ENVIRONMENTAL FACTORS DETERMINE NUMBERS OF OVERWINTERING EUROPEAN STONECHATS SAXICOLA RUBICOLA* - A LONG TERM STUDY

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In this study the relationship between the number of European Stonechats Saxicola rubicola at a winter site in Israel and the local rainfall, air temperature, and arthropod abundance was examined. In some years population size declined to about one third of the initial size, while in others it remained almost constant. The decline of bird numbers was mainly due to the disappearance of young, unpaired individuals. The magnitude of the decline in numbers was correlated with timing and amount of winter rainfall, which is crucial for the growth of the vegetation after a long dry summer period. Early winter rainfalls had a much stronger impact than total winter rain. The decline in numbers was also correlated with arthropod density in pitfall traps; however, it was not correlated with air temperature. The relative extend to which density-dependent and density-independent factors determine the size of the wintering population of European Stonechats is evaluated.

Key words: Saxicola rubicola - pairing - winter territory - density dependence - rainfall - climatic changes - arthropod food

*Saxicola rubicola, formerly known as Saxicola torquata rubicola

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INTRODUCTION

Several studies have shown that mortality rates of migrating birds during the nonbreeding season are high (Berthold 1973; Morel 1973; Hogstad 1984; Baillie & Peach 1992; Rappole & McDonald 1994). The mortality risk of an overwintering individual is influenced by environmental factors (Hogstad 1984; Greenwood & Baillie 1991) and by density-dependent competition for space and food (Newton 1992). Environmental factors can show large fluctuations in areas where migrating birds winter, especially in semiarid and arid areas. Few of the previous studies on the density of wintering populations took this high variability into account. Consequently, the role of environmental factors limiting a population during a critical period may be misinterpreted in short-term studies (Feinsinger & Swarm 1982). To understand how environmental factors influence population density and the behavioural responses of birds it is important to account for variation over the whole season in different years (Morton 1980; Klomp 1980; Cuadrado 1992; Wiens 1993; Cuadrado et al. 1995; Rothery et al. 1997).

This paper focuses on environmental constraints and presents data for European Stonechats Saxicola rubicola, an overwintering bird in the Negev, Israel, using data from seven non-breeding seasons (1989/90 and 1993/94 to 1998/99). A previous study showed that the number of wintering European Stonechats is not constant; population size may shrink considerably in the course of one winter (Rödl 1994). In order to assess the impact of environmental factors on the number of wintering European Stonechats, I have investigat-
ed whether the amount and timing of rainfall, air temperature, and arthropod abundance were correlated with population size. I predicted a positive correlation for all three factors with the number of birds overwintering. Each of the factors, when encountered at above-average levels, can be expected to increase a bird’s ability to balance its energy needs and thus increase its fat stores or gain time for other requirements such as defence of a winter territory or predator avoidance. While above-average winter temperatures might act directly on the condition of the bird, the influence of the amount of rainfall and arthropod abundance are more indirect, affecting food availability.

Unlike other migratory insectivorous birds, European Stonechats form heterosexual pairs upon arrival on their winter grounds and defend territories throughout the winter (Gwinner et al. 1994; Rödl 1994). A similar situation is known for the White Wagtail Motacilla alba (Zahavi 1971; Davies 1976), but pairs of wagtails form very loose congregations compared to the obvious and more stable alliances seen in European Stonechats. Since in European Stonechats winter partners are very unlikely to stay together until the next breeding season (Rödl 1994), winter pairing does not seem to enhance reproductive output. Instead, its advantages are more likely linked to survival during the winter itself. For a functional explanation of the advantages of winter pairing in the European Stonechat it is essential to understand the character and relative importance of environmental constraints during the winter.

METHODS

The study area is situated in the Negev Desert in southern Israel. It consists of smooth hills transected by wadis, which form long stretches of sparse vegetation. European Stonechats establish winter territories in the wadis. The hilly structure and the predominantly arid, low vegetation of the area enable rather easy observation of the perching birds.

During five winter seasons (1989/90, and 1993-1997) birds were trapped with baited bowtraps on the ground and colour-banded for individual recognition. Birds were aged according to the moult patterns of wing-feathers (Flinks 1994). The trapping effort was concentrated around the beginning of the winter season, during November and December. Presence and location of all birds were recorded on a regular basis every second week (and every week in 1989/90) from mid-October to the beginning of March. Additional information apart from the scheduled observations was included whenever available. Locations of bird encounters were indicated on a map with a scale of 1:20 000. On average 33% (16% to 47%, n = 5 years) of all birds present in November and December were colour-banded and thus could be identified individually.

If a known territorial individual was not present in its territory nor at other places in the study area during several consecutive days, and did not reappear at a later time, it was labelled as being ‘vanished’. This, however, applied only to birds that were present between mid-November and mid-February, to exclude a possible bias by migrating birds on temporary stop-over. Many unbanded individuals were attributable to a fixed location; this was possible when neighbouring birds were banded. When a non-banded bird was missing and in other parts of the study area no extra bird showed up, it was assumed that this individual had ‘vanished’. This was justified by the observation that banded birds that abandoned a territory were either seen in the close vicinity, or were not found anywhere else in the study area. During the last two winter seasons (1997/98, 1998/99) no birds were individually banded, but all birds were counted from November until January to determine a change in population size for the first part of the winter.

To quantify a change in bird numbers during each winter, the monthly decrease in bird numbers was divided by the total decrease in number during the whole winter to give the percentage of the overall population decline that occurred during each month (see Table 1). To avoid bias through non-territorial vagrant individuals these numbers exclude the migration time (about two weeks at
Plate 1. The habitat of a European Stonechat territory after early rains in February 1995

Plate 2. The habitat of a European Stonechat territory after late rains in February 1997
Table 1. Relative population decline of Stonechats during each month in three years with declining numbers. Data represent the difference between the number of birds at the beginning of each month and the number of birds at the end of that month, divided by the total of birds that vanished during the whole season.

<table>
<thead>
<tr>
<th>Year</th>
<th>November</th>
<th>December</th>
<th>January</th>
<th>February</th>
<th>Vanished birds</th>
</tr>
</thead>
<tbody>
<tr>
<td>1989/90</td>
<td>52.8</td>
<td>11.1</td>
<td>36.1</td>
<td>0</td>
<td>36</td>
</tr>
<tr>
<td>1995/96</td>
<td>56.7</td>
<td>30.0</td>
<td>13.3</td>
<td>0</td>
<td>30</td>
</tr>
<tr>
<td>1996/97</td>
<td>44.0</td>
<td>48.0</td>
<td>0</td>
<td>8</td>
<td>25</td>
</tr>
<tr>
<td>Average</td>
<td>51.2%</td>
<td>29.7%</td>
<td>16.5%</td>
<td>2.7%</td>
<td></td>
</tr>
</tbody>
</table>

Table 2. Initial maximum number of Stonechats in seven winters and the number of vanished birds during the period mid-November till end-December.

<table>
<thead>
<tr>
<th>Season</th>
<th>Initial maximum no. (November)</th>
<th>Vanished birds (until 31 December)</th>
<th>Proportion vanished (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1989/90</td>
<td>62</td>
<td>23</td>
<td>37.1</td>
</tr>
<tr>
<td>1993/94</td>
<td>34</td>
<td>6</td>
<td>17.6</td>
</tr>
<tr>
<td>1994/95</td>
<td>53</td>
<td>2</td>
<td>3.8</td>
</tr>
<tr>
<td>1995/96</td>
<td>66</td>
<td>26</td>
<td>39.4</td>
</tr>
<tr>
<td>1996/97</td>
<td>35</td>
<td>21</td>
<td>60.0</td>
</tr>
<tr>
<td>1997/98</td>
<td>31</td>
<td>3</td>
<td>9.7</td>
</tr>
<tr>
<td>1998/99</td>
<td>27</td>
<td>19</td>
<td>70.4</td>
</tr>
</tbody>
</table>

To estimate the amount of potential prey active on the ground, 36 long plastic cups were embedded in the wadi bottom in six rows (see also Rödl and Flinks 1996). For trapping, the cups’ lids were removed in the early morning and cups were left open during the whole day, to be closed only in the hour before sunset. No detergents or preservation agents were used. Two territories were sampled this way during four seasons and the data averaged. Each year the same locations were used, but the cups were dug in anew. I installed cups one to two weeks before the first trapping day to avoid digging-in effects (Greenslade 1973). Data were collected twice a month in 1989/90 and once a month during 1993/94, 1994/95 and 1995/96. The complete schedule of trapping-dates was determined a priori. If rain fell during the last two days before a scheduled trapping-date, trapping was delayed until there had been two consecutive days without rain.

Rainfall and temperature data were obtained from the meteorological unit of the Jacob Blaustein Institute for Desert Research in Sde Boqer. The measurements were taken 5 to 10 km from the study area. In one season estimates of operative temperature were simultaneously made in the study site itself using an aluminium cast having about the volume of a European Stonechat (Walsberg & Weathers 1986). Measurements taken at the study site were significantly correlated with air temperature measured at the meteorological station (Pearson correlation, $r = 0.485$, $df = 87$, $P < 0.001$). The data for air temperature were used for the analysis.

To compare annual rainfall of different years
with a long-term average, I calculated a mean normalised anomaly of rainfall \( r_n \) (in mm) according to the equation

\[
r_n = \frac{r - mr}{s}
\]

where \( r \) represents the amount of rainfall for the respective season; \( mr \) the long-term mean for the amount of rain per season; and \( s \) the standard deviation of \( mr \) (Nicholson 1985).

**RESULTS**

**Variable population size**

Fig. 1 shows the number of European Stonechats at the study site during five different winters (1989/90, 1993/94 - 1996/97) plus the numbers during the first half of the winter in two additional seasons (1997/98 - 1998/99). Two main patterns are discernible. First, the number of European Stonechats decreased significantly from mid-November until mid-February in 1989/90 (Spearman correlation, \( r_s = -0.9, n = 12, P < 0.01 \), 1996/97 \( r_s = -0.9, n = 6, P < 0.05 \), and a similar trend was observed in 1995/96 \( r_s = -0.72, n = 6, P = 0.07 \) and in 1998/99. Second, during three other years, in 1993/94 \( r_s = 0.1, n = 6, \text{n.s.} \), 1994/95 \( r_s = 0.3, n = 6, \text{n.s.} \), and 1997/98, the population remained more or less constant at the initial maximum value of November.

On average about 80% of the birds missing at the end of the winter vanished during the time span from mid-November until end-December, hence during the early wintering season (Table 1). Focusing on this early phase only, the proportional decrease from mid-November until end-December is compared between the different years in Table 2, and will henceforth be referred to as the proportion of vanishing birds. Table 2 shows a large difference between the proportion of vanishing birds in two outstanding years that will be focus of further comparisons, 1994/95, during which there was almost no decrease, and 1996/97, when more than half of the birds vanished until the end of December.
Fig. 2. Total amount of rainfall during the whole rainy season and amount of rainfall until 31 December in each winter period. The horizontal lines indicate the long-term average values.

Rainfall

In Israel, after a dry summer, rainfall usually starts in October or November, but the onset of rainfall is highly variable. The last rains occur during March and April, and only exceptionally in May (the rest of the year remains dry). Fig. 2 shows the total amount of rain during each of seven winter seasons. In 1994/95 and 1996/97 rainfall was above a long-term average of 97.5 mm \((n=23\text{ years, 1976-1998})\). Nevertheless the pattern

of overwinter change in numbers of birds was rather different in these two years (Fig. 1). Accordingly, rainfall would not seem to be directly related to the decline in bird numbers in 1996/97. This seems to be supported by the fact that the total amount of rain and the vanishing proportion of birds in the course of the winter (from mid-November until mid-February, in this case a longer period than specified above) were not significantly correlated (Spearman correlation, \(r_s = -0.61, n = 7, P = 0.17\)).

However, it is known that the time of onset and the regularity of rainfall have a more pronounced influence on the start of the growing season and amount of annual vegetation, and on the flowering period of perennial plants, than the overall total of winter rainfall (Danin 1983). Consequently, Fig. 2 shows the amount of rain for early winter, i.e. from the onset of rains until Decem-

Fig. 3. Correlation between rain anomaly of early rains until 31 December (see methods) and the vanishing proportions of birds during the same time span. Rain anomaly of zero represents the mean of the seasons 1976/77-1998/99.

Fig. 4. The amount of total rain during the winter seasons from 1976/77 until 1998/99 (A) and separately for the period until 31 December (B). Solid lines represent long-term average; stippled lines the fit for a linear regression.
ber 31. The end of this time span was chosen to be the same as in Table 2. Fig. 2 reveals clear differences between the years 1994/95 with early rains and 1996/97 with late rains. Although the total amount of rain in both years is above the long-term average of 97.5 mm, the amount that fell early in 1994/95 was far beyond the long-term average of 29.8 mm as compared to 1996/97. Plates 1 and 2 illustrate the consequences of this difference for the growth of vegetation. The vegetation in a European Stonechat territory was much more developed in mid-February 1995 after early rains than in February 1997. There is a significant relationship between rain until the end of December and the vanishing proportion of birds (Fig. 3, Spearman correlation $r_s = -0.811$, $n = 7$, $P = 0.03$).

Out of seven winters only one had above-average amount of rain until end of December. This is in contrast to years before the study period, where the amount of early rainfall was fluctuating around the long-term mean (Fig. 4B). Although not significant, a curve-fit over all 23 years shows a decline in the amount of early rains, which is not paralleled by the amount of total winter rains (Fig. 4A). There was no significant serial correlation between subsequent years (Durbin-Watson $d = 2.05$, critical $d = 1.47$, $df = 22$, $P > 0.05$) what could lead to wrong interpretations. Thus the results show that early winter rains were more scarce in the last few years (with one exception of the winter 1994/95) than in previous years.

Temperature

Rain influences the development of arthropod prey directly via the amount of vegetation. However, ambient temperature may limit the availability of prey to birds by influencing prey mobility. The birds may react accordingly with a change in activity patterns (East 1980; Elgar 1986; Caraco et al. 1990). Furthermore, temperature affects the metabolic rate and hence food consumption of the birds (Aschoff and Pohl 1970; Grubb 1975; Walsberg 1993). Through these relationships ambient temperature may influence the numbers of birds present during a specific winter. However, I found no significant correlation between the monthly average air temperature in November and December and the vanishing proportion of birds. Since monthly average values can be biased by a few outliers, I also related the number of days below and above a long-term average value (minimum and maximum daily temperatures) to the proportion of vanishing birds. Neither estimate was significantly correlated with the proportion of vanishing birds.

Density of ground-active arthropods in pitfall traps

Table 3 summarises pitfall results for four study years. Both the total number of arthropods and the number of species rose considerably from January to February. High December values were found only in 1993 and 1994, the years when no significant decline in the number of birds was found. It was during these years that rainfall started well before December 31 (see Fig. 2). In the years 1989 and 1995 rainfall started after January and arthropod numbers did not rise before February. According to the distinction between early and late rains (Fig. 2), I divided the winter period into two phases, and for each of four years averaged the number of arthropods and the number of species trapped during the early phase in November and December, when prey numbers are still

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Fig. 5. Relationship between the mean number of prey items (A) and prey species per territory (B) and the proportion of vanishing birds in four years.
Table 3. Number of potential prey individuals and number of potential prey species of Stonechats in pitfall traps. Each number is the average over two territories during one day of open traps.

<table>
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<tbody>
<tr>
<td>November</td>
<td>n_{indiv}</td>
<td>3</td>
<td>4</td>
<td>8</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>n_{species}</td>
<td>3</td>
<td>3</td>
<td>5</td>
<td>6</td>
</tr>
<tr>
<td>December</td>
<td>n_{indiv}</td>
<td>4</td>
<td>22</td>
<td>17</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>n_{species}</td>
<td>3</td>
<td>8</td>
<td>11</td>
<td>11</td>
</tr>
<tr>
<td>January</td>
<td>n_{indiv}</td>
<td>10</td>
<td>12</td>
<td>37</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>n_{species}</td>
<td>6</td>
<td>8</td>
<td>16</td>
<td>8</td>
</tr>
<tr>
<td>February</td>
<td>n_{indiv}</td>
<td>114</td>
<td>28</td>
<td>76</td>
<td>67</td>
</tr>
<tr>
<td></td>
<td>n_{species}</td>
<td>22</td>
<td>18</td>
<td>27</td>
<td>24</td>
</tr>
<tr>
<td>March</td>
<td>n_{indiv}</td>
<td>115</td>
<td>45</td>
<td>75</td>
<td>153</td>
</tr>
<tr>
<td></td>
<td>n_{species}</td>
<td>42</td>
<td>24</td>
<td>23</td>
<td>43</td>
</tr>
</tbody>
</table>

relatively low. Fig. 5 shows that the proportion of vanishing birds declines with the average number of arthropods in early winter (Fig. 5A, Spearman correlation with arc-sin-transformed proportional values, \( r_s = -1.0, n = 4, P < 0.01 \)), and possibly as well with the average number of species (Fig. 5B, \( r_s = -0.8, n = 4, P = 0.2 \)) during the early phase of the winter.

**Status and age of vanishing birds**

Up to one third of the males present during a season were unpaired. Both paired and unpaired males defended territories, the existence of non-territorial floater males could not be shown. Each year male numbers exceeded female numbers by about 20%. Out of the males that vanished at least 82% (33) disappeared alone, leaving the female partner behind. In only six cases both partners of a pair disappeared simultaneously. Thus most birds vanished singly (sign test, \( n = 39, P < 0.01 \)). Usually, unpaired females occurred only when a male vanished and left his female partner behind; in most cases the female moved to the territory of an unpaired male. When a female vanished out of a pair, the single male stayed in its territory, either alone or it was soon accompanied by a new female partner. A total of 55 males were aged during trapping. Out of these, the vanishing males were significantly younger than males that stayed (\( \chi^2 = 3.50, n = 55, P < 0.01, \) Table 4). The vanishing males were significantly more often unpaired than paired (\( \chi^2 = 4.65, n = 53, P = 0.03, \) Table 4). Furthermore, unpaired males were more often yearlings, paired males more often adult (\( \chi^2 = 9.04, n = 53, P < 0.01 \)).

**Site fidelity**

On average 27% of the birds banded in one season returned the following winter (\( n = 25 \) in four seasons, Table 5). Eighty-two percent of all returning males (\( n = 17 \)) were paired during the winter they were banded. Two males and one female reappeared in more than one subsequent winter period. One male, banded in 1989, was
seen last in spring 1995; it was thus at least five and a half years old. Fifteen out of 17 individuals were observed in the same territory in which they had been banded a year before. In two cases both banded individuals of a pair were observed again the subsequent winter. However, none of these former couples was paired again, the females staying in a different territory paired with a different male. One of the males succeeded in expelling an already established unbanded male and reoccupied its former territory (Rödl 1994).

### DISCUSSION

The studied population of wintering European Stonechats declined in some winters, but not in others. So far it cannot be decided whether the vanishing birds left the area or whether they died at the study site. I only found the body or feather-remains on two occasions. Theoretically, a second phase of migration triggered by lack of food might have occurred (Gwinner et al. 1988). However, further south, west, and east of the study area the birds only find unsuitable, very dry habitat which extends into the Sahara and Arabian deserts, and which is only interrupted by the Red Sea and some small oases. In these more arid areas as European Stonechats do not winter (Cramp 1988). If vanishing birds were to go back further north into sites with more precipitation, they would encounter conspecifics with already established territories in a much higher density than in the Negev (unpubl. results). The apparent lack of alternative sites in any direction, together with the fact that most of the birds vanished at a time when food was scarce, temperatures were low, and body masses of birds were at a minimum (Rödl 1994), makes it almost impossible that vanishing birds succeeded in establishing a new territory once they left an initial winter site. Vanishing birds most likely either died at the site, or experienced a drastic fitness reduction by leaving their territory. However, in years with abundant rainfall almost no birds vanished. Therefore an evaluation of the factors responsible for the vanishing of birds is of great importance for an understanding of the dynamics of the wintering population.

Although an influence of ambient temperature on bird behaviour was expected, neither average nor minimum/maximum air temperature values showed a significant correlation with the population size. The correspondence between the ambient temperature, in one year measured with an aluminium cast, and the air temperature at the meteorological station although significant, was low (\( r = 0.49 \)), which may account for the apparent lack of an influence of temperature. Alternatively, temperature might really have played a minor role for the condition of wintering stonechats in the investigated population. Greenwood and Baillie (1991) also found an insignificant influence of air temperatures on the population size of wintering birds in Britain.

In contrast to air temperature, the amount of rain during early winter correlated significantly with population size. An influence of the amount of rain on avian populations had been demonstrated in many other studies (e.g. Marchant 1992; McCleery 1998; Foppen et al. 1999). The present data show that the timing of the rain had also strong impact on the population size. The effect of rain on the birds’ environment was cumulative (unless the rain was totally erratic and unevenly distributed). Once the rainy season had started every additional rainfall increased the magnitude of this environmental factor. An early start of rain resulted in the lush development of vegetation and arthropods. This emphasises the need to investigate the whole season in detail in order to understand the factors regulating population size (Feinsinger & Swarm 1982).

<table>
<thead>
<tr>
<th>Year</th>
<th>Number Returned</th>
<th>Proportion Returned (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1989/90</td>
<td>8</td>
<td>38.1</td>
</tr>
<tr>
<td>1995/96</td>
<td>4</td>
<td>29.4</td>
</tr>
<tr>
<td>1996/97</td>
<td>7</td>
<td>26.9</td>
</tr>
<tr>
<td>1997/98</td>
<td>6</td>
<td>15.4</td>
</tr>
</tbody>
</table>

Table 5. Number of returned birds (n) and proportion of returning birds on the number of all birds banded in the previous winter.
The number of arthropods in pitfall traps was a function of rainfall and the ensuing growth of the vegetation (Ayal unpubl. data). It was negatively correlated with the proportion of vanishing birds during the same winter, which most probably reflected a correlation with the development of the vegetation. In years with much early rainfall the vegetation became correspondingly lush (Plate 1), which presumably directly enhanced the number of arthropods. Here interdependence of several factors is probably blurring the functional character of the relationship between number of European Stonechats and each environmental factor. Therefore a multivariate statistical approach would have been appropriate, but was not feasible with a sample size of a few years.

Pitfall trapping as a tool for estimating the numbers of ground-active prey animals is very common (Southwood 1978; Poulin and Lefebvre 1997). However, it is not always a reliable measure of the amount of prey available to birds, because density and activity of prey animals cannot be distinguished by that method (Smith 1982; Cooper & Whitmore 1990; Wolda 1990). In contrast to many other environments, the Negev is a structurally simple, arid habitat. Most arthropods occur - and European Stonechats predominantly search for food - on the ground or between low annual herbs (Rödl & Flinks 1996). Therefore it can be assumed that the amount of prey caught in pitfalls is a good approximation for the amount of prey that is available to European Stonechats (Hutto 1990). Ants were excluded from the analysis due to their clumped occurrence.

There are factors that have not been considered in this study. The most important one is density regulation via intraspecific competition. To what degree do environmental factors on the one hand and competition on the other influence bird number, and how variable is the relative importance of the two factors (Newton 1998; Dunning & Brown 1982; Conell 1983; Wiens 1983; Greenwood & Baillie 1991)? Certainly, environmental factors and competition could vary both temporally and spatially in their relative importance. At a different study site with Mediterranean vegetation, some 100 km north of the Negev Desert site, rainfall is more common (average annual precipitation=400 mm). The more intense rainfall at the Mediterranean site corresponded to a bird density that was about three times higher and more stable than that in the Negev (T. Rödl & M. Räss unpubl.data). In two winter seasons (1995/96 and 1996/97), the number of birds at the Mediterranean site stayed roughly the same from autumn to spring, whereas in one of these seasons, in 1996/97, the number of birds in the Negev decreased significantly during the same time. The population in the Mediterranean was probably closer to satiation than the population in the Negev site. Therefore competition might have been stronger at the Mediterranean site than in the Negev. In some dry years population size in the Negev may have been limited by density independent environmental factors. Incomplete satiation in the Negev was likely if a low population density in one year was influencing the initial density in the next year. This could have been the case in the seasons 1996/97 - 1997/98 where the high proportion of vanishing birds in one winter could have resulted in low initial maximum numbers at the beginning of the next winter. A close look at Fig. 1 and Table 2 shows a general tendency towards a decline (increase) in the initial maximum numbers from one year to the next when many (few) birds vanished during the first of two consecutive seasons. Thus, there could be a potential bias through serial correlation when different years are compared as separate units (Conell & Sousa 1983).

The high variability of European Stonechat populations in the Negev has two important implications. First, assuming that vanishing reduces the fitness of birds, a high proportion of overall mortality in the European Stonechat population can be attributed to adverse rain and food conditions during a critical early period in some winter seasons. There might be a threshold of the amount of early rains below which winter populations decrease (Fig. 3). Although this effect may be insignificant in years with average or above-average (above-threshold) food supply, critical years
can crucially affect population size (Pulliam & Dunning 1987). The contribution of winter mortality to total annual mortality has been discussed in several studies (Klomp 1980; Dhondt 1983; Hogstad 1984; Goss-Custard et al. 1995). In 1996/97 60% of the European Stonechat population vanished during a period of three months. According to return-rates of banded birds adult European Stonechats in western Europe show annual mortality rates 64% and 69% at most (Glutz von Blotzheim & Bauer 1988). This means that in one dry winter almost the total value of annual mortality (breeding and non-breeding season) for adults was reached. Such high mortality values cannot be sustained in the long run and must be compensated by more favourable seasons or in other areas. As the Negev is at the southern limit of the winter distribution of European Stonechats, it is possible that winter mortality rates were higher than in most other wintering areas. Although the study site may not represent conditions for the whole population the high variation of behavioural responses to environmental conditions in marginal wintering areas is of particular interest in view of climatic changes and habitat degradation that are experienced by many migrants, for example in the Sahel zone (Batten & Marchant 1977; Baillie & Peach 1992; Kelsey 1992; Marchant 1992). Populations in marginal areas will be affected most severely by these changes. A delay of winter rains in the last few years (see Fig. 2) could have had a strong impact on the population sizes of European Stonechats.

Secondly clear inter-seasonal differences in environmental constraints at the Negev study site help to clarify the function of winter pairing. A comparison between certain individual traits of those birds that vanished and those that stayed may be revealing. More unpaired than paired males vanished from the area. Unpaired males were significantly younger than paired males. When a paired male vanished, its female partner usually stayed behind. An individual that was present until the end of the wintering period was more likely to return in the next winter than a bird that vanished before the end of the season. Evidently then, vanishing from the study area is disadvantageous. Given that affected birds are mainly unpaired males, winter pairing in the European Stonechat must offer immediate advantages for the winter period. I suggest that the nature of these advantages varies in the same way as the relative influence of environmental factors versus competition on the population density varies over time and place. A functional explanation for the winter pairing can be found only with due consideration of the variable influences of environmental constraints on a bird’s behaviour.

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REFERENCES


SAMENVATTING

In de Israëlische Negevoestijn bevindt zich de zuidgrens van het overwinteringsgebied van de Roodborsttapuiten Saxicola rubicola die in Europa broeden. Opmerkelijk is dat in dit woestijengebied veel van de Roodborsttapuiten paarsgewijs voedselterritoria verdigen. Deze paartjes zijn elkaar van jaar op jaar overigens niet trouw en ze broeden later ook niet samen. In deze studie worden de relaties tussen de lokale populatiegrootte in de Negevoestijn en de lokale regenval, temperatuur en hoeveelheid insecten onderzocht. In sommige jaren liep de populatiegrootte in de loop van de winter terug tot een derde van de aantallen die zich in het najaar vestigden, terwijl in andere jaren de populatiegrootte redelijk constant bleef. Het waren vooral onvolwassen, ongepaarde mannetjes die in de loop van de winter uit het gebied verdwenen. Het is waarschijnlijk dat deze reductie de werkelijke sterfte weergeeft. De grootte van de winterse aantalsvermindering was gecorreleerd met de hoeveelheid regen en hing ook af van het moment waarop de regen viel. Regen die vroeg in het winterhalfjaar viel, zorgde voor een uitbundige plantengroei (zie de kleurenfoto’s) en relatief veel voedsel in de vorm van insecten. In zulke winters zullen de meeste Roodborsttapuiten het seizoen overleven. De rol van dichtsheidsafhankelijke en dichtheidsonafhankelijke processen voor populatiegrootte aan de rand van het verspreidingsgebied worden bediscussieerd. (TP)

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