BETWEEN COHORT VARIATION IN DISPERsal distance in
THE EUROPEAN KESTREL FALCO TINNUNCULUS AS SHOWN BY
RINGING RECOVERIES

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Ringing recoveries of European Kestrels from north-western Europe have
shown that a very low proportion of this population is migratory, and that
even large-distance movements can be attributed mainly to dispersal move-
ments of young birds. Several studies have shown the importance of food
availability on dispersal rates in raptors, including the European Kestrel.
Based on recovery data, we show here that dispersal rate, as well as disper-
sal distance, of nestling Belgian kestrels varied strongly between cohorts
born in different years. Both were negatively correlated with measures of
the quality of the year in terms of food, as indicated by the number of fledg-
lings per nest and the energy content of the natural seed crop (acorns plus
beechnuts) in deciduous woodland in the preceding winter. In good years
dispersal activity was lower than in bad years. Dispersal activity also
showed a negative trend over the whole study period (1967-1989).

Key words: Falco tinnunculus - movement patterns - dispersal - ringing

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INTRODUCTION

Natal dispersal is, according to Greenwood
(1980), the movement an animal makes from its
point of origin to the place where it reproduces or
would have reproduced if it had survived and
found a mate. Natal dispersal is an important pro-
cess in population dynamics. Many costs and
benefits have been discussed in the literature, but
very little is known about the underlying mecha-
nisms (Johnson & Gaines 1990). Also little is
known about yearly variation in dispersal rate and
distance. Ringing recoveries are usually not suit-
able for analyses on dispersal since the accuracy
of general ringing scheme data is insufficient for
the short distances involved. In north-western Eu-
rope, however, ringing recovery data of the Euro-
pean Kestrel Falco tinnunculus include many
long distance movements which, by detailed anal-
yses, have been shown to be mainly dispersal
movements of first year birds. Only a very low
proportion of the population is truly migratory
(seasonal bi-directional movement; Belgium, Ad-
riaensen et al. 1997; British Isles, Mead 1973; The
Netherlands, Cavé 1968, Bijlsma 1993). Recorded
dispersal distances range from zero to well over
hundred kilometers in most European countries
(Belgium, Adriaensen et al. 1997; British Isles,
Snow 1968; Mead 1973; Spencer & Hudson 1982,
Mead & Clark 1987; Germany, Siefke & Klein
1988; The Netherlands, Cavé 1968; Bijlsma 1993).

Detailed field data together with modelling
work on Dutch kestrels (Daan et al. 1990) has
shown that food availability (acting mainly
through laying date) is a very important factor in
adult breeding performance, but that in young
birds the quality of the year of birth remained de-
tectable at least until their second winter. In this
study the proportion of locally surviving adult
and juvenile kestrels, compared with overall sur-
vival in a wider area, was positively correlated with food abundance (vole density) in the previous winter. This could be interpreted as a higher tendency to disperse with increasing deterioration of the food supply (Daan et al. 1990). In this paper we use recovery data of nestling European Kestrels from the Belgian Ringing Scheme (ringed in Belgium and Luxembourg) to look at yearly variation in dispersal activity. We try to relate this variation to measures of food abundance.

MATERIAL AND METHODS

The data set included 551 recovery records of European kestrels ringed between 1967 and 1990. Data were coded according to the EuriRg Data Bank code (EURING 1979). Of these 551 recoveries, 384 (70%) birds were reported dead when found. The probability that a bird was found alive decreased with recovery distance from 32% alive within 25 km onto a 8% at more than 200 km (Adriaensen et al. 1997).

We used the proportion of nestlings recovered at more than 100 km from the nest as one estimate of yearly dispersal activity. A second measure was calculated as the average recovery distance (log-transformed for Normality) of all recoveries away from the ringing place. The first measure of dispersal intensity gives a measure of what proportion of the population was involved in movements over longer distances, while the latter takes the recovery distance of all birds into account. In calculating the proportion of long-distance dispersers, the cut-off point was arbitrarily set at 100 km (although setting it at 25 km resulted in qualitatively similar results). About one fifth of Belgian kestrels which were ringed in the nest and recovered in the next breeding season were recovered more than 100 km away (Adriaensen et al. 1997).

Since Adriaensen et al. (1997) argued (1) that probably only a very limited proportion of the nestlings are migratory and thus return after their initial movement, and (2) that birds, once settled, only rarely show movements over larger distances, we did not limit the data to the first season, but instead used all recovery data available. Thus we actually compared recovery distances per cohort from 1967 to 1989. Nestlings ringed before 1967 were not used since too few were recovered each year. Because the data set only included recoveries up to 1990, we did not use the 1990 records because the time available for recovery of these birds was too short.

We used two measures for the quality of the year in terms of food availability for the kestrel: (1) the number of chicks ringed per kestrel nest and (2) the energy content of the natural seed crop (acorns and beechnuts) in deciduous woodland in the preceding winter as a measure of prey abundance (see below). The number of fledglings per nest is, in many raptors including the European Kestrel, closely linked to food availability during the breeding season (e.g. Daan et al. 1990; Korpimäki & Norrdahl 1991; Wiehn & Korpimäki 1997). The number of nestlings ringed per nest were retrieved directly from the Belgian ringing lists. These data were collected from 1989 backward to 1972. A minimum of 28 nests was available per year. We did not have an index of mouse and/or vole abundance, but since the density of small rodents is positively correlated with the seed crop in the preceding winter (R. Verhagen, L. Wauters, pers. comm.), we used the energy content of the seed crop of acorns and beechnuts (kJ m⁻²) in northern Belgium (as retrieved from Wauters & Lens 1995) as a measure of food abundance for the kestrels. Seed crop data were available from 1984 onwards.

Data were analysed using SAS V6.12. Exact probabilities were calculated using StatXact V3.0 (Cytel Software, Cambridge, US, 1995).

RESULTS

The proportion of birds recovered at more than 100 km and the average recovery distance were strongly correlated ($r = 0.84$, $n = 23$, $P < 0.001$). The two variables fluctuated considerably over the years and showed a decreasing trend from 1967 to 1989 ($r = -0.54$, $n = 23$, $P = 0.008$, identi-
Fig. 1. Time series of the proportion of European Kestrel nestlings recovered more than 100 km from ringing site and the log-transformed average recovery distance (km) for all recoveries away from the ringing site. For statistics see the results section.

Fig. 2. (A) Proportion of nestlings of European Kestrels recovered within 100 km of ringing site versus the average number of chicks ringed per nest. (B) Time series of the proportion of nestlings of European Kestrels recovered within 100 km of ringing site and average number of chicks ringed per nest.
Both the proportion of Belgian kestrel nestlings recovered at more than 100 km from the breeding site and the average recovery distance (for birds not recovered on the ringing site), vary strongly, and in parallel, from year to year. Birds move less far in good years, i.e. in years with a good seed crop in the previous winter and a higher number of nestlings per nest during the breeding season. Because we looked at recoveries of nestlings ringed in one year, but irrespective of the recovery year, this is a cohort effect, shown by all individuals born in a certain year. Field data in combination with modelling work on Dutch kestrels (Daan et al. 1990) also showed that yearly food availability generated long lasting differences between cohorts of young.

Is this effect of the quality of the year of birth on mobility an effect on true natal dispersal, or an effect on the feeding range of young birds prior to settlement? Not all kestrels breed in their first season, and in breeding populations a considerable number of non-breeding birds may occur (Village 1990). Part of the differences in mobility between good and bad years in this study are indeed due to differences in feeding range of young birds before they may return to settle. However, several arguments can be raised to support the hypothesis that natal dispersal distance is also markedly influenced by quality of the year of birth: (1) detailed analyses of recovery data on Dutch as well as Belgian recovery data led to the conclusion that natal dispersal over large distances regularly occurs (Cavé 1968; Adriaensen et al. 1997); (2) 24% of the birds in the data set analysed here were recovered at least two years after banding; and (3) the relationship between average brood size and average distance seems also to hold if only recoveries of birds during the breeding season and at least two years after banding are considered, although this result is just not significant ($P = 0.076$), perhaps due to the small sample size ($n = 45$).

Our data confirm the hypothesis of Daan et al. (1990) that the correlation between the proportion of local survival over total survival and vole abundance 'could be explained by an increased tendency to disperse with deterioration of the food supply'. On top of the year effect, we also showed an effect of ringing date within years. Irrespective of the quality of the year, laydate (as measured through the date of ringing of the chicks) seems to have an effect on the dispersal
tendency of the young birds. However, this is probably also an effect of food availability because laydate is strongly influenced by food availability in early spring (Daan et al. 1990). Dutch data on the European Kestrel, as well as a British study on the Goshawk, suggest that the most crucial phase in terms of food availability for young birds occurs in the period after fledging, perhaps around the time the young birds become independent (Daan & Dijkstra 1982; Daan et al. 1990; Kenward et al. 1993). In bad years kestrels are probably forced to move away from the place they were born in their search for food. Dispersing over long distances is always risky, and doing so when food is scarce may cause high mortality among young kestrels in poor years. However, some do survive, not least because kestrels are strong flyers (Adriaensen et al. 1997) and because they are efficient at locating areas with high food abundance while on the move, using the distinct UV radiation of the scent marks of their prey (Viitala et al. 1995). The annual intensity of dispersal has decreased markedly since the mid-1970s. Whether this can be explained in the same way as the variation within and between years is unclear. If it can, then food availability for young kestrels may have increased over these years.

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SAMENVATTING

Voor de meeste vogelsoorten zijn ringgegevens niet goed bruikbaar voor de studie van dispersie (beweging
van de geboorteplaats naar de plaats waar de eerste keer gebroed wordt), omdat de dispersie over te kleine afstanden gaat in relatie tot de nauwkeurigheid van de ringgegevens. Voor de Torenvalk *Falco tinnunculus* lieten gedetailleerde analyses van Belgische en Nederlandse terugvangstgegevens echter zien dat de veel verplaatsingen over grote afstanden geen migratiebewegingen (seizoenstrek) waren, maar eerder dispersieverplaatsingen van jonge dieren. Onder andere uit studies van Nederlandse Torenvalken is gebleken dat voedsel, vooral in de periode dat de jonge dieren onafhankelijk worden, hierbij een belangrijke factor is.

In deze studie tonen terugvangstgegevens van Belgische Torenvalken die in het nest geringd werden (511 terugvangsten), aan dat zowel het aandeel dieren dat zich over meer dan 100 km verplaatst als de gemiddelde afstand die afgelegd werd, sterk varieerde tussen jaren (Fig. 1). Beide dispersie-maten zijn negatief gecorreleerd met twee maten voor de beschikbaarheid van voedsel: het aantal jonge valken per nest (neemt af met dalende voedsel beschikbaarheid) en de totale energie inhoud van de zaadoogst in loofbos (een goede zaadoogst maakt dat er veel wintervoedsel is voor mieren) in de voorafgaande winter (Fig. 2, 3). Hoe meer voedsel er dus in een jaar is, hoe lager de dispersie activiteit erna is.

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