	NS	0.71
d. LP = 6.72 + 1.14WT**	0.004	0.78
e. LP = 4.20 + 0.99WT** + 1.24VR	0.006	0.87
f. LP = 4.41 + 0.92WT - 0.01SC + 1.31VR	0.03	0.87

key factors in buzzard breeding performance (Kostrzewa and Kostrzewa 1990). In general, there was little evidence for any influence of winter weather on the buzzard population.

*Northern Goshawk.*—Density of territorial pairs (2.3–2.9 per 100 km<sup>2</sup>;  $\bar{x} = 2.6 \pm 0.21$ ; coefficient of variation = 0.04; cf. Kostrzewa and Kostrzewa 1990), and laying pairs (2.1–2.2 per 100 km<sup>2</sup>) showed little yearly variation. We found neither influence of winter weather on density of territorial or laying pairs nor relationship between winter weather and breeding success (Table 2).

DISCUSSION

*Effects of density.*—We suggest that the density of kestrel territorial pairs was related to winter conditions. From all observations (Fig. 1) and correlations (Table 3: eqs. a–c), we believe that winter temperature acts as an ultimate factor and food availability as a proximate factor for kestrel survival and density of territories in the next spring. This may hold because the density of pairs was reduced by mortality due to food shortage, starvation, and cold (cf. Olsen and Olsen 1989). Causes of death are hard to discriminate in the field. Winter weather affects the number of sparrowhawks in southwest Scotland (Newton and Marquiss 1986). Kestrels and sparrowhawks are similar in body mass (150–300 g). Presumably, they are more sensitive to low temperature and food shortage than larger nonmigrating raptor species. But kestrels and sparrowhawks differ in ecology. During winter more kestrels than sparrowhawks die of starvation (Newton et al. 1982). Sparrowhawks seem to catch enough songbirds. Kestrels take more songbirds, as they do in Germany, because voles are hidden under the snow. The density of territorial pairs (13 per 100 km<sup>2</sup>) changed little after a mild winter, which was followed by the year (1984) of the lowest vole level. But after the hard winters of 1985 and 1987, when vole populations were intermediate (Fig. 1), the kestrel territorial-pair density (9 per 100 km<sup>2</sup>) dropped despite the possibility of a food shift to songbirds.

In severe winters starvation in kestrels is likely (Fig. 3), especially in years with prolonged snow cover (Village 1990). From body mass data (Piechocki 1982, Dijkstra et al. 1988, Village 1990) and energetic work by Masman (1986: 205), we

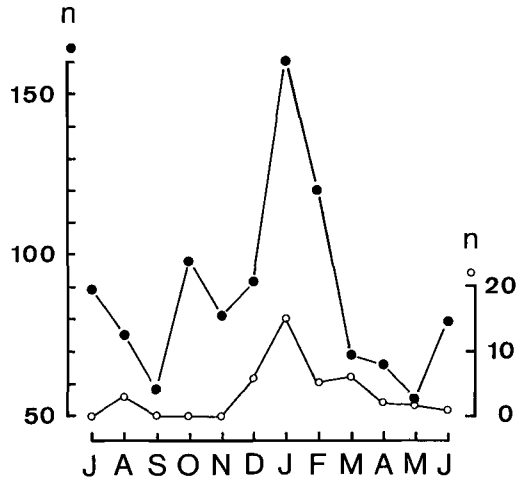


Fig. 3. The upper graph (●) shows kestrel mortality according to monthly ring recoveries (taken from the national ringing scheme) irrespective of death causes in the northern part of Germany during 1909–1987 (n = 1,041). The lower graph (○) shows monthly mortality due to cold and starvation (n = 40).

estimate that both sexes starve after 5 days, with a daily loss of body mass (ca. 12 g) on no or little food intake. Starved kestrels were found at mean values of 135 g (range: 102–160 g) (Piechocki 1982: 11). Under similar circumstances, the time that kestrels should withstand starvation is comparable to that of sparrowhawks (Newton 1986).

The density of territorial buzzards observed in the same area from 1981–1988 was not related to winter temperature or days with snow cover. Buzzards are much heavier (average winter body mass for both sexes: 762–1,018 g; cf. Cramp and Simmons 1980) than kestrels. Buzzards will die within 2 weeks after losing 25% of body mass (Piechocki 1970). Goshawk territorial pairs did not change after severe winter weather. This species feeds mostly on birds, but it has a body mass similar to the buzzard.

Kestrels and sparrowhawks appear more sensitive than the larger Common Buzzard and Northern Goshawk to low temperature and food shortage because of the species' relatively greater energy demands (cf. Aschoff and Pohl 1970).

*Effects on breeding.*—In raptors one of the most crucial elements of being able to breed is female body mass (Newton 1986). In sparrowhawks mass increases by 40–50 g in 10–20 days before laying. The increase depends on the male's abil-

ity to provide food to his mate (Newton et al. 1983). A shortfall of 15% in female body mass will prevent females from laying. Similar observations were made on kestrels (Village 1983). Body mass is not only important shortly before egg formation, but also much earlier in the year (Cavé 1968). In our study nonlaying kestrels may have been unable to attain the stage of laying, because they could not increase body mass adequately before laying (Village 1990). This seems likely from the negative correlation of nonlaying pairs and April temperature (R. Kostrzewa 1991).

Buzzards and goshawks were unaffected by similar winter conditions (Table 2). With their higher body mass they were able to withstand >10 consecutive days with little or no food. Such "long" periods of poor weather never occurred during our study, and were also judged unlikely from long-term weather records. Apparently unusually high mortality due to starvation caused by winter weather is extremely rare for either species in our area.

We believe that the vole-eating Eurasian Kestrel is disadvantaged by low body mass during cold weather in temperate areas. The heavier Common Buzzards and Northern Goshawks survived despite their different feeding ecology. Body mass seems to be more cogent to winter survival than food availability, because larger mass has advantages in thermoregulation and presumably buffers longer periods of starvation.

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