

LONG-TERM RESEARCH REVEALS EFFECTS OF PEAT MOOR REGENERATION ON A CORE POPULATION OF RED-BACKED SHRIKE *LANIUS COLLURIO*

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Abstract.

This study investigates the impact of peat moor restoration on the population dynamics of a core population of the Red-backed Shrike (Lanius collurio) in the Bargerveen nature reserve, The Netherlands. The restoration of raised bogs, initiated in the 1970s and 1980s, aimed to rehydrate desiccated peatlands, enhancing habitat heterogeneity and prey availability for the species. Through a combination of long-term monitoring (1993-2023) of breeding pairs, nest site location, and diet composition, this research examines how restoration measures influenced the distribution and population trends of Red-backed Shrikes. The results show a significant increase in population size, particularly after 2017 with fluctuations in water levels and changes in prey availability as key drivers of the population trend. During raised bog restoration the birds abandon the central part of the peat area and colonize the buffer zones. Nesting opportunities have increased due to the development of thorny shrub vegetation and adapted management practices ensuring that habitat restoration does not reduce nesting sites. Furthermore, climatic factors, particularly warm and dry weather; have positively influenced reproductive success. The findings support the hypothesis that large-scale, landscape-level restoration of peat bogs, including the surrounding lagg-zones and buffer areas, is essential for sustaining Red-backed Shrike populations. The study highlights the importance of integrated habitat management and the influence of external factors, such as climate change, on species recovery.

Keywords: Red-backed Shrike; Peat moor restoration; Habitat heterogeneity; Population dynamics; Buffer zones; Climate change; Landscape-scale conservation.



*This article is dedicated to Hans Esselink (1954-2008)

Hans Esselink (1954-2008) ringing Red-backed shrike nestlings in 1992 in the Bargerveen Nature Reserve.

1. INTRODUCTION

The Red-backed Shrike (Lanius collurio, Linnaeus, 1758) was once a common breeding bird in the Netherlands, with an estimated population of 10,000 breeding pairs at the turn of the 20th century. However, habitat destruction due to changes in land use caused a sharp nationwide population decline, with only 200-280 breeding pairs remaining between 1985 and 1990 (Hustings & Bekhuis, 1993). The Bargerveen nature reserve, a remnant peat moor near the German border, was one of the few places that preserved a small population of Red-backed Shrikes. In clear contrast to almost every other population in North-West Europe, this population began to increase from the late 1980s, coinciding with the implementation of nature restoration measures. It eventually became the national core population for the species. This raised the question of whether peat moor regeneration could save the Redbacked Shrike in the Netherlands (Esselink et al., 1995).

The Bargerveen shrike population has been studied in detail since 1993, focusing on changes in population size, nesting and breeding success, reproduction and recruitment, diet composition, and prey availability. Aspects of the development and breeding ecology of the Bargerveen population have been described in several publications (e.g., Hornman et al., 1998; Geertsma et al., 2000; Hemerik et al., 2015). From the outset of this study, it was hypothesized that restoration measures aimed at regenerating peat moor habitat would reduce habitat suitability and cause a population decline, as living raised bog itself is not a suitable habitat for Red-backed Shrikes. Targeted management and the development of a peripheral laggand transition zone between the restored raised bog core and the surrounding agricultural and urban areas would be necessary to supplement suitable habitat in a (semi-) natural landscape setting (Esselink et al., 1994 and 1995).

This article describes the development of the core Red-backed Shrike population between 1993 and 2023, in relation to changes in landscape structure and management, and concludes with the overall ecological lessons learned from this long-term research project.

2. RESEARCH AREA

The Bargerveen peat moor (Fig. 1) is a nature reserve under the European Natura 2000 legislation, located in the province of Drenthe, The Netherlands (52°40'40''N, 7°802'08''E), near the German border. Managed by the State Forestry Service, it is the largest remnant of the former Bourtanger Moor, a raised bog system that once spanned 1600 to 3000 km². Large-scale peat harvesting continued until the 1970s, with extraction ceasing completely only in 1992. The remaining unexcavated peat moor was secured in 1968, followed by the acquisition and protection of surrounding excavated areas, expanding



Figure 1. Topographic map of the study area, Bargerveen peat moor reserve, including buffer zones (red-hatched areas).

the protected area to 2083 ha in 1992 (the official Natura 2000 area) and approximately 3000 ha by 2023, including buffer zones.

Habitat changes in the Bargerveen area in relation to management

To restore a functioning raised bog ecosystem, a range of small and large-scale measures have been implemented in the core area of Bargerveen and its surrounding buffer zones. These efforts aim to retain rainwater, stabilize groundwater levels, and reduce evaporation and shading from tall grasses, shrubs, and trees, thereby promoting conditions for the growth of peat mosses (Sphagnum spp.). Starting in the 1970s, a small network of low dikes was constructed around the intact peat bog core, followed by larger dikes built around excavated plots in the 1980s and 1990s. Over time, the Bargerveen transitioned from a drained and excavated, mineralizing raised bog remnant into a varied landscape, featuring small regenerating raised bog areas, wet and dry heathland, mesotrophic grasslands and meadows, and large open water areas. Between 1997 and 1999, a central drainage canal used for peat transport was filled, and a concrete road was removed from the area. The creation of buffer zones with large water basins surrounding the Natura 2000 area further prevented water seepage and stabilized groundwater levels throughout the entire region. As a result, groundwater levels rose by several decimeters (Fig. 2).

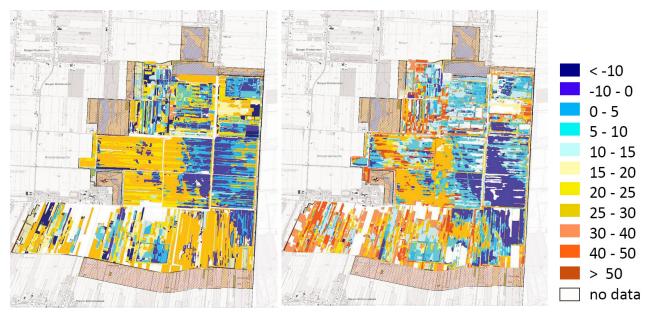


Figure 2. Representation of the area's hydrology (water level relative to ground level, in cm) in 1997 (left) and 2014 (right), extrapolated from vegetation surveys. Note that the decrease in groundwater levels in the central part of the area does not indicate a drop in groundwater but an increase in peat moss development in open water areas. Calculations were made only for the Natura 2000 area and do not include the surrounding buffer zones.

Small trees and shrubs, particularly Birches (Betula spp.) and Willows (Salix spp.), which had colonized significant areas of the dry, excavated peat, died when water tables were raised. At the same time, sheep and cattle grazing were introduced to counteract the encroachment of Purple Moor grass (*Molinia caerulea*), and shrubs and low trees were removed mechanically. As a result, the central part of Bargerveen transformed into a very open and wet landscape between the late 1990s and 2015, while the surrounding buffer zones had not yet been developed. The last large-scale measures were taken between 2015 and 2018, with the raising of several parts of the larger dike system and the expansion of the buffer zones in the southern part of the area. In addition to the construction of several large water basins, many parts of these buffer zones were converted from arable farming to extensive grasslands, thorny shrubs, and hedges with Blackthorn (Prunus spinosa) and Common Hawthorn (Crataegus monogyna), as well as encroachment by Blackberry (*Rubus* spp.), providing suitable nesting sites for shrikes and other birds (Fig. 3).

3. Methods

Population trend of Red-backed shrikes

From the 1970s to the present, monitoring of Redbacked Shrikes has been conducted through annual integral censuses using nationally standardized criteria to determine the number of territories (Vergeer et al., 2023). This method is based on occupied territories but does not account for the breeding status of each pair or individual bird (such as solitary males), nor does it correct for movements of pairs or individual birds after disturbances or nest failures. Since 1993, counting the breeding population has been based solely on the number of (potentially) reproducing pairs, including only sites where a) a nest was found, b) a resident pair was observed, or c) young immobile fledglings were detected. Differences between



Figure 3. Typical habitat of the central part of the Bargerveen in 1993 (left), showing large areas of regenerating peat moor vegetation with a mosaic of open water, Cottongrass (*Eriophorum angustifolium*), Birches (*Betula* spp.), and Willows (*Salix* spp.). The surrounding buffer zones in 2021 (right) now feature a mosaic of peat moor (*Sphagnum* mosses), flower-rich grasslands on dike slopes, and mixed shrub areas with Birches, Willows, as well as Blackthorn (*Prunus spinosa*) and Common Hawthorn (*Crataegus monogyna*).

territory estimates and counts of actual breeding pairs are explained by the presence of solitary males and the correction for dispersion of breeding pairs within the season after initial breeding attempts had failed. With these corrected counts, the most reliable estimate of the actual year-by-year size of the breeding population in the Bargerveen area has been made. Data for this began being collected in 1996. For 1993, 1994, and 1995, the population size was retrospectively estimated by using the mean difference between surveys and actual counts during 1996-1999. From 1994 to 2013, a significant portion (approximately 60-80%) of the Bargerveen population was individually marked with color rings, which improved the accuracy of counting separate breeding pairs and allowed for corrections of within-season dispersion of breeding birds. The locations of all breeding pairs' nests have been recorded as accurately as possible in a GIS environment.

Habitat change

Changes in habitat resulting from restoration measures are monitored every 6 to 12 years through full-coverage vegetation surveys, which map the total area and location of specified vegetation types (in accordance with Natura 2000 guidelines) and the distribution of characteristic plant species. Using the GIS toolkit Iteratio (Holtland et al., 2010), the mean highest groundwater level (in spring) for the entire area is calculated based on the mapped vegetation types.

Field surface level territories

Field surface level (meters above sea level) for all breeding pair territories (either nest location when found or the center of breeding pair field observations) was calculated using ArcGIS Pro with digital elevation maps AHN1 (1993-2011), AHN2 (2012-2019), and AHN3 (2020-2023). This calculation was necessary as the construction of dikes during the research period has locally altered field surface levels within the monitoring period 1993-2023.

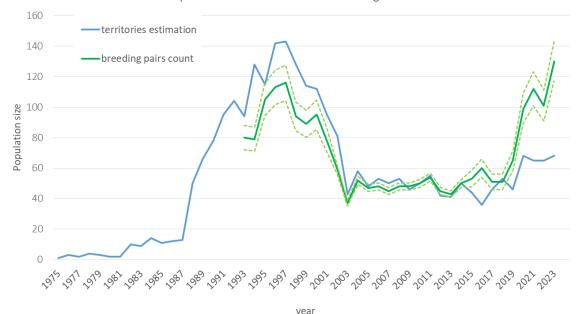
Diet composition

Diet composition was studied from 1993 to 1996 through visual observations from a shelter at the nest site. To improve the identification of prey items fed to the nest-lings, photographs were taken of prey items that could not be identified in the field. The taxon (species, genus, or family) and the size of prey fed to the nestlings were recorded. In total, data on 11,485 prey items from 29 nests were collected. In 2017, diet composition was again studied using automatic Bushnell camera traps. That year, an additional 1,761 prey items from 7 nests were identified.

4. RESULTS

Development of the Red-backed shrike population

The Red-backed Shrike population in the Bargerveen area has been monitored from 1977 to 2023 (Fig. 4). In the 1970s and early 1980s, only a small population of 2-4 territories was present. Numbers increased from the early 1980s to approximately 13-14 territories in 1985-1987, followed by a sharp rise to over 140 territories in 1996-1999. The small population size in the early years and the sudden increase in the following period must be interpreted with caution, as monitoring intensity was relatively low. Redbacked Shrikes can be secretive during the early breeding season, which may lead to an underestimation of the number of pairs. Additionally, solitary birds (mainly males) and dispersing breeding pairs after failed nesting attempts could result in an overestimation of the population. The count of 113-116 actual breeding pairs in 1996-1997 provides a reliable representation of the population size at its peak. After this peak in the late 1990s, the population declined sharply to 37 breeding pairs in 2003, followed by a relatively stable, slightly fluctuating population size of 43 to 60 breeding pairs until 2018. From 2019 onward, the population increased rapidly, reaching 130 breeding pairs in 2023, with only a small dip in 2022.



Population trend Red-backed shrike Bargerveen

Figure 4. The number of territories (1977-1999) and actual breeding pairs (1993-2023) in the study area, including the protected Natura 2000 area and surrounding buffer zones of Bargerveen, are presented here. The estimation of territories in 1977-1999 is based on standardized monitoring of all individuals and pairs. Counts from 1993 to 2023 are exclusively based on actual breeding pairs (see Materials and Methods). Confidence intervals are estimated retrospectively, taking into account the monitoring intensity in relation to the total population size.



Figure 5. The distribution of breeding pairs of Red-backed Shrikes in the Bargerveen reserve, including the buffer zones surrounding the protected Natura 2000 area, varied over the years. Between 1993 and 1999, there were 624 nest locations. From 2000 to 2016, the number of nest locations increased to 966. However, in the period from 2017 to 2023, the number of nest locations slightly decreased to 770. These figures illustrate the changes in the spatial distribution of breeding pairs over time, with a significant increase in the early 2000s, followed by a small decline in the most recent years.

Distribution of breeding pairs in the Bargerveen

The location of nest sites within the Bargerveen changed significantly during the period from 1993 to 2023 (Fig. 5). During the initial phase (1993-1999), many breeding pairs were present in the northern and southern sections, as well as along the edges of the central section. Areas surrounding the nature reserve were practically unoccupied. In the subsequent period (2000–2016), breeding pairs almost completely disappeared from the edges of the central section, while nesting density increased in many parts of the northern section. Additionally, the first buffer zones and abandoned agricultural areas within the nature reserve were slowly colonized. In the period from 2017 to 2024, nesting sites in the northern section, and to a lesser extent in the southern section, became concentrated along higher dike systems, and the northern buffer zones were

increasingly colonized, contributing significantly to the population increase.

This shift in spatial distribution of breeding pairs is also visible in average field surface level of nest locations for Red-backed shrikes in the Bargerveen (Fig. 6). The average level increased by approximately 40 to 60 centimeters (from 18,6 meter to 19.2 meter above sea level) during the period 1993-1999 as breeding pairs moved from the lower central area to the higher fringes and dikes on the edges of the area. Between 2000 and 2012, the average ground surface level of nest locations remained nearly constant. A notable decline is observed from 2013 onwards when breeding pairs choose to nest in the buffer zones, which are situated at lower field surface levels compared to the elevated raised bog system.

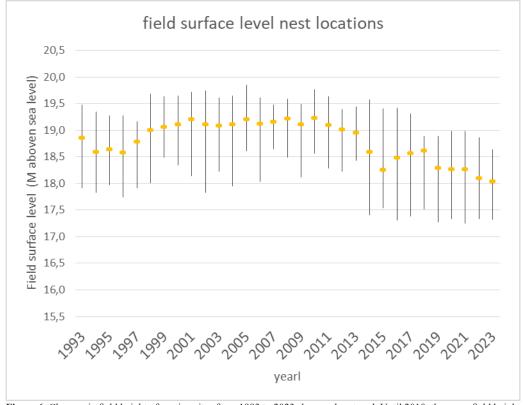


Figure 6. Changes in field height of nesting sites from 1993 to 2023 show a clear trend. Until 2010, the mean field height increased as nesting sites shifted within the raised bog system. This shift was due to the regeneration and development of the central bog area. After 2010, many breeding pairs began to colonize the surrounding buffer zones, which are situated at lower field elevations compared to the raised bog. This shift resulted in a decrease in the average field height of nesting sites as more pairs moved into these lower-lying areas.

Changes in diet composition

The diet of Red-backed Shrike nestlings shifted significantly between 1991-1996 and 2017. During the earlier period, the diet was primarily composed of day-active moths and their caterpillars (*Lepidoptera*; 24.9%), beetles (*Coleoptera*, mainly water beetles Dytiscidae and Scarabid beetles Scarabidae; 15.3%), and dragonflies (*Odonata: Zygoptera* and *Anisoptera*; 12.2%). However, by 2017, the importance of these groups had decreased sharply, while grasshoppers (*Orthoptera*: true grasshoppers *Acrididae* and Bush-crickets *Tettiginiidae*; 29.7%) became a substantial part of the nestling diet.

Some groups remained equally important in both periods, such as bees and wasps (Hymenoptera, mainly

Bumblebees *Bombus* spec.; 10.9-13.7%) and spiders (Araneae; 10.3-9.4%). The total number of vertebrates (or parts of them) did not differ significantly between the two periods (11.8% vs. 14.3%), but notable changes were observed within specific species. The frequency of Viviparous lizard (*Zootoca vivipara*) in the diet dropped from 5.3% to 1.3%, while the proportion of pond frogs (Amphibia, Ranidae) increased from 0.4% to 5.5%.

These percentages reflect the number of individual prey items fed to the nestlings. However, when considering the share of total weight and protein content of the prey, vertebrates likely represented a greater proportion of the diet compared to invertebrates (Table 1).

Invertebrates (order)		1991-96	%	2017	%	trend
Moths & Butterflies	Lepidoptera	1585	15.7	129	9.1	▼
Beetles adults	Coleoptera	1546	15.3	114	8.1	▼
Dragonflies and damselflies adults	Odonata	1165	11.5	74	5.2	▼
Bees, Wasps and ants	Hymenoptera	1099	10.9	193	13.7	
Grasshoppers & bush crickets	Orthoptera	1056	10.4	419	29.7	
Spiders	Araneae	1041	10.3	133	9.4	
Caterpillars	Lepidoptera larvae	929	9.2	80	5.7	▼
Flies and mosquitos adults	Diptera	488	4.8	89	6.3	
True bugs	Hemiptera	230	2.3	22	1.6	
Beetle larvae	Coleoptera larvae	84	0.8	7	0.5	
Dragonfly larvae	Odonata larvae	73	0.7	18	1.3	
Worms	Opisthopora	56	0.6			
Woodlice	Isopoda	24	0.2			
Scorpionflies	Mecoptera	17	0.2			
Fly and mosquito larvae	Diptera larvae	9	0.1			
Harvestmen	Opiliones	8	0.1	1	0.1	
Millipeds	Diplopoda	5	0.0			
Centipeds	Chilopoda	2	0.0			
Earwigs	Dermaptera	2	0.0			
Snails	Stylommatophora	1	0.0	11	0,8	
invertebrates unknown		790	6.9	248	14.1	
vertebrates (class)						
Amphibians	Amphibia	43	0.4	77	5.5	
Reptiles	Reptilia	540	5.3	19	1.3	▼
Birds	Aves	31	0.3	10	0.7	
Mammals	Mammalia	93	0.9	14	1.0	
Vertebrates unknown		568	4.9	103	5.8	

Table 1. The diet composition of nestling Red-backed Shrikes in the Bargerveen area during the period 1991-1996 (11,485 prey items from 29 nests) and in 2017 (1,761 prey items from 7 nests) was based on nest observations. The data are presented as counts of prey items without corrections for prey size or nutritional value.

5. DISCUSSION

In 1995, Esselink et al. posed the question of whether peat moor regeneration could help rescue the Red-backed Shrike population in the Netherlands. The authors hypothesized that this would only be possible if the restoration efforts included the full natural gradient of raised bog systems at a landscape level, encompassing the lagg-zones and transition zones surrounding the living peat moor. As presented in this paper, monitoring of the Red-backed Shrike population from 1993 to 2023 fully supports this hypothesis, based on both the population trend over time and the spatial distribution of breeding birds in relation to the effects of restoration measures taken. Several driving factors can explain the population's response to these measures, both in terms of prey availability and nesting opportunities. These factors interact and can only be partially unraveled.

The primary factor driving population trends and the redistribution of breeding pairs is the fluctuation in water levels within the core of the raised bog reserve (Figure 6). Retaining nutrient-poor rainwater and maintaining a stable water level are essential for the growth of *Sphagnum* mosses, which form living raised bogs. Growing bogs absorb rainwater and create a gradient of nutrient-poor, acid-ic rainwater transitioning to slightly nutrient-rich, buffered groundwater in the surrounding area.

From the 1970s and 1980s, efforts to retain rainwater in the Bargerveen led to a substantial initial increase in habitat heterogeneity. Formerly excavated, desiccated, and drained peatlands were locally re-wetted, resulting in vegetation succession toward Sphagnum bogs, wet heathlands, and willow thickets. More elevated, dry areas retained mesotrophic grasslands and ruderal vegetation on roadside verges and embankments. In the lowest locations, woodland growth died off due to elevated water levels. Although the retained rainwater was nutrient-poor, the upper layer of the desiccated peat had undergone widespread mineralization prior to rewetting, likely enriching the water bodies with nutrients. However, the low pH and isolated location of the water bodies prevented the presence of fish and strongly limited the numbers of amphibians. This led to very high densities of invertebrate aquatic fauna, including dragonflies, water beetles, and aquatic bugs (Heteroptera, mainly *Notonectidae* and *Corixidae*) during the 1990s.

Additionally, the landscape provided a highly suitable habitat for *Viviparous Lizard* and supported a rich floral abundance in wet heathlands with *Erica tetralix* and mesotrophic grasslands, maintaining large populations of bumblebees and diurnal moths. During this period, the recovering raised bog functioned as a large-scale ecotone, offering a high abundance and diversity of prey for Red-backed Shrikes. As water levels further increased, the influence of peat mineralization decreased in relation to acidic, nutrient-poor rainwater, resulting in a decline in aquatic fauna density. Moreover, permanent inundation and the development of *Sphagnum* vegetation reduced the extent of flower-rich heathlands and grasslands, consequently impacting flower-visiting insects.

Only following the acquisition and development of buffer zones did prey availability for Red-backed Shrikes increase again, albeit with significant changes in prey composition. Populations of *Viviparous Lizards* declined markedly, but grasslands, rough grassy verges, and nutrient-rich, buffered waters supported high densities of grasshoppers and pond frogs.

Increasing water levels and removing shrub growth to mitigate evaporation and shading resulted in a decline in nesting opportunities within the central part of the Bargerveen reserve. This affected thornless shrubs, birch (Betula spp.) and willow (Salix spp.), as well as bramble (Rubus spp.). During the 1990s, Red-backed Shrikes often nested in relatively tall, thornless shrubs, which possibly contributed to higher predation rates and lower breeding success during this period. With the development of thorny shrubs such as bramble, blackthorn (Prunus spinosa), and hawthorn (Crataegus monogyna) at the edges and buffer zones of the raised bog, nesting opportunities significantly increased. Although not specifically studied, it is reasonable to assume that the proportion of successful nests-and thus the average annual reproductive success-has subsequently increased. In recent years, management practices to limit woodland encroachment for peatland recovery have been adjusted to avoid reducing nesting opportunities for shrikes. Rather than cutting birch and other trees at the ground level, stems are partially cut at a height of 50-80 cm and then pushed over (Figure 7). This promotes bramble overgrowth, creating new, secure nesting sites for shrikes and other bird species while effectively limiting birch growth.

Several publications have documented the population development up to 2015. Esselink et al. (1995) initially attributed the significant increase in Red-backed Shrikes entirely to improved habitat quality, particularly the increased prey availability in the Bargerveen. However, subsequent studies on reproductive success and recruitment indicated that this could not explain the growth, and immigration must have played an important role in at least several years during the growth of the population (Geertsma et al., 2000). Hemerik et al. (2014) later estimated that for the observed yearly population growth, approximately 20% of the Red-backed Shrikes breeding in the



Figure 7. Nest of Red-backed Shrike on a location with specific management to limit woodland encroachment by partially cutting Birch stems at a height of 50–80 cm and subsequently pushed over, thereby providing nesting sites for shrikes and other bird species while effectively limiting birch growth.

Bargerveen were immigrants. An untestable hypothesis suggests that during the 1990s and early 21st century, habitat loss in neighboring Germany due to ongoing peat extraction led to the displacement of breeding populations. It is even possible that the Bargerveen may have temporarily functioned as an ecological sink. Research on individually color-ringed shrikes revealed minimal exchange between the Bargerveen population and other Dutch populations (Geertsma et al., 2000). The idea that the Bargerveen acted as a source population for the recovery of Red-backed Shrikes across the Netherlands is likely incorrect. Nonetheless, since the 1990s, the Bargerveen has consistently supported the largest Red-backed Shrike population in the Netherlands. Recent unpublished reproductive data suggest that current population growth is primarily driven by local recruitment.

Since 2019, there has been a significant increase in the Red-backed Shrike populations in the Netherlands and other parts of Northwest Europe. In the Netherlands, the estimated population has increased more than sixfold since the 1990s (Sovon, 2024), growing from an estimated 450-550 breeding pairs in 2018 to 1,250-1,550 breeding pairs in 2023 (Boele et al., 2024). In general, the distribution of Red-backed Shrikes is limited by climatic factors (Nijssen, 2020), avoiding very warm and dry conditions in southern Europe, probably facing a mismatch with vegetation greenness on their late arrival from the breeding grounds (Pedersen et al., 2020), as well as high precipitation and low summer temperatures in the north. Søgaard Jørgensen et al. (2013) showed for the Bargerveen and a Danish population that sunny, warm, and dry weather increases reproductive success, with significant effects on the number of fledglings per (successful) pair and lower nestling mortality. Hornman & Nijssen (1996) have demonstrated that weather conditions significantly influence prey availability in the Bargerveen, and Pedersen et al. (2011) found a negative correlation between prey diversity and temperature, indicating that Red-backed Shrikes feed on preferred prey items in warmer summers (low diversity) while being forced to feed on a larger variety of species in colder summers. Moreover, under warm and dry conditions, predation decreases, and fewer subsequent replacement clutches occur (Stichting Bargerveen, unpublished data), leading to a higher average number of fledged young per breeding pair. Additionally, these young fledge earlier in the season, significantly increasing their chances of survival until the next breeding season. In the Bargerveen population, the positive effects of warm and dry weather during the breeding seasons of 2019, 2020, and 2022 almost certainly played an important role, while the population dip in 2022 was likely due to the unfavorable wet weather during the 2021 breeding season.

This research shows that peat moor restoration can indeed facilitate Red-backed Shrike populations, but only when applied on a landscape scale, including the restoration of lagg-zones and buffer zones that belong to a functioning raised bog landscape. Although the role of the Red-backed Shrike as a suitable indicator for the integrity of ecosystems (Esselink et al., 1994) is still valid, it should be considered that an increase in populations of this species can also temporarily occur in disturbed ecosystems or be driven by factors outside the research area, such as climatic changes.

ACKNOWLEDGMENTS

This article is dedicated to Hans Esselink (1954-2008), a pioneer of shrike research in the Netherlands, a highly valued member of the international shrikeologist community, and the initiator of the Bargerveen Foundation. Since 1991, the foundation's staff has been investigating the opportunities and threats facing the Red-backed Shrike in the Netherlands and surrounding countries. Shrike monitoring in the Bargerveen reserve was initiated and, for many years, carried out by Hans van Berkel (1947-2013), with support from the managers of the State Forestry Service, particularly Jans de Vries and Piet Ursem. The research conducted in 2017 was financed by the province of Drenthe, The Netherlands.

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