Reduced adult survival and increased reproduction in Swedish kestrels

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Summary. The decline of the Swedish kestrel population during the 1950s and 1960s is probably caused by a decrease in yearly adult survival rate, from $0.66 \pm 0.03$ S.E. to $0.48 \pm 0.03$ S.E.

Contrary to what would be expected from generally harmful effects of pesticides on reproduction, brood size increased from $3.4 \pm 0.4$ S.E. to $4.2 \pm 0.2$ S.E. during the same period.

We found no relationship between brood size and breeding density. The increased reproduction therefore does not seem to be a density-dependent effect of reduced population size. The increase in brood size may rather be an evolved adaptation, selected for by increased optimal reproduction as a consequence of higher adult mortality.

Introduction

During the last two decades there has been an increased awareness of pesticide damage to wildlife populations, such as the catastrophic decline of the peregrine falcon, Falco peregrinus (Tunstall), which became almost extinct in large areas (Ratcliffe 1980). Several other raptors have also declined markedly, such as the sparrowhawk, Accipiter nisus (Linnaeus), buzzard, Buteo buteo (Linnaeus), kestrel, Falco tinnunculus (Linnaeus) and merlin, Falco columbarius (Linnaeus) (e.g. Newton 1979; Wallin unpublished).

These declines are generally explained by the influence of pesticides on reproduction (e.g. Newton 1979; Caufield 1981), DDT and its metabolites being the most well-known. DDE causes eggshell thinning, which leads to a low hatchability and decreased reproduction (e.g. Newton 1979).

Depending on the rate of intake and excretion of pesticides, the concentrations in adult raptors may increase over several years. As a result, species with low adult mortality are expected to be more affected than birds with short-lived adults, and older age-classes to suffer more than young ones (Johnels and Westermark 1968). Sparrowhawks showed an increased organochlorine concentration in eggs during the first two years of life (Newton et al. 1981). The concentrations in the egg and in the laying female are well correlated (Henny and Meeker 1981).

Besides a reduced reproductive rate, a lowered adult survival due to increased pesticide load might also explain the population declines of raptors. However, this is often more difficult to establish than a reduced reproductive rate, and has rarely been documented (Newton 1979).

To test if a reduced survival has contributed to the decline of kestrels in Sweden, we examine their age-specific survival rate using ringing recovery data. We compare first year and adult survival rates during two periods: a pre-pesticide and a pesticide period. We also examine the reproductive rate during the same periods, and the influence of population density on reproduction of kestrels in SW Sweden 1980-1982.

Material and methods

Survival rates

Survival rates were estimated from ringing recoveries, obtained at the Bird Ringing Office of the Swedish Museum of Natural History. We only used those individuals marked as nestlings before 1972, and with a reliable age at death (recovery circumstances beginning with the OLD EURING codes 0, 3-9 and total code 100 are all excluded). The 197 recoveries were divided into two time periods. The first, a "pre-pesticide" period, consisting of birds ringed 1923–1955, and a second, a "pesticide" period 1956–1971. Eighty-five recoveries belong to the pre-pesticide and 112 to the pesticide period. The recoveries are fairly even distributed over the years (Table 1). The results are therefore not dependent on a few exceptional years, which could bias the survival estimates.

The choice of 1955 as the boundary between the pre-pesticide and pesticide period is not obvious. Methyl-mercury began to be used as early as 1940 (Johnels et al. 1979), and DDT was introduced at the end of 1940s (e.g. Ratcliffe 1980). There may have been a time-lag before pesticides become widely used and geographically spread. There may also be a delay while concentration in individuals accumulates to a deleterious level. For these reasons one might expect a time-lag between the introduction of pesticides and their serious effects on the population. This has been documented in several raptors, for instance peregrine falcon, sparrowhawk, merlin, kestrel and common buzzard (Ratcliffe 1980; Wallin unpublished).

It is not known when Swedish kestrels started to decline. However, there are some indications; the number of migrating kestrels at Falsterbo began to decrease in the mid 1950s (Wallin unpublished), coinciding with a drastic decline in a breeding population around Kvismaren, in S. Sweden.
The population was relatively stable at 6–10 pairs until the mid 1950s, when it declined rapidly and became extinct at the end of the decade (A. Enemar in litt.; Sondell 1968; Pettersson 1977). During the same period the kestrel disappeared from several other parts of the country, or at least became drastically reduced (Otterlind and Lennerstedt 1964). For these reasons, we use 1955 as the last pre-pesticide year.

The recoveries are arranged in composite dynamic life-tables (Table 2). From these we estimate age-specific survival rates as suggested by Cave' (1977) and North and Morgan (1979). Since there are no significant differences in the age composition between different recovery circumstances ($\chi^2_{10} = 11.1, P = 0.35$), all recoveries are pooled within each of the two periods. This property is important as different recovery circumstances may lead to different reporting probabilities.

**Brood size**

The reproductive rate is also examined from a sample, provided by the Swedish Ringing Office. We here define "brood size" as the number of chicks ringed in a nest. The broods are grouped according to time (1930–1955 and 1960–1980) and area (north or south of 61°N). This later division is motivated by much higher spread of pesticides in southern Sweden (e.g. ref. in Johnels et al. 1979).

The influence of population density on brood size was studied in a local kestrel population near Göteborg, SW Sweden, 1980–1982. As a measure of population density, we use the distance from a nest to the nearest neighbor nest (or to the mid-point of the territory in one case in which the nest was not found).

**Results**

**Survival rate**

The estimated juvenile (first year) survival was higher in the pre-pesticide period 0.38 ± 0.04 S.E. then in the pesticide period 0.31 ± 0.04 S.E., but the difference was not significant ($P > 0.20$).

However, adult survival decreased significantly from 0.66 ± 0.03 S.E. in the former period to 0.48 ± 0.03 S.E. in the latter ($\chi^2 = 13.16, P < 0.005$). Inspection of Table 1 suggests that this difference might arise because of unusually many recoveries from two year old birds during the pesticide period. However if this year class is outweighted the significance still remains, although at a lower level ($\chi^2 = 10.22, P = 0.017$). Hence the many recoveries of two year old birds, do not affect the general conclusion that adult survival had decreased.

A simplified model based on an age-specific first year survival rate, and thereafter a constant yearly survival rate, agrees fairly well with the observed distributions (Table 2).

We conclude that adult survival and possibly also juvenile survival, have decreased during the pesticide period. The decrease in survival rate might be responsible for the decline of the Swedish kestrel after the middle of 1950s.

**Brood size**

Contrary to what might be expected from the harmful effects of pesticides on raptor reproduction (Newton 1979), the brood size was higher during the pesticide than during the pre-pesticide period. Brood-size in south Sweden was on average 0.8 nestlings larger during the pesticide period ($t = 3.80, P < 0.001$). There was no such increase in the northern part of Sweden ($P > 0.50$), but the sample size for the pre-pesticide period in the north is small ($n = 12$, Table 3).

As high population density may depress reproduction...