

# What is going on with the silver Y, *Autographa gamma*?

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## KEY WORDS

Climate change, decline, Lepidoptera, migratory moth, the Netherlands

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The silver Y, *Autographa gamma*, the most abundant moth of the Netherlands, has declined by 56% over the last 30 years. An analysis shows that adult mortality caused by weather conditions may be severe. There is a strong geographic component in the decline, which is interpreted as larval mortality associated with deposition of deleterious components. The number of immigrants is declining as well, but this plays a much smaller role. However, it is predicted that deteriorating conditions around the Mediterranean region caused by global change will further reduce the number of immigrants in the near future.

## Introduction

Of the around 2300 species of micro and macro moths of the Netherlands, the silver Y, *Autographa gamma* (Linnaeus) is the most numerous by far. Counts of hundreds, sometimes even thousands of moths during one observation night are no exception; the highest recent total annual numbers amounted to 606,981 and 606,981 (1991, 1996). Unlike most moths, the species is active also during the day, which, together with its unmistakable wing pattern (figure 1), makes it probably the moth species that is best known to the general public.

The Working Group Lepidoptera Faunistics and Dutch Butterfly Conservation possess a powerful tool to monitor the ups and downs of the Lepidoptera fauna of the Netherlands in their common database 'Noctua'. In the case of the silver Y the database testifies of a worrying decline. A total of over 150 thousand observations of this species provide sufficient information to analyse this development in more detail.

## Importance

As an abundant species, the silver Y plays various important roles in the ecosystem. First, moths pollinate nocturnal flowering plants (Kephart et al. 2006, MacGregor et al. 2014, Schoonhoven et al. 2014, Sexton 2014, Winkler et al. 2005). Actually, the silver Y is considered one of the less effective pollinators (Huigens & Mol 2013, Kwak 2012), but this is amply compensated by its large numbers.

Second, larvae and adults of moths are important prey for insectivorous birds and bats, and this is particularly true for numerous species that are not too small, such as the silver Y (e.g. Jooris & Faquet 1977, Skals et al. 2003). The adult moth for instance is one of the more important resources for the red-backed shrike (*Lanius collurio*), and the disappearance of this bird from the Dutch dunes has been associated with a reduction of prey availability, including the silver Y (Kuper et al. 2000).

A third important effect of the silver Y on the ecosystem may be in its role as larval grazers. It is a central tenet in nature conservation that structure, composition and succession of the vegetation is to a high degree determined by animal grazers. In discussions on this topic the attention generally alternates between small grazers, like rabbits, and the large ones, like

bovids and horses. However, long standing exclusion experiments involving invertebrates (insects, molluscs) have demonstrated that in many instances the role played by invertebrates equals that of vertebrates (Allan & Crawley 2011, Crawley 1989, Louda & Rodman 1996, Root 1996, Stasny & Agrawal 2014). The long-time negligence of invertebrates in nature conservation can be understood from the difference in scale, coarseness, and thereby the immediate visibility of their effects (Kotanen & Rosenthal 2000). The larvae of the silver Y can cause considerable damage to crops, especially in circum-Mediterranean regions, but their impact on natural ecosystems is not well understood. Taking into account their abundance, strong polyphagy (they are known from 311 plant species, all herbs) and the species' strong reproductive potential (a female may lay 500-1500 eggs), their impact must be considerable (Chumakov & Kuznetsova 2014).

## From migrant to summer guest

The silver Y is well known because of its migratory behaviour, the classical definition of migration being 'a periodic, more or less unidirectional, continued movement, assisted by the efforts of the animal, and in a direction over which it exerts a control, which results in the animal passing away from its previous daily field of operations' (Williams, 1930). A useful review of migration in Lepidoptera in general is given by Vervloet (2002).

Many pages have been filled describing the migration of the silver Y (Baker 1978, Dingle 1978, Lempke 1972, De Vos 1992). During the winter, the species lives in the Mediterranean region, mainly in North Africa. Regularly it is reported as a pest of local crops. In spring, part of this southern population migrates to Northwest Europe, becomes quite numerous in the course of several generations, then dies out. Many authors have wondered about this seemingly paradoxical course of events (Johnson 1969, Lempke 1972, Stinner et al. 1983, Williams 1957). Only recently the availability of vertically looking high resolution radars has led to the discovery that, unlike previously assumed, southward migration in autumn does occur (Chapman et al. 2012). The return migration occurs at an altitude of several hundred meters, where the moths are able to find a suitable air current. Most surprisingly, they have the ability to adjust their



1. A silver Y drinking on a flower head of *Pulicaria dysenterica* Bernh., Koudekerke (province of Zeeland). Photo: Albert de Wilde  
1. Een gamma-uil drinkend op een bloemhoofdje van heelblaadjes, Koudekerke.

flight direction in order to compensate for an oblique wind direction. Chapman *et al.* (2008, 2013) conclude that the silver Y has a compass, and an innate flight direction.

The larvae of the silver Y need a fairly high humidity (Chumakov & Kuznetsova 2014), and mainly for that reason the ecological carrying capacity of the Mediterranean region is only one fifth of that of Northwest Europe. Therefore the silver Y should perhaps be considered a summer guest, in the ornithological terminology, rather than a migrant – obviously with the difference that in the moth several generations are involved each year.

One may expect that at least the two other common ‘migrants’ in the Netherlands, the red admiral and the painted lady (*Vanessa atalanta* Linnaeus and *V. cardui* Linnaeus) demonstrate the same behaviour, but this still has to be confirmed.

### ‘Migrant Lepidoptera Registratie Nederland’

In 1940, BJ Lempke started his long-term project on the documentation of migrant moths and butterflies in the Netherlands (De Vos 1992, Van der Meulen *et al.* 2015). It has been enormously successful. Even at present migrants are reported on a regular basis, and a large part of the data used in this paper indirectly stem from that project.

However, there is a limitation to the usefulness of these data. In order to estimate the abundance of a species one needs to know not only the number of specimens, but also the number of collection events, in the period of the year that a species can at all be recorded. For a given species, collection events where the species is missing are important, because they implicitly provide zero-observations. Unfortunately, the lists sent in for the migrant project are limited to the few migrant species, moreover omitting collection events when none of these species was observed. In the present study, in calculations that touch upon abundance or otherwise depend on the number of collection events, data from the migrant Lepidoptera registration therefore had to be disregarded.

## Decline

Although the silver Y still remains the most common moth of the Netherlands, the species is declining sharply (figure 2). The silver Y is well known for its strong yearly fluctuations in abundance (Lempke 1972, figure 2) but since the turn of the century, these fluctuations are much less obvious. Instead, a strong trend of decline is obvious: in the course of the last 30 years the abundance has dropped by 56%. This corresponds to the situation in Great Britain. Working with a very different monitoring scheme and using different algorithms, a decline of 46% in the period 1968-2007 has been reported (Fox *et al.* 2013). To a large extent this is a concealed phenomenon, partly because the species is still numerous, partly also because the growing popularity of moth study generally results in increasing total numbers that are yearly recorded. However, relative to the number of collection events, this increase in observed numbers lags behind.

An estimate of the abundance of a moth or butterfly species is mostly, and in many cases entirely, based on the observed numbers of adults. In the short run this may be misleading, because a high adult mortality may follow an essentially healthy larval generation. Only a protracted mortality in either stage will result in a recognisable decline. Moreover, larval and adult mortality do not necessarily have the same cause. In the case of the silver Y, a third component, which is decreased immigration, may contribute to the decline. All three elements will be discussed in the following sections.

## The anatomy of a bad year

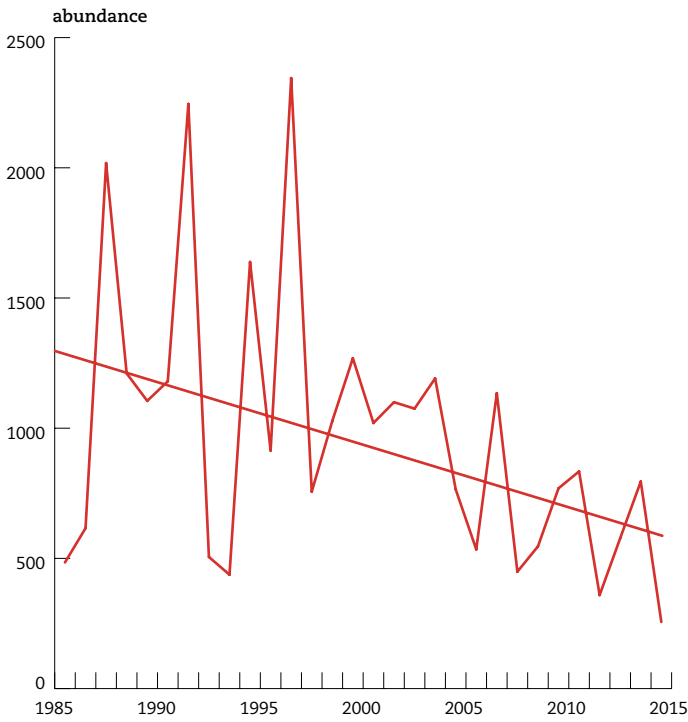
As is obvious from figure 2, the abundance observed in 2014 was exceptionally low, even when taking into account the declining trend. It is therefore interesting to investigate that year in more detail.

Figure 3 compares the daily observed number of adult moths in 2014 to that number in the 30-year period between 1985 and 2014. The discrepancy in average height of the two lines reflects the low abundance of the silver Y in 2014. In 2014, the two peaks in adult abundance start earlier than on average in the 30 years before. That currently is a common phenomenon, our data demonstrate that almost all spring and summer species show this trend. More importantly, the numerical development strongly lags behind normal in the months of June and August.

To obtain a better insight in the situation over the course of the year, data on the entire Lepidoptera fauna were analysed. For each day the average number of species was calculated that was yielded by a collection event. These values for 2014 were compared to the corresponding values over the last 30 years. The daily difference in species-yield is cumulatively plotted in figure 4. The graph is best understood by realising that each datapoint that is lower than its immediate predecessor represents a day with a lower than average yield. The graph clearly shows a sequence of negative values in June, and an even more striking sequence of deeply negative values in August. Clearly, the silver Y was just one of the many species that performed badly in June and August of 2014.

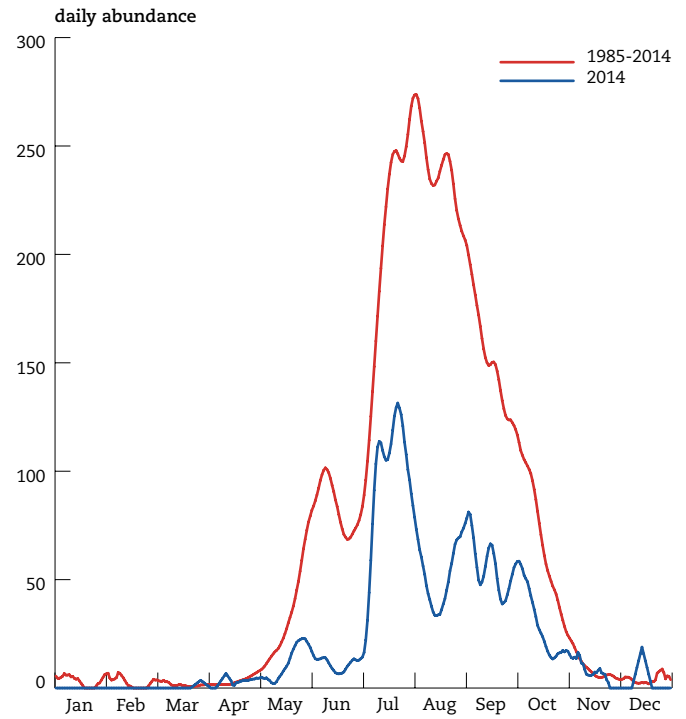
Reasonably it can be expected that the explanation behind figure 4 must be found in the prevalent weather conditions. Indeed, a stepwise regression analysis could explain 42% of the variance in the anomalies with six weather-variables (table 1). Taking the results together, one could say that in general yields are maximal on warm, dry, somewhat hazy and overcast days with winds from the south. August 2014, to the contrary, was cold and wet.

Although the graph of figure 4 is calculated over all species, the congruence with the abundance of the silver Y as shown in



**2.** Trajectory of the annual abundance during the last 30 years, with the regression line ( $y = 50,590 - 24.815x$ ;  $R^2 = 0.1709$ ). Abundance is calculated essentially as the number of specimens per collection event (in the time of year that the species can be observed); for details see Ellis et al. (2014). A collection event is defined as the fact that a person on a date on a place has been observing Lepidoptera. Like in all following illustrations, numbers of specimens have been transformed as  $x \Rightarrow \log(x+1)$ ; larvae and pupae count for 1/100th of an adult.

**2.** Verloop van de jaarlijkse talrijkheid gedurende de laatste 30 jaar, met de regressielijn ( $y = 50,590 - 24.815x$ ;  $R^2 = 0.1709$ ). De talrijkheid wordt essentieel berekend als het aantal exemplaren per collection event (in de tijd van het jaar dat de soort kan worden waargenomen); voor details zie Ellis et al. (2014). Een collection event ('waarnemingsactiviteit' - een goed Nederlandse woord is er niet) is het feit dat een persoon op een plaats op een datum vlinders heeft waargenomen. Aantallen exemplaren zijn, evenals in de volgende figuren, getransformeerd als  $x \Rightarrow \log(x+1)$ , met dien verstande dat rupsen en poppen tellen voor 1/100e imago.



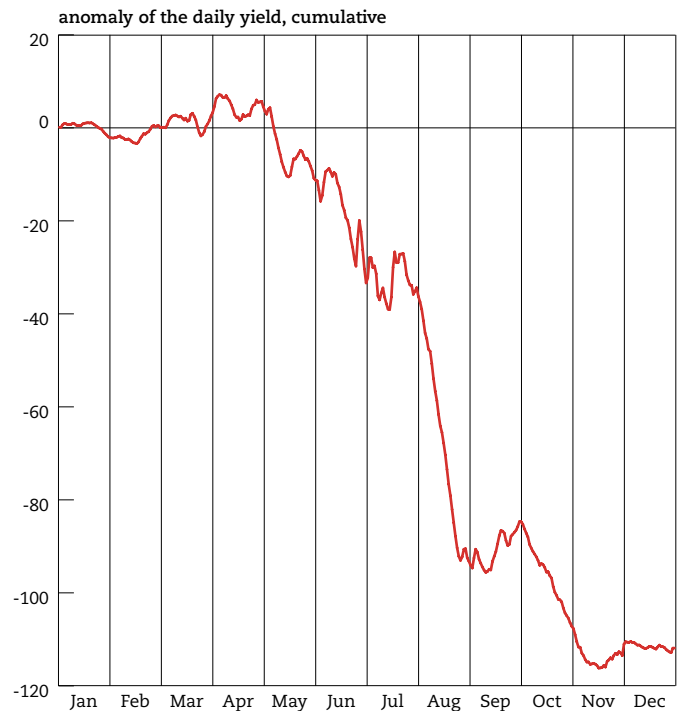
**3.** Daily abundance of the silver Y in 2014, compared with the average value of the daily abundance over the last 30 years. Abundance is calculated as the daily number of specimens divided by the daily number of collection events involving macro-lepidoptera (times 10,000, to get rid of trailing zeroes).

**3.** De dagelijkse talrijkheid van de gamma-uil in 2014, vergeleken met de gemiddelde waarde van de dagelijkse talrijkheid over de laatste 30 jaar. Talrijkheid is berekend als het dagelijkse aantal exemplaren, gedeeld door het dagelijkse aantal collection events waarbij macro's werden genoteerd (maal 10.000, om voornullen kwijt te raken).

figure 3 is remarkable. It demonstrates that the daily weather conditions take an immediate effect upon the observed adult population.

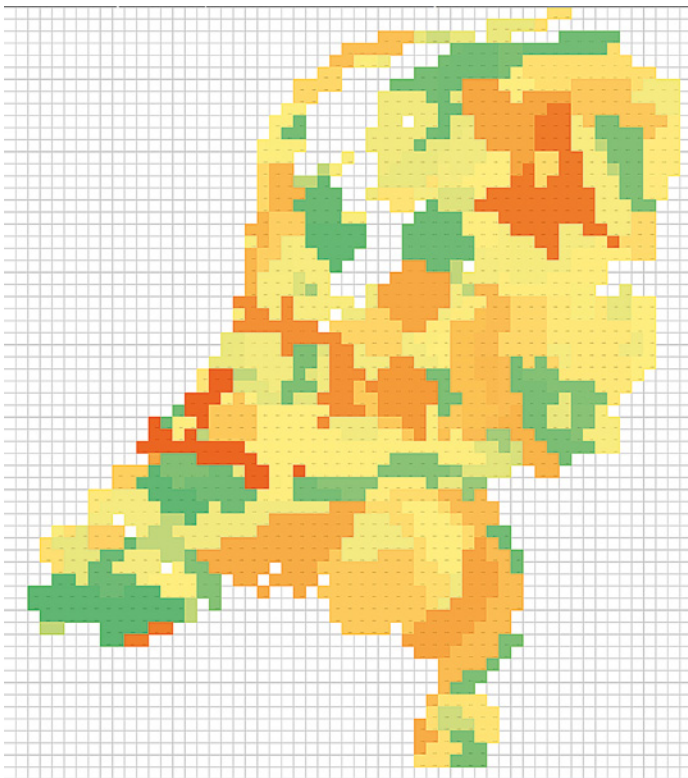
It still remains to be seen whether the lows in abundance in figure 3 reflect mortality or non-detection. After all, one could imagine that the moths go into hiding and remain inactive until the weather conditions improve. However, one would then expect a surge of the reappearing moths augmented with newly emerging ones when favourable conditions return. There are no indications of such a surge. Also, when all species of macro-moths are combined in a similar approach (not shown), the number of specimens does recover after an unfavourable period, but never exceeds the norm. These patterns support the conclusion that unfavourable weather conditions are a major mortality factor for the adult moths.

The importance of weather-determined mortality compared to other factors like light pollution and limited nectar availability is difficult to assess. A point in case certainly is the higher generality of the first.



**4.** Comparison between the daily average number of Lepidoptera species observed per collection event in 2014 and during the last 30 years. The difference, the 'anomaly' is plotted cumulatively (the value on a day x is added to the total over all preceding days).

**4.** Vergelijking van het dagelijks gemiddeld aantal vlindersoorten dat wordt waargenomen tijdens een collection event in 2014, en in laatste 30 jaar. Het verschil, de 'anomalie', wordt cumulatief weergegeven (de waarde op dag x wordt opgeteld bij het totaal over alle voorafgaande dagen).



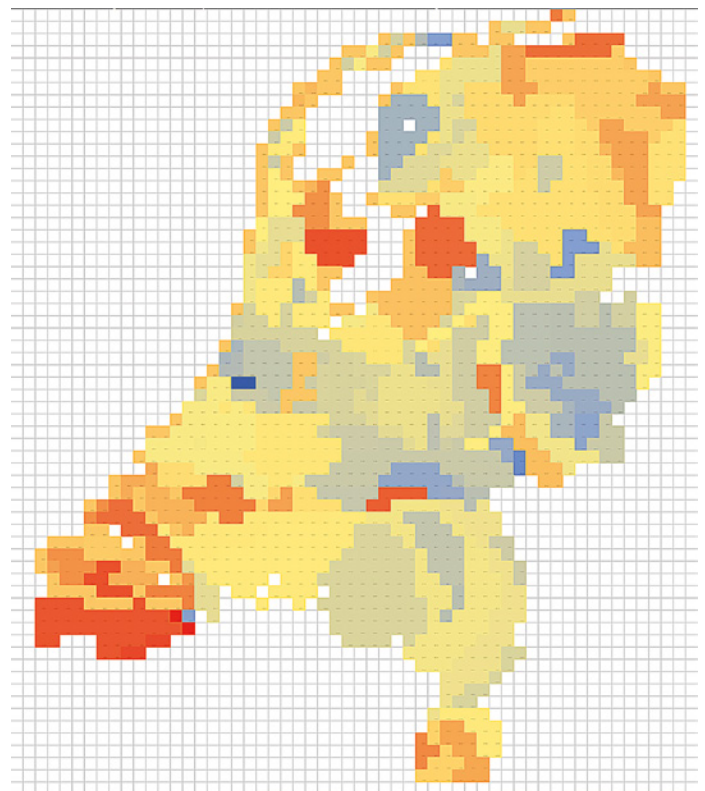
5. Results of a G-test of the change in of the silver Y in the last 15 years, compared with the previous 15 year period. The test is based on the number of specimens and the number of collection events (in the relevant period of the year) per landscape and period (Yates' correction was applied; if the number of collection events in either period was  $\leq 10$ , G was set to zero). Shades of light to dark green indicate increase (G: 11 to 34,849), shades of yellow to dark red mean decrease (G: -4 to -57,307).

5. Resultaten van een G-test op de af- of toename van gamma in de laatste 15 jaar, vergeleken met de 15 jaar daarvoor. De test is gebaseerd op het aantal waargenomen exemplaren en het aantal collection events (in de tijd van het jaar dat gamma überhaupt waargenomen kan worden) per landschap en periode. (Met Yates' correctie; indien het aantal collection events  $\leq 10$  was werd G op nul gezet). Tinten van licht- naar donkergroen duiden een toename aan (G: 11 tot 34,849), tinten van geel tot donkerrood een afname (G: -4 tot -57,307).

## Regional patterns in decline

In order to understand the long-term decline of the silver Y, regional differences were investigated. To this end a digitalised version was used of a map published in the atlas of the Netherlands (Atlas van Nederland 2014). The particular map, accessible on the internet (<http://avn.geo.uu.nl/16landschap/04/04.html>) divides the country in 167 landscapes, classified in 19 landscape groups. For technical reasons it is not possible to reproduce this map, but the data obtained in the calculations were translated into hour squares, defined as 5x5 km squares based on the national grid.

A G-test was executed to compare the abundance per landscape of the silver Y in the periods 1985-1999 and 2000-2014 (Sokal & Rohlf 1996). The results are shown in figure 5 with shades of yellow to red reflecting significant decline, while shades of green reflect increase. It is immediately clear that the decline is concentrated in specific regions. Repeating the analysis on the 19 landscape groups demonstrates that the decline is deepest in the dunes, the urban landscapes (which can be understood more or less as the conurbation of Western Holland), the river valley landscapes (large parts of the provinces of Drenthe and adjacent Friesland and Groningen, western Overijssel and the southern half of Noord-Brabant). This



6. Density distribution per landscape of the silver Y in The Netherlands, ranging from relatively scarce (deep blue) to relatively abundant (deep red). The abundance is essentially based on the number of specimens per collection event in the last 30 years, but specimen numbers observed are weighted more for more recent observation years. See Ellis et al. (2013) for details.

6. De verdeling van de talrijkheid over de landschappen van de gamma-uil over Nederland, verlopend van relatief schaars (donkerblauw) tot relatief zeer talrijk (donkerrood). De talrijkheid is gebaseerd op het aantal exemplaren per collection event tijdens de laatste 30 jaar, met dien verstande dat aantallen exemplaren zwaarder wegen naarmate de waarneming recenter is. Zie Ellis et al. (2013) voor details.

is followed by a series of landscape groups that are much less affected, including the middelhoge zandgronden ('middle-high sands', mainly around the city of Hengelo). The only landscape group with signs of increase practically coincides with Zeeuws Vlaanderen, although, as shown in figure 5, several more local foci of increase exist.

## Congestion and immigration

The distribution, in terms of local abundance per landscape, of the silver Y in the Netherlands is far from homogeneous (figure 6). The species is strikingly numerous in the province of Zeeland and adjacent Zuid-Holland, the region West-Friesland, around the cities of Enkhuizen and Hoorn, and in the north-eastern corner of the country. This pattern fits well with that displayed by several other migrants, most notably the hummingbird hawk-moth (*Macroglossum stellatarum* Linnaeus). Somehow these moths, arriving from the south, seem to 'hesitate' when confronted with large bodies of water. This translates into high abundances south of these major water bodies. Especially interesting is the landscape of Maaskant, a small area between 's Hertogenbosch and the river Meuse, which runs from east to west at that point. Apparently, even such a rela-

**Table 1.** Stepwise regression of the daily anomaly of the weather variables (weather station De Bilt, against the 30-year average) on the anomaly in daily species values of figure 4, executed with the programme DataDesk. Data were provided by KNMI. The wind vector was calculated as follows 360 = north, 90 = east, 180 = south, 270 = west, 0 = windless / variable. F-ratio of the regression = 45.6, R<sup>2</sup> (adjusted) = 42.4%.

**Tabel 1.** Stapsgewijze regressie van de dagelijkse afwijking van de weer-variabelen in de Bilt (tegenover het 30-jarig gemiddelde) op de anomalie die samengevat is in figuur 4, uitgevoerd met het programma DataDesk. De data zijn afkomstig van het KNMI. Met betrekking tot de windrichting geldt: 360 = noord, 90 = oost, 180 = zuid, 270 = west, 0 = windstil/variabel. F-ratio van de regressie 45.6, R<sup>2</sup> (gecorrigeerd) 42.4%.

Variable	Coefficient	SE (coefficient)	t-ratio	P-value
Maximum temperature	0.024639	0.0021	11.8	≤ 0.0001
Vector mean wind direction	-3.12310e-3	0.0007	-4.46	≤ 0.0001
Percentage of maximum potential sunshine duration	-0.014824	0.0035	-4.18	≤ 0.0001
Daily precipitation amount	-4.81194e-3	0.0013	-3.73	0.0002
Potential evapotranspiration	0.038825	0.0142	2.73	0.0066
Maximum visibility	-0.022415	0.0084	-2.67	0.0079

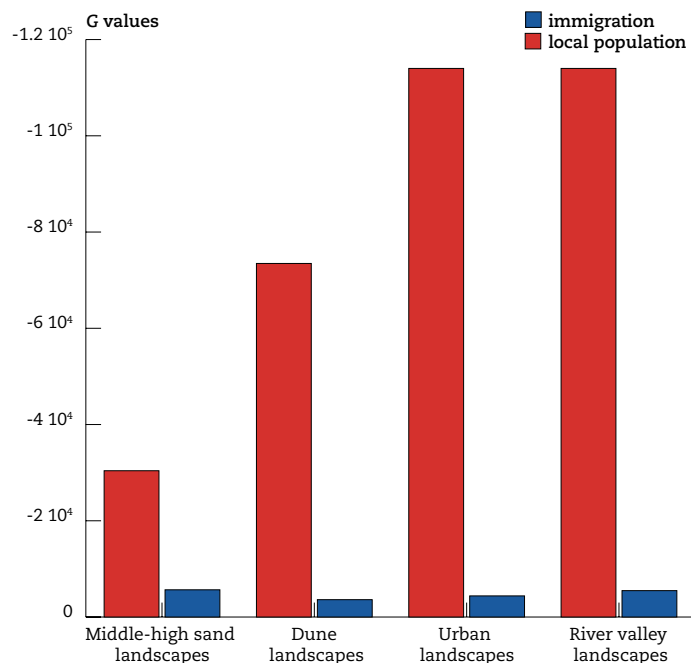
tively narrow strip of water is sufficient to cause stagnation.

On the other hand, most silver Y's on their spring journey have to cross the Mediterranean Sea, and the North Sea apparently is not an impregnable barrier either.

Sparks *et al.* (2007) found a significant correlation between the numbers of migrants, silver Y included, that annually arrive in the south of England, and the rising yearly temperatures. This can indicate an increase in supply from far southern Europe with rising temperatures. But it is also conceivable that higher temperatures reduce the 'reluctance' of the moth to cross the North Sea. Not quite improbable, because a similar effect would ease the crossing of the Mediterranean Sea. A possible mechanism could be that at higher temperatures the moths might be flying in higher air layers.

This begs the question if the decline of the silver Y in the Netherlands is the outcome of reduced immigration, or derives from a reduced success of the local, established population. Moreover, a possible reduced immigration can stem from a reduced supply from the south, but could also be caused by an increase of moths that, coming from the south, do not touch down but continue their flight and cross the sea.

As can be seen in figure 3, the flight diagram of the silver Y shows two waves. The first one must, at least for the largest part, be interpreted as associated with the immigration, the second one with the development of the local population. A first country-wide calculation, comparing the situation before and after day number 174 (June 23rd), showed a decline in both periods, but the degree of decline, in terms of G-value, was a



**7.** Results of a G-test as described under figure 5 for the four most important landscape groups, separately on silver Y-moths recorded before June 23rd (presumed immigrants, red) and those recorded after date (presumed locally born, blue)

**7.** Resultaat van een G-toets als beschreven in figuur 5 voor de vier belangrijkste landschapsgroepen, enerzijds voor de imago's van de gamma-uil waargenomen vóór 23 juni (veronderstelde immigranten, rood) anderzijds voor de na die datum waargenomen vlinders (veronderstelde gevestigde dieren, blauw).



**8.** Distribution of the deposition of potential acid (nitrogen and sulphur compounds) in 2015, with gradient from light to dark indicating increasing deposition levels. Map derived from the 'Large scale concentration and deposition maps' of the RIVM, (<http://geodata.rivm.nl/gcn/>)

**8.** Verdeling van de depositie van potentieel zuur (stikstof- en zwavelverbindingen) in 2015, waarbij de gradiënt van licht naar donker toenemende depositieniveaus weergeeft. Kaart ontleend aan de 'Grootschalige concentratie en depositiekaarten' van het RIVM (<http://geodata.rivm.nl/gcn/>)

twentyfold higher in the second period (G 46.699 and 877.492 respectively).

To try and disentangle the decline in immigration and local success, another G-test was performed per landscape group; figure 7 shows the results for the four most relevant landscape groups. The result shows in all cases a relatively weak decline in the immigration concomitant with a much stronger decline in the established populations, suggesting that the decline of the silver Y should be largely explained by a reduced quality of the habitat of the Netherlands. One still could assume that the decline of the established population would be caused by a reduced immigration input. However, this seems unlikely because in the middle-high sands immigration has declined to a similar degree as in the other three landscape groups, while the decline in the established population there is much less strong. Some of the congestion zones show a clear increase in numbers, in contrast to the general trend. In five of the seven landscapes with sufficient data in the immigration period there was a significant increase both in the number of immigrants and in the size of the established population.

## Conclusions

The first section of this study showed that adult mortality of the silver Y can be considerable, and is largely determined by the daily weather. Long-term changes in the weather pattern therefore are expected to have strong effects, although precise predictions are difficult to make.

Given the small size of the Netherlands as a country, weather may be considered a global phenomenon. The fact that the decline of the established population contrariwise shows a strong geographical component means that weather conditions, or global change, are an unlikely cause. The most probable candidate of this regionally different decline lies in the distribution of the deposition of chemical compounds, leading to larval mortality either directly through toxicity or indirectly by reducing the food quality. In fact, Wallis de Vries (2013) found that high nitrogen deposits are strongly deleterious to the local Lepidoptera fauna; see also Dise (2011), Fox *et al.* (2014), Throop & Lerdaun (2004), Wallis de Vries & Van Swaay (2006). The congruence between the pattern of decline shown in figure 5 and the

deposition map in figure 8 is obvious. A more definite answer of course will have to come from a point to point comparison of the data behind figure 5 and those behind this or a similar deposition map.

For the moment the decline of the silver Y can be attributed to reduced immigration only to a limited extent. However, this is expected to change in the future. Larvae of the silver Y need lush vegetation for their development. One of the most explicit predictions of the global change scenario is a strong drying of the circum-Mediterranean area (Giorgi & Lionello 2008). This certainly will reduce the carrying capacity of that region for the silver Y and will be responsible for a diminished immigration further north.

In the long run, the fate of the silver Y will be decided in the south. It is conceivable that the silver Y might adapt to new opportunities; but it seems highly improbable that the speed of its evolutionary change will match the pace of climate change. For the present, regional, persistent larval mortality due to pollution, and the erratic ups and downs in adult survival coupled with weather conditions shape the abundance of our still commonest moth.

## Postscriptum

Not all data for 2015 are available as yet (mid-December, 2015), but it is possible to make a reasonable prediction of the abundance of the silver Y in this year. That amounts to an annual abundance of 813. This value is almost double the value of 2014, yet close to the value that is predicted by the regression line of figure 2.

## Acknowledgements

Over 3800 observers have at any moment contributed to the information in Noctua about the silver Y – either directly, through reports or papers, or through the internet portals 'Waarneming.nl' or 'Telmeel.nl'. Without this huge body of information this paper could not have been written. I am grateful to Ties Huigens (Dutch Butterfly Conservation) for critically reading the manuscript of this paper.

## References

- Allan E & Crawley MJ 2011. Contrasting effects of insect and molluscan herbivores on plant diversity in a long-term field experiment. *Ecology Letters* 14: 1246-1253.
- Baker RR 1978. The evolutionary ecology of animal migration. Holmes & Meyer.
- Chapman JW, Bell JR, Burgin LE, Reynolds DR, Pettersson LB, Hill JK, Bonsall MB & Thomas JA 2012. Seasonal migration to high latitudes results in major reproductive benefits in an insect. *Proceedings of the National Academy of Sciences of the United States of America* 109: 14924-14929.
- Chapman JW, Lim KS & Reynolds DR 2013. The significance of midsummer movements of *Autographa gamma*: implications for a mechanistic understanding of orientation behavior in a migrant moth. *Current Zoology* 59: 360-370.
- Chapman JW, Reynolds DR, Mouritsen H, Hill JK, Riley JR, Sivell D, Smith AD & Woiwod I 2008. Wind selection and drift compensation optimize migratory pathways in a high-flying moth. *Current Biology* 18: 514-518.
- Chumakov MA & Kuznetsova TL 2014. AgroAtlas, interactive agricultural ecological atlas of Russia and neighboring countries: economic plants and their diseases, pests and weeds. Available at [http://www.agroatlas.ru/en/content/pests/Autographa\\_gamma/](http://www.agroatlas.ru/en/content/pests/Autographa_gamma/). [Accessed 8.iii.2015]
- Crawley MJ 1989. Insect herbivores and plant population dynamics. *Annual Review of Entomology* 34: 531-564.
- De Vos R 1992. Handleiding bij het waarnemen en registreren van Nederlandse trekvlinders. *Trekvlinderregistratie Nederland*.
- Dingle H (ed) 1978. *Evolution of insect migration and diapause*. Springer Verlag.
- Dise NB 2011. Nitrogen as a threat to European terrestrial biodiversity. In: *The European nitrogen assessment* (Sutton MA, Howard CM, Erisman JW, Billen G, Bleeker A, Grennfelt P, Van Grinsven H & Grizzetti B eds): 463-494. Cambridge University Press.
- Ellis W, Groenendijk D, Groenendijk M, Huigens T, Jansen M, Van der Meulen J, Van Nieuwerkerken E & De Vos R 2013. *Nachtvlinders belicht: dynamisch, belangrijk, bedreigd*. De Vlinderstichting.
- Fox R, Parsons MS, Chapman JW, Woiwod IP, Warren MS & Brooks DR 2013. The state of Britain's larger moths 2013. *Butterfly Conservation and Rothamsted Research*.
- Fox R, Oliver TH, Harrower C, Parsons MS, Thomas CD & Roy DB 2014. Long-term changes to the frequency of occurrence of British moths are consistent with opposing and synergistic effects of climate and land-use changes. *Journal of Applied Ecology* 51: 949-957.
- Giorgi F & Lionello P 2008. Climate change projections for the Mediterranean region. *Global and Planetary Change* 63: 90-104.
- Hill JK & Gatehouse AG 1992. Genetic control of the pre-reproductive period in *Autographa gamma* (L.) (silver Y moth) (Lepidoptera: Noctuidae). *Heredity* 69: 458-464.
- Huigens T & Mol M 2013. *Nachtvlinders als bestuivers*. *Vlinders* 4: 14-17.
- Johnson CG 1969. *Migration and dispersal of insects by flight*. Methuen.
- Jooris R & Faquet M 1977. Over een 'zomervreetplaats' van vleermuizen in een ijskelder. *De Levende Natuur* 80: 274-275.
- Kephart S, Reynolds RJ, Rutter MT, Fenster CB & Dudash MR 2006. Pollination and seed predation by moths on *Silene* and allied Caryophyllaceae: evaluating a model

- system to study the evolution of mutualisms. *New Phytologist* 169: 667-680.
- Kothanen PM & Rosenthal JP 2000. Tolerating herbivory: does the plant care if the herbivore has a backbone? *Evolutionary Ecology* 14: 537-549.
- Kuper J, Van Duinen G-J, Nijssen M, Geertsma M & Esselink H 2000. Is the decline of the red-backed shrike (*Lanius collurio*) in the Dutch coastal dune area caused by a decrease in insect diversity? *Ring* 22: 11-25.
- Kwak MJ 2012. Generalisten en specialisten op duifkruid: wie bestuift wanneer het beste? *Entomologische Berichten* 72: 94-102.
- Lempke BJ 1972. De Nederlandse trekvlinders. 2e druk. Bibliotheek van de Koninklijke Nederlandse Natuurhistorische Vereniging 12: 1-151.
- Louda SM & Rodman JE 1996. Insect herbivory as a major factor in the shade distribution of a native crucifer (*Cardamine cordifolia* A. Gray, bittercress). *Journal of Ecology* 84: 229-237.
- MacGregor CJ, Pocock MOJ, Fox R & Evans DM 2014. Pollination by nocturnal Lepidoptera, and the effects of light pollution: a review. *Ecological Entomology* 40: 187-198.
- Root RB 1996. Herbivore pressure on goldenrods (*Solidago altissima*): its variation and cumulative effects. *Ecology* 77: 1074-1087.
- Schoonhoven L, Biesmeijer K, Oostermeijer G & Roos R 2014. Niet zonder elkaar: bloemen en insecten. *Natuurmedia*.
- Sexton R 2014. The moth pollinators of greater butterfly orchids *Platanthera chlorantha* in central Scotland. *Journal of the Hardy Orchid Society* 11: 14-22.
- Skals N, Plepys D & Löstedt C 2003. Foraging and mate-finding in the silver Y moth, *Autographa gamma* (Lepidoptera: Noctuidae) under the risk of predation. *Oikos* 102: 351-357.
- Sokal RH & Rohlf FJ 1996. *Biometry: the principles and practice of statistics in biological research*. 3rd edition. Freeman.
- Sparks TM, Dennis RLH, Croxton PJ & Cade M 2007. Increased migration of Lepidoptera linked to climate change. *European Journal of Entomology* 104: 139-143.
- Stasny M & Agrawal AA 2014. Love thy neighbour? Reciprocal impacts between plant community structure and insect herbivory in co-occurring Asteraceae. *Ecology* 95: 2905-2914.
- Stinner RE, Barfield CS & Stimac JL 1983. Dispersal and movement of insect pests. *Annual Review of Entomology* 28: 319-335.
- Throop HL & Lerdau MT 2004. Effects of nitrogen deposition on insect herbivory: implications for community and ecosystem processes. *Ecosystems* 7: 109-133.
- Van der Meulen J, De Vos R & Vliegenthart A 2015. Nederlands jubileum: 75 jaar trekvlinderonderzoek. *Vlinders* 2015(4): 12-15.
- Vervloet A 2002. Long-distance migration in butterflies and moths: a cross-species review. MSc thesis, University of Utrecht.
- Wallis de Vries MF 2013. Hoe stikstof de vlinders laat stikken. *Entomologische Berichten* 73: 158-163.
- Wallis de Vries MF & Van Swaay CAM 2006. Global warming and excess nitrogen may induce butterfly decline by microclimatic cooling. *Global Change Biology* 12: 1620-1626.
- Williams CB 1930. The migration of butterflies. *Biological Monographs and Manuals* 9.
- Williams CB 1957. Insect migration. *Annual Review of Entomology* 2: 163-180.
- Winkler K, Wäckers FL, Buitrago L & Van Lenteren JC 2005. Herbivores and their parasitoids show differences in abundance on eight different nectar producing plants. *Proceedings of the Netherlands Entomological Society Meeting* 16: 125-130.

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## Samenvatting

### Wat is er aan de hand met de gamma-uil, *Autographa gamma*?

De gamma-uil, de talrijkste nachtvlinder van Nederland, met een navenant belangrijke ecosysteemfunctie, is in de laatste dertig jaar op landelijk niveau 56% in aantal teruggelopen. De achtergronden kunnen zijn mortaliteit van de volwassen vlinders, mortaliteit van de rupsen, en teruglopende immigratie. Weersomstandigheden, zoals die optraden in 2014, kunnen een sterke mortaliteit van volwassen vlinders veroorzaken. Op lokaal niveau zijn er grote verschillen in de mate van achteruitgang: in de duinen, de randstad en de beekdallandschappen is de achteruitgang veel sterker dan elders. De achteruitgang treedt op zowel in de immigratie van deze trekvlinder als, in nog veel sterkere mate, de ontwikkeling van de lokale populatie later in het jaar. Zoals wel meer trekvlindersoorten vertoont de gamma-uil een duidelijke opstuwung aan de zuidkant van brede watermassa's. De teruglopende immigratie kan daarom het gevolg zijn van een verminderde aanvoer van uit het zuiden, maar het is eveneens denkbaar dat hogere temperaturen dit stuwings-effect verminderen, waardoor een relatief groter aantal de Noordzee oversteekt. Verondersteld wordt dat de achteruitgang van de lokale populatie samenhangt met de depositie van schadelijke stoffen. Verondersteld wordt eveneens dat in de toekomst de overlevingskansen van de soort in het Middellandse Zeegebied door verdroging zullen verminderen, waardoor de aanvoer vanuit het zuiden zal stagneren.



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