FOOD AND HUNTING BEHAVIOUR

IS THE DECLINE OF THE RED-BACKED SHRIKE (*Lanius collurio*) IN THE DUTCH COASTAL DUNE AREA CAUSED BY A DECREASE IN INSECT DIVERSITY?

Jan Kuper, Gert-Jan van Duinen, Marijn Nijssen, Marten Geertsma and Hans Esselink

ABSTRACT

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Like other bird species predating on large invertebrates, the Red-backed Shrike strongly declined in the Dutch coastal dunes. Still common throughout the whole dune area in the fifties, in 1997 and 1998 only one last territory was occupied on Ameland – a Wadden Sea island. We suppose that affected invertebrate diversity led to deteriorated prey availability that caused this dramatic downfall. Therefore, we compared food ecology data of the 1997 and 1998 breeding pair with data from 1989 on Ameland, with a growing population in a Dutch peat-moor reserve Bargerveen and (from literature) with a stable population in Germany.

Comparison of Ameland 1997 and 1998 with other areas showed some remarkable results: (1) mean invertebrate prey size in adult and nestling diet was smallest on Ameland (1997 and 1998), (2) prey availability in terms of densities and weight on Ameland (1997 and 1998) was lower compared to Bargerveen, (3) prey availability was stronger reflected in the diet when availability was low (Ameland), (4) present availability of *Scarabeidae* on Ameland is low nowadays.

These results support our hypothesis that affected invertebrate diversity caused the downfall of the Red-backed Shrike in the Dutch dunes. For successful dune restoration, knowledge about the causes of the decrease of invertebrate diversity is strongly needed.

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Key words: *Lanius collurio*, degrading habitats, food ecology, food availability, insect diversity

INTRODUCTION

The Red-backed Shrike is a bird species of structure-rich landscapes like small-scale agricultural landscapes, edges of bogs and coastal dunes (Cramp and Perrins 1993). In most Western European countries, numbers of the Red-backed Shrike are decreasing (Hustings and Bekhuis 1993, Tucker and Heath 1994, Hagemeijer *et al*. 1997). Its diet consists of a broad spectrum of large invertebrates and small vertebrates (Mansfeld 1958, Korodi Gál 1969, Esselink *et al.* 1995).

Several hypotheses have been proposed to explain the decline of the Red-backed Shrike (summarised in Esselink *et al.* 1995 and in Lefranc and Worfolk 1997). Hypothesis like climatic changes (wetter and cooler summers in the breeding areas), human persecution during migration, expansion of the Sahara Desert, changes on the wintering grounds, and accumulation of pesticides in the food web on the wintering grounds would affect breeding populations in general. Nevertheless, apart from declining populations, stable and growing populations still occur. Therefore, we suggest that causes for the decrease must be situated on the breeding grounds (Esselink *et al.* 1994). Beside habitat destruction, we suppose that the decrease of the Red-backed Shrike is caused by affected faunal diversity that led to deteriorated prey availability.

The Red-backed Shrike's broad food spectrum suggests that a decline in prey species diversity is buffered (Ash 1970, Lefranc 1973, Cramp and Perrins 1993). We suggest, however, that the Red-backed Shrike depends on great prey species diversity (Esselink *et al.* 1994). Faunal activity is confined to certain parts of the day (depending on weather characteristics and diurnal activity) and season (phenology and peak abundance). Therefore, prey species are only temporarily available as a food source, forcing the Red-backed Shrike to switch constantly between prey species (Hornman *et al.* 1998). In degrading breeding habitats we suggest that food links have been affected in such way that prey availability at the top of the food chain is too low to sustain a healthy shrike population (Esselink *et al.* 1994). Comparative studies on diet composition and food availability in relation to reproductive success and adult survival within and between ecosystems with different population trends (increasing, stable, declining, or vanishing) might help trace the links within food webs affected in degrading habitats (Esselink *et al.* 1994). Throughout the Dutch coastal dune area, the Red-backed Shrike was still common in the fifties (Teixeira 1979, Hustings and Bekhuis 1993). In 1997 and 1998, only one last territory was occupied in the dune area on the Wadden Sea island Ameland (Fig. 1). Population trend on Ameland showed a continuing decrease from 1964 (30 pairs) until 1999 (extinct) with a short revival in 1987-1989 (18-21 pairs). The Bargerveen peat-moor reserve is inhabited by the single growing population in the Netherlands, which increased from 3 territories in 1978 to 145 territories in 1997 (Esselink *et al.* 1995, Geertsma *et al.* 2000). In the present study, we compare food ecology data from the

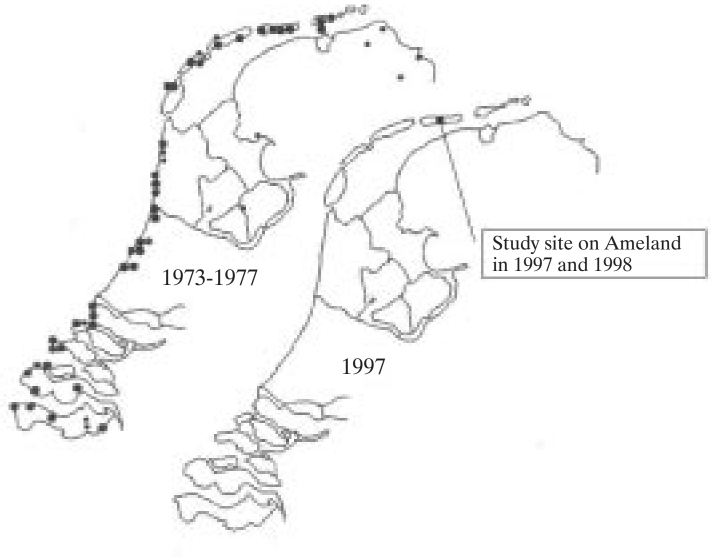

Fig. 1. Decline of the Red-backed Shrike population in the Dutch dune area between 1973-1977 (from Teixeira 1979) and 1997/1998. The single dot indicates the last pair on the Wadden Sea island Ameland of the Dutch dunes.

vanishing population of Ameland in 1997 and 1998 with data from a growing population of the Bargerveen peat-moor reserve in 1995 (Hornman *et al.* 1998). To compare adult diet composition we also used data from the Ameland population in 1989 (18 pairs – population perhaps already decreasing) and data from stable population in Nordrhein-Westfalen in Germany (Wagner 1993).

The following data of these populations were compared: (1) invertebrate prey size of nestlings and adults, (2) nestling food intake, (3) prey availability, (4) adult diet composition.

MATERIAL AND METHODS

Data on nestling diet composition and food availability were collected on Ameland in 1997 and 1998, and in the Bargerveen area – in 1995 (Hornman *et al.* 1998). Pellets were collected in 1989 (end of May, June) on Ameland. In the 1990s, when the population on Ameland was vanishing, pellets were collected in 1993 (August), 1994 (beginning of August), 1997 (June) and 1998 (end of June, July), in the Bargerveen area – in 1994 (end of May-July). For comparison, a pellet analysis of a stable population in a small-scaled agricultural landscape in Nordrhein-Westfalen, Germany (Wagner 1993 – pellets were collected in 1990 and 1991 from May to August), was used.

Study area

In 1997 and 1998, the last single territory of the Dutch coastal dunes was located at the same spot on Ameland (*A98* and *A97*). The territory was situated at the inner border of dune landscape, neighboured by intensively used farmland. It was dominated by a mosaic of open grass encroached shrub dune-land, two moist pastures and Creeping Willow (*Salix repens*) bushes. The pastures normally were mown at the end of June. In 1997 and 1998, mowing was done after the breeding season in August. Bare ground patches were present. Only little open water was present in a small, eutrophicated pond.

Bargerveen peat-moor reserve is a raised bog remnant, where nature management by the State Forestry Service is focused on peat moor regeneration. This management resulted in mosaic landscape with transitions from wet to dry and from nutrient-poor to nutrient-rich conditions. In 1995, four successive territories of the Red-backed Shrike were observed (*B I*, *B II*, *B III*, and *B IV*). Territory *B I* was dominated by heather vegetation (*Calluna vulgaris* and *Erica tetralix*) and Purple Moor-grass (*Molinea caerulea*). It was richly structured by the presence of trees and bushes. Open water was present. Low Bramble (*Rubus fruticosus*) bushes and mosses, alternated with *E. tetralix* and *M. caerulea*, dominated vegetation of *B II*. Open water and large bare ground patches were present. Vegetation structure and vegetation composition of territory *B III* resembled *B I*, but open water surface was larger in *B III*. Territory *B IV* was structure-rich by the presence of trees, and vegetation was dominated by *E. tetralix*, *C. vulgaris* and *M. caerulea*. Within *B IV*, a section of cultivated grassland (Perennial Ryegrass *Lolium perenne* dominated) was found. No open water was present (Hornman *et al.* 1998).

Nest observations

Nest observations on Ameland and Bargerveen were carried out every other day from 6.00 *a.m.* until 9.00 *p.m.* (Table 1). On Ameland in 1997 and 1998, one nest each year was observed. In Bargerveen, four successive nests were observed during the 1995 breeding season.

Nestling diet composition was determined from a hide at 2-3 m distance from the nest. Every prey item was determined to the highest possible taxon. If necessary, a slide of the prey item was taken for later determination. Time of delivery and prey size as a relative estimate of parental bill volume were noted.

Pellet analysis

Adult diet was analysed by determining prey remains in pellets to the highest possible taxon. Pellets were crumbled and body parts of prey that were suitable for identification, were collected. Species identifications were performed and prey lengths were found using identification literature and reference collection.

Table 1
Periods, during which nest observations and food availability counts were carried out. *A97* and *A98* are the Ameland nests in 1997 and 1998, *B I-B IV* are the four nests in Bargerveen in 1995. Age is age of the nestlings during the observation period (day 0 is day of hatching). No. days is number of observation days. Mean *T* is mean maximum diurnal temperature, between brackets is temperature range. No. rainy days is number of days during nesting period with regular rain fall during the day. Survival is number of surviving nestlings from hatching until fledging.

Nest:	*A97*	*A98*	*B I*	*B II*	*B III*	*B IV*
Period	06-13/06-21 1997	06-29/07-09 1998	06-07/06-21 1995	06-24/07-02 1995	07-08/07-18 1995	07-25/08-01 1995
Age	5-13 days	1-11 days	1-15 days	3-11 days	2-12 days	6-13 days
No. days	5	6	8	5	7	5
Mean *T*	18.3 (15-20.5)	17.3 (16-18.5)	14.4 (9.5-22)	22.4 (17-28)	23.8 (17.5-28.5)	24.4 (21.5-28)
No. rainy days	1	2	5	0	1	0
Survival	3 → 1	3 → 1	5 → 3	5 → 5	4 → 3	4 → 4

Prey availability

Prey availability was estimated by counting potential prey in line transects. Transects were situated in characteristic vegetation types within the hunting range of the Red-backed Shrike. All territories contained five transects. Transects were five meters wide, transect length varied from 75 to 200 m. Species and numbers were counted by walking slowly through the vegetation. This method allowed determination of numbers of flying, vegetation dwelling and flower visiting invertebrates. Determined invertebrates comprised only part of the Red-backed Shrike's nestling diet. Especially ground-dwelling species (for instance carabid beetles and spiders) could not be surveyed with this method, but also some vegetation-dwelling insects (like caterpillars) could not be included. During the nestling phase transects were counted six times per day every three hours, starting at 6.30 *a.m*. Availability of potential prey species was determined by adding up densities of potential invertebrate prey species per transect count.

The relationship between nestling diet composition and prey species availability (as established in transects) was determined by calculating linear regression between prey species diet contribution in a three hour period and potential prey species availability coinciding with the midpoint of the corresponding three hour period of nest observation.

Calculation of prey weight

Fresh weight of prey were determined in several ways:

(1) Mean weight of freshly killed specimens was measured for damselflies and dragonflies (without *Aeshnidae*), the daily active nocturnal butterfly *Autographa gamma*, some hover-fly species.

(2) A general relationship between bill volume and length of invertebrate prey (except earthworms and *Aeshnidae* dragonflies) was calculated by obtaining lengths of 33 prey species from previous studies and calculating mean volume estimated during nest observations. This relation was incorporated in the length – dry weight formula by Rogers *et al*. (1976). Dry weight was converted into fresh weight by measuring water content of species of different taxonomic orders. If unknown, water content was assumed to be 70% of fresh weight.

(3) Fresh body weight of *Aeshnidae* dragonflies prey could not be determined by using methods 1 and 2 as they were fed mostly in parts. Dragonflies have also different length – weight relationship compared to Rogers *et al*. (1976) as they have different body dimensions. A length – fresh weight relationship for dragonflies was calculated by measuring mean fresh weight and mean body length of freshly killed specimens. The relationship between prey volume (nest observations) and length was calculated, as well, and incorporated in the length – fresh weight relationship. This was used to estimate fresh weight of *Aeshnidae* prey items.

(4) Length of Viviparous Lizards (*Lacerta vivipara*) was estimated from pictures taken during nest observations. Size in bill volumes of the same specimens was estimated during nest observations. General length – volume relation was calculated from these data. This relation was incorporated in a length – fresh weight formula modified after Van Heereveld and Schraven (1978). The relation was used for all vertebrate prey. This relation was also used for earthworms as these were supposed to have corresponding body density.

(5) Dry weight of undetermined prey with known volume was calculated using method 2, assuming that these were all invertebrate prey. Water content was assumed to be 70% of fresh weight.

(6) Undetermined prey with unknown volume was assumed to have a mean fresh weight of invertebrate prey smaller or equal to 1.0 bill volume. It was assumed that these prey items were small invertebrates as they were rapidly swallowed by the nestlings and could not properly be seen in the bill of the parent.

RESULTS

Weight of nestling prey

Determination of nestling invertebrate prey weight was based on prey deliveries by the parents. Mean weight of nestling invertebrate prey was lower in both Ameland nests compared to all four Bargerveen nests (t-test, $p < 0.05$; Table 2). In 1998, large part of prey delivered to the nest by the male was consumed by the female (45% of invertebrate prey), while covering the young. Mean weight of these invertebrate preys was also significantly lower compared to all four Bargerveen nests (t-test, $p < 0.05$).

Mean weight of invertebrate prey on taxonomic levels ranging from order to species was lower on Ameland for most prey groups compared to Bargerveen, combining all data from Ameland and Bargerveen (Fig. 2).

Table 2
Mean fresh weight of invertebrate prey in grams. *A98Y* is nestlings on Ameland 1998; *A98F* is female covering nestlings, Ameland 1998; A97 is nestlings Ameland 1997; *B I-B IV* is nestlings Bargerveen nest *B I* to nest *B IV*

Nest	*n*	Mean weight (g)
A98Y	305	0.085
A98F	254	0.067
A97	822	0.096
B I	1254	0.134
B II	894	0.116
B III	862	0.143
B IV	868	0.110

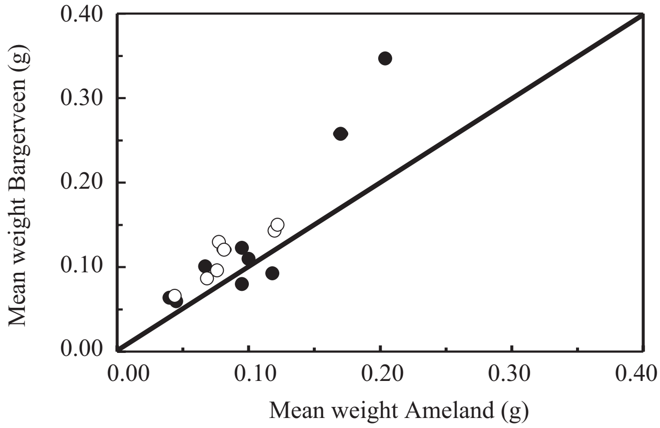

Fig. 2. Mean weight of nestling invertebrate prey of Ameland in 1997 and 1998 and Bargerveen in 1995. Bold dots indicate prey types at taxonomic level of order, open dots indicate prey types at taxonomic level of family to species. The diagonal line indicates 'weight Bargerveen' = 'weight Ameland'.

Size of adult prey

Determination of adult prey length was based on pellet analysis. Contribution of the smaller prey size classes on Ameland in the period between 1993 and 1998 was higher compared to all other areas (Fig. 3). Peak of prey size was in the range of 5 to 10 mm (43%). Prey in size class 0-5 mm contributed substantially (36%), whereas prey larger than 15 mm were hardly found (4%). Peak of adult prey length on Ameland in 1989 had been also in the range from 5 to 10 mm (54%), but prey contribution in length class 10-15 mm had been larger (39%). Prey smaller than 5 mm and larger than 15 mm had contributed little to the diet. Frequency distribution of prey

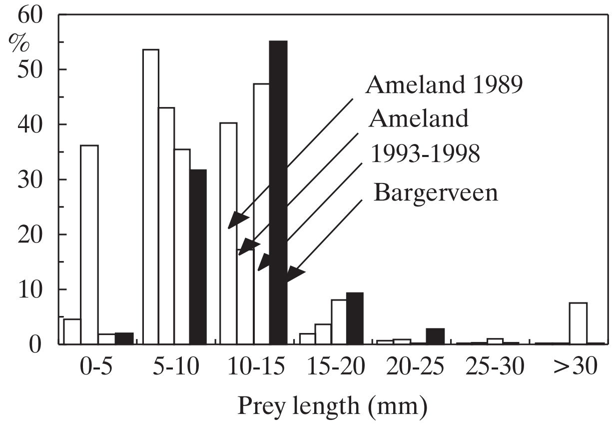

Fig. 3. Relative contribution of different size classes in adult diet. Data from Germany after Wagner (1993).

length in Bargerveen and in Germany (Wagner 1993) was comparable, although the latter showed higher contributions in size classes 10-25 mm compared to Bargerveen. Peak of prey length in both areas was in length class 10-15 mm. Contribution of prey in length class 5-10 mm was large, but contribution of prey smaller than 5 mm was only *ca* 2%. Prey larger than 15 mm contributed more than 10% to the diet. In Bargerveen prey larger than 30 mm still contributed 7.3% (dragonflies *Libellula quadrimaculata*).

Nestling food consumption

Nestling food consumption on Ameland in 1997 was relatively low compared to three of the Bargerveen nests (Fig. 4). Nestling food intake in 1998 on Ameland

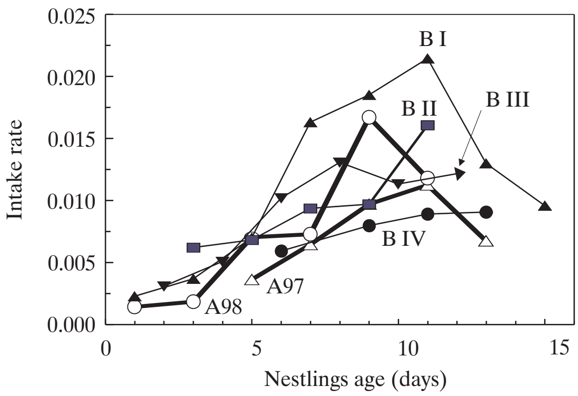

Fig. 4. Daily nestling food intake in gram per minute per nestling during nestling phase. *A97* and *A98* are data from Ameland 1997 and 1998 respectively. *B I-B IV* are data from Bargerveen nest *B I* to *B IV*.

went up to the level of Bargerveen after two nestlings had died at the age of four and six days, respectively. Food intake of *B I* nestlings raised strongly after two nestlings had died at the age of six days (bad weather period).

Prey species diversity and availability

On Ameland, 38 and 50 potential prey species were found during transect counts in the nestling phase in 1997 and 1998, respectively. In Bargerveen, numbers of potential prey species found during transect counts throughout nestling phase ranged from 44 to 56 species.

Mean number and biomass of available invertebrate prey during six daytime periods in the nestling phase was lower in both years on Ameland compared to nests *B III* and *B IV* in Bargerveen (Fig. 5). Mean prey availability in both years on Ameland did not differ from nest *B II* in Bargerveen. Weather during Bargerveen *B I* nestling phase was cold and rainy (Table 1), resulting in low activity of prey in transects.

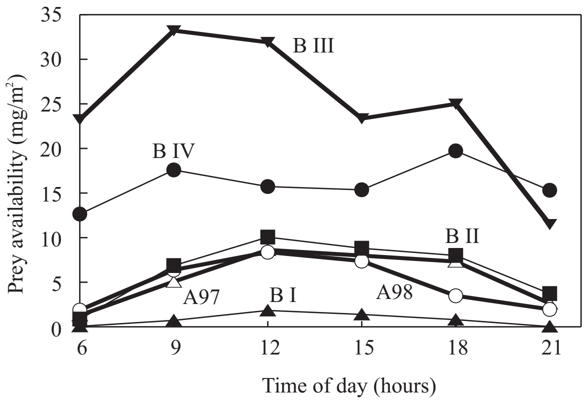

Fig. 5. Mean biomass of potential prey availability (mg/m^2) in transect counts during six daytime periods during nestling phase. Thick line - significant positive correlation, thin line - no correlation between prey species availability and nestling diet composition. Symbols as at Fig. 4.

In both years on Ameland, significant positive correlation between nestling diet composition and prey species availability was observed (Fig. 5). In Bargerveen, only nest *B III* showed such significant positive correlation, whereas three other nests showed no correlation.

Adult diet composition

Adult diet composition on Ameland 1993-1998, Ameland 1989, in Bargerveen 1994 and Germany 1990-1991 consisted mainly of beetles and hymenopterans (Table 3). Between and within these groups, large differences in contribution were

found. Contribution of hymenopterans on Ameland between 1993 and 1998 was much higher compared to Ameland 1989, Bargerveen and Germany, where beetles were contributing strongly. On Ameland in 1989, at the end of the short Red-backed Shrike population revival, *Scarabeidae* beetles contributed almost 50% to the total adult diet. Between 1993 and 1998 on Ameland this group almost disappeared from the diet, contributing only 4%. In Bargerveen and in Germany contribution of *Scarabeidae* was of importance with 11% and 21%, respectively. Other important beetle groups were *Carabidae* and *Elateridae*, although contribution of *Carabidae* on Ameland was less important compared to Bargerveen and Germany.

Table 3
Adult diet composition in pellets on Ameland in 1989 (*A89*), on Ameland in 1993-1998 (*A93-98*), Bargerveen in 1994 (B94) and a German population (After Wagner 1993) in 1990 and 1991 (*G90-91*)

	A89	*A93-98*	*B94*	*G90-91*
Beetles	**79.0**	**34.5**	**59.9**	**51.3**
Scarabeidae	49.5	3.9	11.1	20.6
Elateridae	11.5	7.9	7.7	3.8
Carabidae	5.5	7.9	22.2	12.9
Other beetles	12.5	14.9	18.9	14.0
Hymenopterans	**17.1**	**55.9**	**22.4**	**37.2**
Bombus sp.	11.9	4.0	9.5	14.3
Formicidae	2.0	44.9	7.1	10.2
Other hymenopterans	3.2	7.1	5.8	12.7
Rest	**3.9**	**9.5**	**17.7**	**11.5**
n pellets	115	48	49	293
n individuals	1381	1041	397	1716

Another difference in adult diet composition was found within hymenopterans. Between 1993 and 1998 on Ameland, ants (*Formicidae*) contributed 45% to the total diet that was much higher compared to ant contribution on Ameland in 1989, Bargerveen and Germany. Here contribution of bumblebees (*Bombus* sp.) was of importance.

DISCUSSION

In this study, food ecology of a vanishing Red-backed Shrike population on Ameland was compared with the growing population of Bargerveen and a stable population in Germany. Our hypothesis was that the decline of the Red-backed Shrike population in Dutch dunes is caused by a decrease in insect diversity. Several results indicate that breeding habitat on Ameland was marginal. Breeding success on Ameland in 1997 and 1998 was low. In both years, just one young survived until or just after fledging (Table 1). In the four Bargerveen nests, three to five nestlings fledged. Although

weather conditions were bad during the nestling phase of *B I*, still three out of five nestlings survived.

Adult and nestling prey size on Ameland was smaller compared to reference areas (Bargerveen and Germany). Moreover, adult prey size between 1993 and 1998, when the Red-backed Shrike population was vanishing, was smaller compared to adult prey size in 1989 on Ameland, when the population was at the end of a short revival (Fig. 3). Nest observations revealed that invertebrate prey on different taxonomic levels were smaller on Ameland compared to similar taxonomic groups in Bargerveen (Fig. 2). Even at species level, this was found for *Bombus terrestris* s.l. bumblebees. In a study in an agricultural landscape it was found that increased frequency of disturbance (*e.g.* mowing, cattle-grazing, heavy manuring) affected diversity of large invertebrates, because these invertebrates had lowered chance to complete their life cycles. Smaller invertebrates were less affected because of their shorter life cycles. Smaller prey became more important in diets of insectivorous birds as abundance of large prey decreased (Siepel 1990). The higher contribution of smaller prey to adult and nestling diet on Ameland compared to Bargerveen and Germany might suggest a comparable background process.

From historical references, it can be concluded that several species of *Scarabeidae*, *e.g. Phyllopertha horticola*, *Amphimallon solstitialis* and *Polyphylla fullo*, were important prey for the Red-backed Shrike in the Dutch coastal dunes (Esselink *et al*. 1998, Nijssen *et al*. 2000). At the beginning of the 20th century, these *Scarabeidae* species were abundant in the dunes (Everts 1903), but later they strongly declined in presence and abundance, although detailed data are lacking (Mahler *et al*. 1996). *Scarabeidae* contribution in the adult Red-backed Shrike diet in recent years on Ameland declined compared to adult diet in 1989 and was not found in the nestlings' diet in 1997 and 1998. It has been found that *Scarabeidae* prey can play an important role in the nestling diet of Red-backed Shrikes (Hornman *et al*. 1998, Bargerveen Foundation unpubl. data). This group serves as an example to support our hypothesis that decreased insect diversity in Dutch dunes has affected Red-backed Shrike populations.

The Red-backed Shrike is an opportunistic eye-hunter, catching moving prey. If possible it will catch the most profitable prey types, *i.e.* prey that are large and/or easy to obtain. In marginal Red-backed Shrike habitat, where numbers of potential prey are low, a correlation between prey species availability and diet composition is expected. In these habitats, shrikes do not have the opportunity to choose the most profitable prey but are forced to catch whatever is available to fulfil food demands. In optimal habitats, where prey species are available in surplus (peak) numbers at the same time, and there is difference in profitability between prey species, the Red-backed Shrike will choose the most profitable prey. No correlation between prey species availability and diet composition will be expected, *i.e.* the ratio, in which prey species contribute to the diet does not reflect the ratio these species are present in the field. In case there is no difference in profitability between prey species in

optimal habitats, a correlation between prey species availability and diet composition might be found, as shrikes will catch their prey more or less randomly.

In this study, determination of availability was subject to some restrictions. First, the transect method allowed determining just part of the total availability as only flying, vegetation dwelling and flower visiting invertebrates could be counted. As a consequence, only these groups were taken into account in calculating a correlation between prey species availability and diet contribution. Second, availability from a shrike's point of view probably differs from availability from a human observer's point of view in this study. Red-backed Shrikes observe their surroundings from a perch, mainly noticing moving prey, which are in motion spontaneously. Using the transect method the human observer slowly walks through the vegetation, thus disturbing many invertebrates that otherwise would have been invisible for some part. Furthermore, the Red-backed Shrike's eye is probably more powerful in detecting potential prey items than is the human eye. Nevertheless, the transect method is the only „shrike" way of prey availability measuring.

As the population on Ameland was vanishing, it was expected that prey availability would be low and correlation between prey species availability and diet composition would be present, whereas prey availability in Bargerveen was expected to be higher compared to Ameland.

In both years prey species availability in transects was lower compared to two Bargerveen nests (Fig. 5). Furthermore, significant positive correlation was found between prey species availability and nestling diet composition. Diet contribution of invertebrates counted in transects was relatively high compared to Bargerveen, being 35% and 38% in 1997 and 1998, respectively. This indicates that prey not counted in transects were less available compared to Bargerveen. As in both years only one young survived, these results suggest that total prey species availability was limited.

Availability as established in transects in *B III* was higher compared to Ameland. In the nestlings' diet, the contribution of prey counted in transects was 29%, which is lower compared to Ameland. This indicates that prey not counted in transects were more available compared to Ameland. These results suggest that total prey availability was higher compared to Ameland. Three out of four nestlings survived. One nestling was accidentally removed from the nest after producing a pellet that got stuck in its bill. When the female tried to remove the pellet she dragged the nestling away.

Availability as established in transects in *B II* was comparable to Ameland, but nestling diet contribution of invertebrates counted in transects was only 18%, indicating that, compared to Ameland, prey not counted in transects were more available. Total prey availability is suggested to be higher compared to Ameland by these results. All five nestlings of *B II* fledged.

Availability, established by transect counts, in *B I* was very low compared to Ameland and other Bargerveen nests. Invertebrates in transects that represented availability, were largely inactive due to bad weather conditions (Table 1). These in-

vertebrates contributed only 13% to the nestlings' diet. Thus 87% of the diet comprised prey that were not counted in transects, indicating that alternative prey were present. Despite very bad weather circumstances, total prey availability was sufficient enough to let three out of five nestlings survive.

Prey availability as established in transects in nest *B IV* was very high. Diet contribution of the invertebrates counted in transects was 62%. The fact that no correlation between prey species availability and nestling diet composition was found, supports the idea that a strong difference was present in relative abundance of prey species in the transects compared to their relative contribution to the diet. For example, bumblebees, several dragonfly and grasshopper species and a daily active nocturnal butterfly *Autographa gamma* were available in high abundance. Of these prey groups one species of grasshopper – *Conocephalus dorsalis*, and *Autographa gamma* were caught in large numbers, whereas the other species were caught much less frequent. Therefore, it can be concluded that abundance of several prey species was so high that the Red-backed Shrike could pick the most profitable prey species. All four nestlings fledged.

Resuming, our results support the hypothesis that affected prey availability is an important factor in the decline of Red-backed Shrike populations of the Dutch dune area:

(1) Mean invertebrate prey size in adult and nestling diet was smallest on Ameland.

(2) Prey availability in terms of densities and biomass on Ameland (1997 and 1998) was lower compared to Bargerveen.

(3) Prey availability was stronger reflected in the diet when availability was low (Ameland).

(4) Present availability of *Scarabeidae* (probably important prey group for the Red-backed Shrike in the Dutch coastal dunes) on Ameland is low nowadays.

Eutrophication, acidification and desiccation strongly affected plant species composition and vegetation structure and therefore microclimate characteristics. Large parts of the Dutch coastal dune area are now covered with grass, moss and shrub encroached vegetation types (Van der Meulen *et al.* 1996). As a consequence, fauna diversity must have been affected. Red data lists for fauna of the Wadden Sea area indicate that present status of many (potential prey) species is susceptible to critical (Von Nordheim *et al.* 1996). Unfortunately, hardly any historical data is present.

Future studies on the Red-backed Shrike's diet composition and food availability in relation to reproductive success and adult survival should be performed in coastal dune systems, where Red-backed Shrike populations are stable or increasing, and must be compared with the affected Dutch coastal dunes. These comparative studies can help us trace affected links in the food web in degrading coastal dune habitats. Possible study areas are located in the dunes along the west coast of Denmark, where numbers of Red-backed Shrikes have increased recently (Grell 1998). When affected links in food webs have been identified, research should focus on how links are affected and how links can be restored. This knowledge will help us in the conservation and effective restoration of dune habitats.

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REFERENCES

Ash J. S. 1970. *Observations on a decreasing population of Red-backed Shrikes*. Brit. Birds 63: 185-205.

Cramp S. A., Perrins C. M. (Eds). 1993. *The Birds of the Western Palearctic*. Vol. 7. Oxf. Univ. Press. Oxford.

Esselink H., Geertsma M., Kuper J. 1994. *Red-backed Shrike: An indicator for integrity of ecosystems?* J. Orn. 135: 291.

Esselink H., Geertsma M., Kuper J., Hustings F., van Berkel J. 1995. *Can peat-moor regeneration rescue the Red-backed Shrike in the Netherlands?* Proc. West. Found. Vertebr. Zool. 6: 287-292.

Esselink H., Nijssen M., van Duinen G. J., Jansen J., Geertsma M., Kuper J., Bravenboer A. 1998. [*Pilot study on effects of eutrophication, acidification, desiccation, and management on fauna, vegetation, and abiotic conditions in the dunes of Ameland and Terschelling. The 'indefinite' loss of the Red-backed Shrike as indicator for insect diversity in the dunes?*] Bargerveen Foundation. Nijmegen. (In Dutch)

Everts E. 1903. [*Coleoptera Neerlandica. The sheath-winged insects of the Netherlands and neighbouring regions. Vol. II*] The Hague. (In Dutch)

Geertsma M., van Berkel H., Esselink H. 2000. *Are high fitness values sufficient to maintain a Dutch population of the Red-backed Shrike (Lanius collurio)?* Ring 22, 1: 79-88.

Grell M. B. 1998. [*Birds of Denmark*.] G.E.C. GADs Forlag & Dansk Ornitologisk Forening. Copenhagen. (In Danish)

Hagemeijer E. J. M., Blair M. J. (Eds). 1997. *The EBCC atlas of European breeding birds. Their distribution and abundance*. London.

Hornman M., Nijssen M., Geertsma M., Kuper J., Esselink H. 1998. *Temporal effects on diet composition in nestling Red-backed Shrike (Lanius collurio) in Bargerveen, the Netherlands.* IBCE Tech. Publ. 7: 83-87.

Hustings F., Bekhuis J. 1993. [*Red-backed Shrikes Lanius collurio in the Netherlands today: remnants of a more glorious past?*] Het Vogeljaar 41: 2-17. (In Dutch)

Korodi Gál I. 1969. *Beiträge zur Kenntnis der Brutbiologie und Brutnahrung der Neuntöter (Lanius collurio L.).* Zool. Abh. Ber. Mus. Tierk. Dresden 30: 57-82.

Lefranc N. 1973. *Notes sur l'histoire recente de la pie-grièche Écorcheur Lanius collurio en Europe occidentale.* Alauda 41: 239-252.

Lefranc N., Worfolk T. 1997. *Shrikes. A guide to the Shrikes of the World.* Pica Press. Sussex.

Mansfeld K. 1958. *Zur Ernährung des Rotrückenwürgers (Lanius collurio collurio L.), besonders hinsichtlinch der Nestlingsnahrung, der Vertilgung von Nutz- und Schadinsekten und seines Einflusses auf den Singvogelbestand*. Beitr. Vogelk. 6: 271-292.

Nijssen M., van Duinen G. J., Geertsma M., Jansen J., Kuper J. T., Esselink H. 2000. [*Effects of acidification, eutrophication and desiccation and influence of management on fauna and flora in the dune areas on Ameland and Terschelling.*] Bargerveen Foundation. Nijmegen. (In Dutch)

Rogers L. E., Hinds W. T., Buschbom R. L. 1976. *A general weight vs. length relationship for insects*. Ann. Ent. Soc. Am. 69: 387-389.

Siepel H. 1990. *The influence of management on food size in the menu of insectivorous animals*. Proc. Exp. & Appl. Ent. 1: 69-74.

Teixeira R. M. 1979. [*Atlas of the Dutch breeding birds*.] Gravenland. (In Dutch)

Tucker G. M., Heath M. F. 1994. *Birds in Europe: Their conservation status*. Cambridge.

Van der Meulen F., Kooijman A. M., Veer M. A. C., van Boxtel J. H. 1996. [*Effect-orientated measures against acidification and eutrophication in open dry dunes. Final report Phase 1 1991-1995.*] Amsterdam. (In Dutch)

Van Heereveld P. J. T. L., Schraven G. A. M. 1978. [*Ecological study on Lacerta vivipara in the Overasseltse and Hatertse fens in 1978*.] Nijmegen. (In Dutch)

Von Nordheim H., Norden Andersen O., Thissen J. (Eds). 1996. *Red Lists of Biotopes, Flora and Fauna of the Trilateral Wadden Sea Area, 1995.* Bonn-Bad Godesberg.

Wagner T. 1993. *Saisonale Veränderungen in der Zusammensetzung der Nahrung beim Neuntöter (Lanius collurio).* J. Orn. 134: 1-11.