



Lost and found: 160 years of Lepidoptera observations in Wuppertal (Germany)

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Abstract

In the light of the current discussion on reduced insect biomass and species decline, we would like to draw attention to the work of amateur entomologists who have been observing the moth and butterfly fauna for decades. Actually, the recording of butterflies and moths has a long tradition in Wuppertal and its surroundings (Germany, North Rhine-Westphalia, Bergisches Land). Therefore, we have access to rather detailed data of the local macrolepidoptera fauna collected over the last 160 years and are able to comment on the trends of moth and butterfly populations during this rather long period. We review historical and current data and provide a comprehensive abundance list of all macrolepidoptera species observed in the study region. We found that, from the mid-twentieth century onwards, the species richness of butterfly and moths species decreased considerably. In terms of the number of species evaluated (537), we see that 27% decreased within the last 160 years while 15% have already been lost. Additionally, 24% are apparently stable at a low level. Particularly affected are highly specialised species of heath, moor, grassland, scrub, coppice and orchard habitats. However, 15% of the evaluated species are observed more frequently. Some of these newly colonised the study region (2.4%). Since Wuppertal is a city that profited from the industrial revolution from the middle of the nineteenth century onwards, we think that our results could serve as a representative example of the loss of species richness due to industrialisation, urbanisation, intensive agriculture and forestry.

Implications for insect conservation If we intend to increase species richness of butterflies and moths again, the focus must be on protecting, restoring and promoting low-nutrient open landscape habitats rather than forests.

Keywords Insect decline · Agriculture · Forestry · Moth · Butterfly

Introduction

In recent years there have been a number of scientifically recognised studies in particular on the decline of butterfly populations, e.g. Maes and van Dyck (2001), van Swaay et al. (2006), van Dyck et al. (2009), Melero et al. (2016), Fartmann (2017), Schmitt and Habel (2018), and Habel et al. (2019a, 2019b). A decline in many moth species has been shown as well, e.g. Conrad et al. (2006), Franzén and Johannesson (2007), Groenendijk and Ellis (2011), Fox et al. (2011, 2014), and Dennis et al. (2019). The ‘Krefeld study’ on the loss of biomass in flying insects received particular public attention (Hallmann et al. 2017). These findings fueled a scientific debate on whether or not, or to which

extent, there is a global negative trend in insect populations (Sánchez-Bayo and Wyckhuys 2019; Crossley et al. 2020). There are indications that freshwater insect populations are stable or recovering (van Klink et al. 2020a) while terrestrial insect populations are declining (Seibold et al. 2019). Findings on freshwater insect populations are still intensively discussed (Desquilbet et al. 2020; van Klink et al. 2020b; Jähnig et al. 2020).

Historical data of butterfly and, especially, moth abundance is fragmented and often focussed on high-quality butterfly habitats or rare species. In this article, we describe and interpret changes in the abundance of macrolepidoptera in Wuppertal (Germany, North Rhine-Westphalia) and the surrounding area over the past 160 years. Thanks to a long tradition of mapping butterflies and moths in the study region—which has never possessed an outstanding habitat for butterflies and moths—we have access to data from the mid-nineteenth century until today, collected by amateur entomologists. The study region experienced a massive

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economic upturn from the middle of the nineteenth century due to the industrial revolution. Therefore, we think that our study can serve as a representative example of the loss of species richness due to industrialization, urbanization, intensive agriculture and forestry.

We begin by collecting and revising historical data, which started with an article on butterfly and moth abundance in 1863 (Weymer 1863). Subsequently, we translate textual data given in historical literature into numerical data in order to make historical sources comparable. Changes in butterfly and moth abundances are a long-term phenomenon, irrespective of annual variation seen in many species (Kühn et al. 2017). Thus, we define a ‘reference period’ covering 19 years (1990 to 2008, the period of our first study on that issue) and compare its species abundance with two historical periods (1863–1908 and 1920–1989). Based on these results, we identify ‘reference species’, which are neither very common nor rare and apparently react robustly to environmental changes. These reference species serve as ‘internal standards’ for normalisation of later datasets. Maes and van Swaay (1997) have already described a similar approach for compiling national Red Lists on butterflies in Flanders and in The Netherlands. We apply that approach to the latest dataset (2009–2019) and deliver the complete data as a Supplement. Based on these data, we subdivide the species into four trend categories: decreasing, constantly rare, constantly common and increasing. Having categorised them, we relate the species and their typical habitats using the guideline published by Hock et al. (1997). The correlation clearly shows which species are under pressure due to habitat destruction. We are also able to identify species that benefit from increasing forestry, industrial brownfield sites and climate change.

Methods

Study region

The study region included the following cities in North-Rhine Westphalia (Germany): Wuppertal, Solingen, Remscheid, Haan (Rheinland), Hilden and Erkrath (in total: 440 km²). Our data can be found online (<http://nrw.schmetterlinge-bw.de/>) with maps and information on the different observation places (6 km × 6 km grid) for each macrolepidoptera species.

Geology

The study region is divided in two major landscapes: a sub-mountainous area with the cities Wuppertal, Solingen, Remscheid and Haan and the Rhine Heath Terrace with the cities Hilden and Erkrath. The area of the three cities Wuppertal, Solingen and Remscheid can be attributed to the large

natural landscape of the Süderbergland, the north-western edge of the Rhenish Massive. Overall, the sub-mountainous area is characterised by largely lime-free greywacke, slates and sandstones, which were formed in the Devonian. From southwest to northeast, a limestone range stretches through the north of Wuppertal. However, settlements, infrastructure and forests cover most of the limestone area. Wuppertal itself is a medium-size city with currently about 362,000 inhabitants, (wuppertal.de) lying in a broad valley formed by the river Wupper. The south-eastern area with its smaller neighbour cities Remscheid and Solingen forms a plateau with heights up to about 379 m, intersected by deep valleys with creeks. The northern area is hilly and reaches 322 m in the north-eastern part. Rhine sediments formed the landscape known as the Rhine Heath Terrace (altitudes about 50 m) with the cities Erkrath and Hilden. The sediments were deposited during the penultimate ice age and were subsequently covered by drifting sands (geoportal.nrw).

Climate

The surroundings of Wuppertal lie on the edge of Atlantic climate influences. This oceanic influence is characterised by precipitation distributed throughout the year with a mean value (1981–2010) of 1175 mm per year for Wuppertal and 798 mm for Düsseldorf. The temperatures are balanced with a mean value (1981–2010) of 10.1 °C for Wuppertal and 10.7 °C for Düsseldorf (Deutscher Wetterdienst, 2019). This means that extended periods of extreme winter cold or summer heat are rare.

Current vegetation

In general, the vegetation can be divided in two main areas: mainly wet forests and intensive agriculture in the sub mountainous region and heathland with pine forests and intensive agriculture on the Rhine Heath Terrace. About half of the area consists of settlements, infrastructure and commercial areas (statistikatlas.nrw.de). The proportion of woodland in the study region is between 25 and 30% for Wuppertal, Solingen and Remscheid and between 16 and 24% for Haan, Hilden and Erkrath. The proportion of softwood to hardwood is about 1/1 (wald-und-holz.nrw.de). Many of the small creeks and their immediate surroundings are nature conservation areas. The Burgholz Forest, the Marscheider Forest and the valleys of the creeks Gelppe and Morsbach have to be mentioned here. While the steep slopes of the Wupper and its tributaries are almost completely afforested, the plateaus are traditionally used for agriculture. Intensive agriculture contributes between 13 and 23% (Wuppertal, Solingen, Remscheid and Hilden) and between 32 and 36% (Haan and Erkrath) to the landscape. As for the Rhine Heath Terrace only small parts (Hildener Heide, Ohligser Heide)

are actively conserved as open heathland. Furthermore, there are a number of brownfield sites like former railway areas (e.g. the railroad yard in Wuppertal-Vohwinkel), quarries (limestone-quarries in Haan-Gruiten) and landfills (e.g. the re-natured Eskesberg landfill in Wuppertal).

Historical vegetation

In the first half of the nineteenth century, the study region was described as ‘woodless’ and ‘covered with heather’ (Sundermann 1979). In the late nineteenth century, Wuppertal and its neighbour cities Remscheid and Solingen were still almost free of forests. Pögt (1998) wrote in his ‘historical views of Wuppertal from the 18th and 19th centuries’: ‘... trees were limited to avenues, parks and orchards. Since the vegetation on hills on both sides of the Wupper valley had been cut down completely and no one reforested them, they were only overgrown with shrubbery’ (translated). People performed woodland coppicing in order to produce charcoal for heating purposes. The Rhine heath terrace, including the Hildener Heide area was an open landscape in the nineteenth century as well. The elevations protruding from the plain were ‘such arid places that nothing else grew there but *Calluna vulgaris*, *Erica tetralix* and *Sarothamnus scoparius*’ (translated from Weymer, 1863).

Data on macrolepidoptera

Species nomenclature is according to Gaedike et al. (2017). Additionally, we supply the species number according to Karsholt and Razowski (1996) in the Supplement.

Current data

From 1990 onwards, we observed moths and butterflies and collected the data in an electronic database (first custom-made, later InsectIS, insectIS.de). In 2005 we published a monograph of the Scientific Association Wuppertal with a first comprehensive list of all macrolepidoptera that had been observed so far in the study region (Laussmann et al. 2005). Based on the data collected until 2008, we discussed the impact of landscape and climate change on the local lepidoptera fauna (Laussmann et al. 2009, 2010). Due to our activities on the internet from 2008 onwards (heidenschaft.de, nvwuppertal.de, melanargia.de), more and more people started observing butterflies and moths in the study region and delivered contributions to our database either directly via InsectIS or in form of excel lists. In the last 2 years, many observers switched to observation.org and the corresponding mobile-phone applications (ObsMapp and iObs) to easily collect and transfer data.

In order to evaluate changes in Lepidoptera populations, we defined the period between the beginnings of our

numerical data collection in 1990 to our first publication on that issue in 2009 as a reference period (19 years). Normalised for 10 years, we had 297 night and 445 day excursions. An average of 23 night excursions took place in the summer half-year (April to September), that is an excursion almost every week, and 7 night excursions in the winter half-year (October to March), that is one excursion roughly every fourth week. Accordingly, there was an average of 36 day excursions per year in the summer half-year (April to September), that is between 1 and 2 observation days per week, and 13 day observations in the winter half-year, that is 1 observation day every 2 weeks (Fig. 1).

We used UV fluorescent lights and commercial light traps for night observations. Between August and April, we additionally applied moth lures (e.g. wine-sugar solution). In order to attract clearwing moth (Sesiidae) we used commercially available pheromones from Pherobank BV (pherobank.com). Since 2005 there are two permanent observation places, one in a rural region (close to Haan) and one in an urban region (close to the centre of Wuppertal-Barmen). Here, we document the observations by inspecting house walls illuminated with UV lamps. Between 1990 and 2008 (19 years), we had a total number of 77,082 observed individuals in our database. Due to much higher observation intensity between 2009 and 2019 (11 years), there were 142,381 individuals in that period.

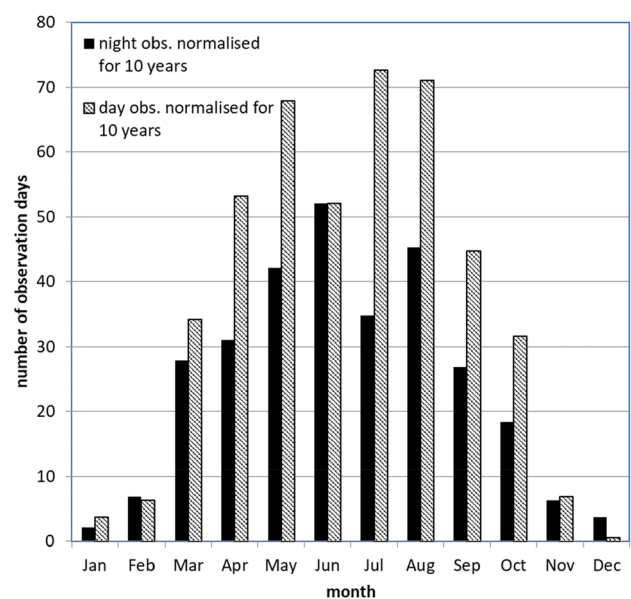


Fig. 1 Number of observation days 1990–2008 normalised for 10 years. The figure shows the observation intensity during the reference period 1990–2008. Excursions are planned observations over several hours at single places (night obs.) or transects through habitats (day obs.). Not included are stationary, permanent observation sites or single adventitious observations

Historical data

Observation and recording of butterflies and moths in the study region has always been in the hands of amateur entomologists. In the middle of the nineteenth century Weymer (1863) published a first comprehensive list of butterfly observations in today's Wuppertal area in the annual reports of the Scientific Association of Elberfeld and Barmen (founded in 1846 by Johann Carl Fuhlrott)—later the Scientific Association Wuppertal—and completed this work in 1878 (Weymer 1878). Subsequently, he published notes about the macrolepidoptera of the Hildener Heide in 1908. We owe our knowledge about the regional butterfly fauna from about 1920 onwards especially to the comprehensive work of four butterfly and moth experts, who gathered data from more than 70 private butterfly collections which originated from the Bergisches Land area. Additionally, they collected information from local publications and private observation lists (Kinkler et al. 1971, 1974, 1975, 1979, 1985, 1987, 1992). Today, the Löbbecke Museum in Düsseldorf (Germany, North Rhine-Westphalia) preserves their 'collection Bergisches Land'. Additionally, we took data from the comprehensive work 'Prodromus der Lepidopteren-Fauna der Rheinlande und Westfalens' (Stamm 1981).

Weymer (1878) often mentioned observations of moth caterpillars on their host plants. Concerning observation of adult moths, we think that Weymer used the same methods as described in e.g. 'Berge's Schmetterlingsbuch' (von Heinemann 1870). Entomologists observed moths by inspecting flowering plants during dusk and dawn or collected them at daytime at their resting places. Observers placed beer-honey bait at tree barks and inspected it using lanterns (described by Weymer 1878 as 'the new sugarplum method'). Additionally, moth were caught when entering illuminated houses or at walls near gas lanterns. From the beginning of the twentieth century, observers used gas mantle lights e.g. 500 W Petromax lanterns to attract moths. From 1968 onwards observers mainly employed blue and

UV fluorescent lights or 125–250 W mercury-vapor lamps (Kinkler et al. 1974).

Evaluation of data

Weymer documented a total number of 662 macrolepidoptera species (Weymer 1863, 1878, 1908). (Kinkler et al. 1971, 1974, 1975, 1979, 1985, 1987, 1992). described 676 species for the study region in their cumulative work, including Weymer's findings. In 2009, we reported 734 species for the last 150 years (545 species were observed in the reference period between 1990 and 2008). In order to make the data of the reference period comparable with the purely textual information provided by (Kinkler et al. 1971, 1974, 1975, 1979, 1985, 1987, 1992). and Weymer (1863, 1878, 1908), we published a translation table (Table 1, see Laussmann et al. 2009) based on consultations with senior observers and based on our own experience.

In this way, we were able to compare data from the reference period with data of historical observations. Since observation intensity increased considerably during the last years, we had to make the new data (2009–2019) comparable to that obtained in the reference period by normalisation. In order to avoid a distortion of the dataset due to strongly varying counts of very common species, we decided to normalise the dataset to counts of species that are and have been neither very common nor rare and apparently react robustly to environmental changes. This means, their abundance varied only slightly in historical data as well as during the reference period (see Supplement, species highlighted in green). These species do not show very special habitat requirements, in most cases feed as larvae on various or ubiquitous plants and are in general no r-strategists. These species can serve as 'reference species' or 'internal standards' for later observation periods. That is, even if the observation density increases or decreases or very common species show a mass propagation, normalisation of numbers of counted individuals to the sum of the observed specimens

Table 1 Translation table: from textual description to numerical data

Abundance class	Textual description	Number of observed individuals in 10 years
0	Lost, not observed	0
1	Very rare, very sparse	1–4
2	Rare, scattered, several observations	5–10
3	Not frequent, locally frequent	11–40
4	Frequent, everywhere, numerous observations	41–200
5	Very frequent	201–500
6	Common	501–1000
7	Very common	More than 1000

For example, the description 'not frequent' assigned to abundance class 3, corresponds to a mean number of 1 to 4 individuals per year (11–40 individuals within 10 years)

of these reference species gives a realistic result regarding trends in species abundance. However, prerequisites are that the methodology does not change fundamentally, that observation takes place over a sufficiently long period (e.g. 10 years) at many different places in the study region and that species counts are not selectively documented (e.g. only rare species). That is now the case with the data collected between 2009 and 2019. Concerning the above mentioned reference species, we found (normalised to 10 years) 3115 individuals in the reference period and 5754 in the period 2009–2019 (see Supplement, spreadsheet: ‘normal. factor’). That means that observation intensity nearly doubled (factor: 1.85) between 2009 and 2019 compared to the reference period. After normalisation, 17 of these species showed a slight to moderate increase and 18 showed a slight to moderate decrease in observed specimens. Therefore, we divided species counts for the period 2009–2019 by 1.85 in order to make the whole dataset comparable to the reference period.

Subsequently, we assigned species to abundance classes (see Table 1) and systematically assessed whether we see a decreasing, steady, increasing or, due to population fluctuations, no trend in the abundance of a species within the covered period of almost 160 years. On this basis, we assign species to the following six trend categories:

(1) *Single observation*. Species mentioned in one or two periods as a single or very rare observation.

(2) *Decreasing*. The abundance of those species shows a clear, continuous decline over the past 160 years of two or more abundance classes. In a few cases, Weymer (1863, 1878, 1908) did not mention a species that was described at least as ‘frequent’ by (Kinkler et al. 1971, 1974, 1975, 1979, 1985, 1987, 1992). We considered these species as decreasing if a clear decline is visible.

(3) *Constantly rare*. Species not observed very frequently, but apparently always present and still occurring in the study region. Fluctuations are possible, but we see no trend.

(4) *Constantly common*. Species frequently observed or even very common. Fluctuations are possible, but we see no trend.

(5) *Increasing*. Species showing an increasing abundance over the past 160 years of two or more classes or which entered the study region in recent years.

(6) *Not rated*. Species excluded from the evaluation, because they are not native, migratory macrolepidoptera, they have been recognised as separate species within the last 160 years or their data is uncertain or doubtful (e.g. Sesiidae and Eupitheciini species).

As a Supplement, we provide the whole dataset. In that Supplement we show the abundance classes for 1863–1908 (Weymer 1863, 1878, 1908), 1920–1989 (Kinkler et al. 1971, 1974, 1975, 1979, 1985, 1987, 1992), 1990–2008 (reference period) and 2009–2019 (recent observations) for each observed species. Additionally, we quote the original

text given in historic literature for each species (in German) and the number of observed and documented individuals during the reference period and the last 11 years.

Concerning the butterfly and moth fauna in North-Rhine Westphalia, the book ‘Praxishandbuch Schmetterlingsschutz’ (translated: ‘Practical Guide to Butterfly and Moth Conservation’, Hock et al. 1997) is most relevant. The authors compiled a list of more or less stenoeccious macrolepidoptera species that are, due to their habitat needs, very typical for certain local habitat types (so called ‘character species’, in the present paper defined as ‘specialist species’). A few species are also characteristic for more than one habitat type. In contrast to specialist species there are relatively undemanding, euryoecious species (so-called ‘ubiquists’, in the present paper defined as ‘generalist species’). For each species in the Supplement, it is described whether it is a specialist species typically found in a certain habitat or a generalist species.

Furthermore, we indicate in the Supplement whether a species is known as a ‘mountainous species’ according to Retzlaff and Seliger (2007). The authors published a list of butterfly and moth species with a distribution focus in North Rhine-Westphalia in the hilly, submountainous and mountainous regions. Finally, we comment on the data of single species if necessary.

Results

Trend categories

Up to now, lepidopterists found a total number of 804 different macrolepidoptera in the study region that appeared at least once during the last 160 years (and of which 560 species were observed between 2009 and 2019). We divided the 804 species into 6 trend categories (see Fig. 2).

While 150 species seemed to be single observations due to drifted individuals or short-term spreading (category 1), we were able to include a total number of 654 species into the evaluation (sum of trend categories 2–6). We considered the data of 537 (sum of trend categories 2–5) species to be sufficiently reliable for interpretation. We excluded not native, migratory species and species whose data are uncertain or doubtful (category 6, 117 species). Among the 147 species in category 2 (decreasing) are 80 species that have not been observed for more than 10 years (considered as ‘lost’ or even regionally extinct). For 85 species in this category the decline is very pronounced (more than 2 abundance classes), 61 of these were formerly frequently observed or even very common. A considerable number of species (131) seem to be stable at a low level (category 3: constantly rare) and 180 species are still found in higher abundance (category 4: constantly common). Furthermore,

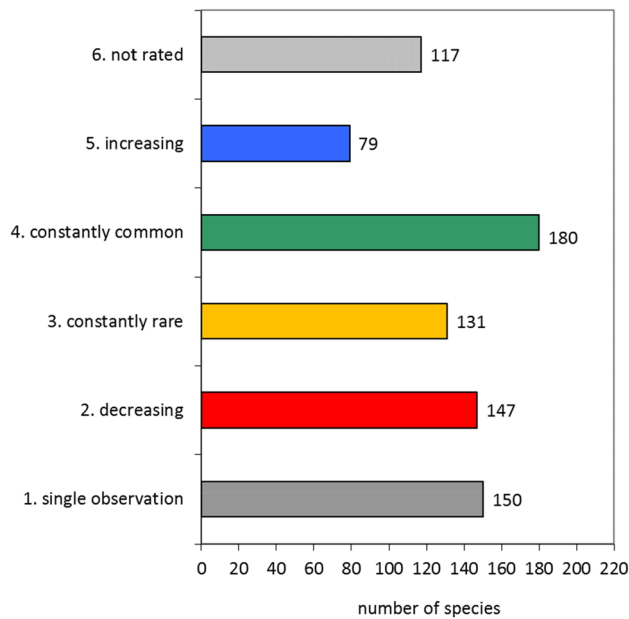


Fig. 2 Numbers of species in trend categories. Macrolepidoptera observed in the past 160 years were classified in 6 trend categories: (1) Single observation. Species mentioned in one or two periods as a single or very rare observation; (2) Decreasing. Species whose abundance show a clear, continuous decline over the past 160 years; (3) Constantly rare. Native species not observed very frequently, but apparently always occurred and still occur in the study region. (4) Constantly common. Species often observed or even very common; (5) Increasing. Species that show an increasing abundance over the past 160 years or which entered the study region in recent years; (6) Not rated. Species excluded from the evaluation, because they are not native, migratory macrolepidoptera, they have been recognised as independent species within the last 160 years or their data is uncertain or doubtful. A coloured version is available online. (Color figure online)

we observed 79 species more often than before (category 5), 48 of these increased considerably (more than 2 abundance classes). Thirteen species are completely new to the study region and are expanding their range from the west and south of Europe. Four of these have just started entering the region and are thus not yet in category 5.

In relation to the number of evaluated species (537) 27% are declining. Some of these are already lost (15%), 24% are virtually stable at low level, 34% are still frequently observed or common and 15% are more often observed. Some species newly colonised the study region (2.4%).

Correlation between population trend of species and their habitat requirements

The correlation between habitat requirements (Hock et al. 1997) and species trends over the last 160 years is of particular interest when interpreting the data. Regarding the evaluated species (537) we had 276 specialist species and

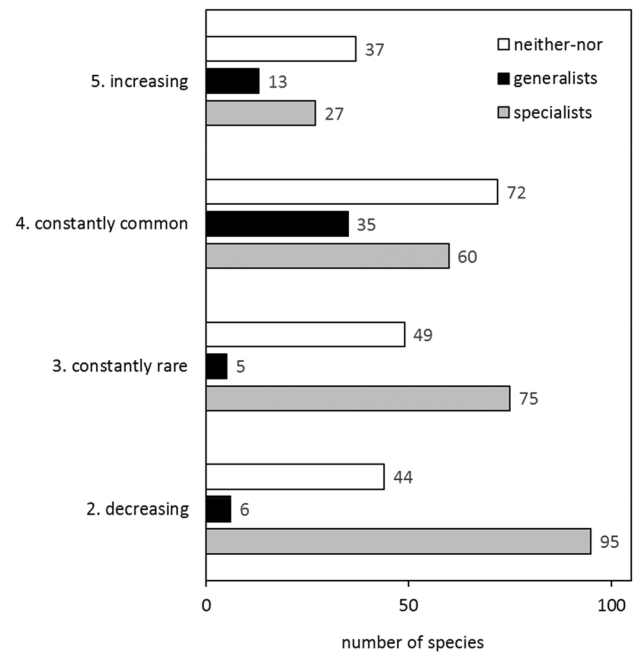


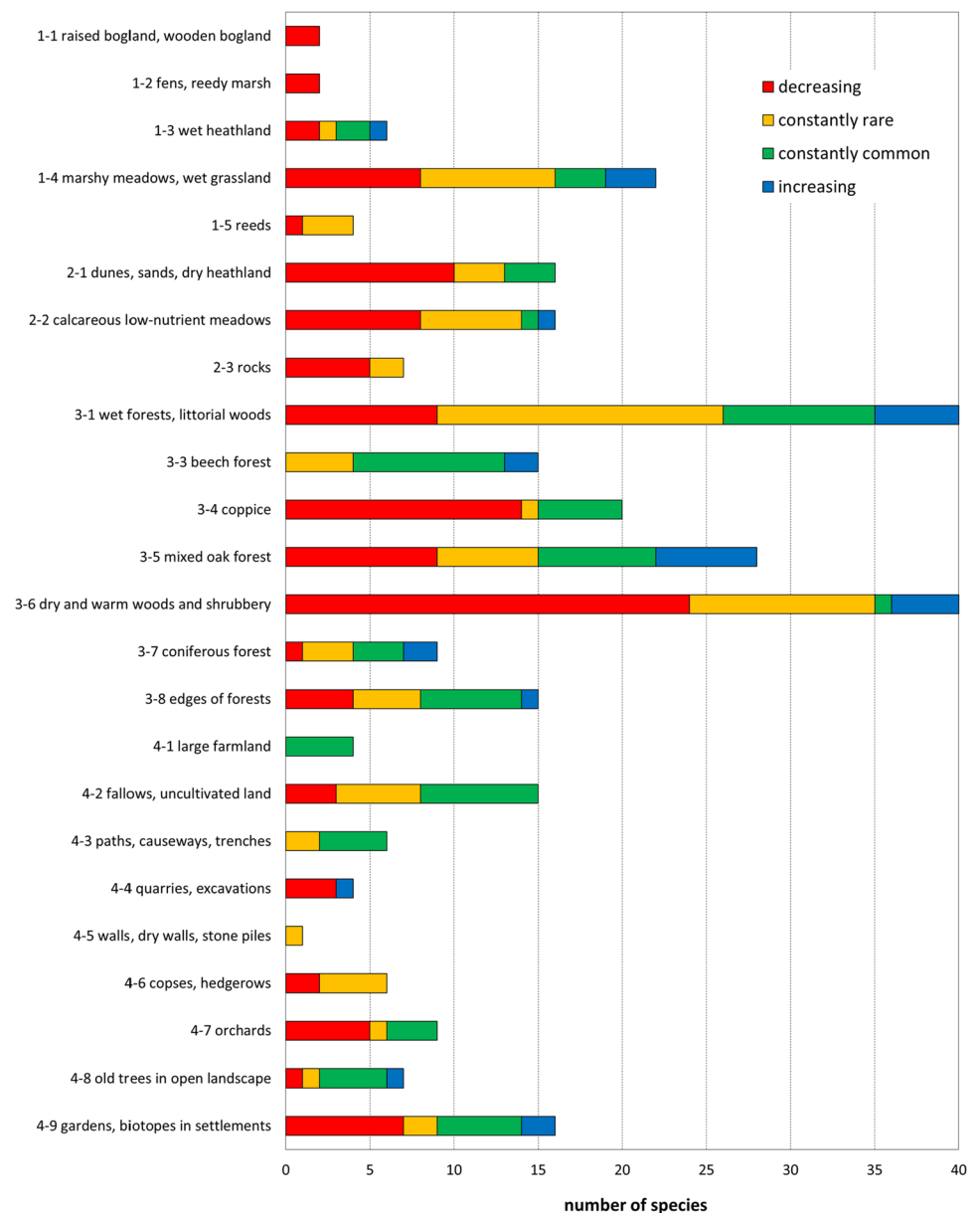
Fig. 3 Number of specialist species, generalists and species that are neither-or in the trend categories decreasing, constantly rare, constantly common and increasing. As an example: we find in the category ‘decreasing’ 95 specialist species, 6 generalists and 44 species that are neither-nor according to Hock et al. (1997). Since the classification of some generalists and specialists was ambivalent in Hock et al. (1997), we excluded 19 of 537 species from this evaluation. A χ^2 test clearly rejects the null hypothesis ($\chi^2=52.6$, d.f.=6, $P<0.001$)

78 generalists in our dataset. However, Hock et al. (1997) listed 19 species as specialist species as well as generalists. These are in particular species typical for forests and anthropogenic habitats like gardens, parks and other habitats in settlements. Since this seems to us rather ambivalent, we decided to exclude these species from this evaluation. We correlated the number of specialist species and generalists to the population trend categories (Fig. 3).

Remarkably, two thirds (66%) of the species in category ‘decreasing’ are specialist species typical for specific habitats (95 of 145). The situation is similar in category ‘constantly rare’ in which 59% (75 of 129) are specialist species. Contrastingly, in these two categories we found only six and five generalists, respectively. Most generalists appear in the category ‘constantly common’. The proportion of specialist species, generalist and neither-nor species in the category ‘increasing’ is quite similar to that found in the ‘constantly common’ category.

In order to interpret these findings, we need to correlate the habitats that the specialist species inhabit and their trend categories. Again, we excluded the 19 species that were described as specialists as well as generalists by Hock et al. (1997). Figure 4 shows that most specialist species of open,

Fig. 4 Number of specialist species in trend categories correlated to their typical habitat. Typical habitats are from Hock et al. (1997): 1–1 to 2–3: open landscape, 3–1 to 3–8 shrubbery and forest habitats, 4–1 to 4–9: more anthropogenic habitats. 52 Species are characteristic for more than 1 habitat. As an example: we had 40 species in our dataset that are specialist species for ‘3–6: dry and warm woods and shrubbery’, 24 of those are decreasing in abundance, 11 are constantly rare, one is still common and 4 are increasing in abundance. When numbers of species of open, extensively used landscape (1–1 to 2–3), coppice, dry woods and shrubbery (3–4 and 3–6), forests (3–1, 3–3, 3–5, 3–7 and 3–8) and habitats with a high anthropogenic impact (4–1 to 4–9) are merged, a χ^2 test clearly rejects the null hypothesis ($\chi^2 = 48,2$, d.f. = 9, $P < 0.001$, see Supplement, spreadsheet ‘Fig. 4’). A coloured version is available online. (Color figure online)



extensively used landscape like bogland, heaths and low-nutrient meadows are found in the category ‘decreasing’. The losses in dry and warm woods, shrubbery and coppice areas are similarly clear. These declines are particularly striking, since there are relatively few species of the categories ‘constantly common’ and ‘increasing’ in these habitat types. Apparently, other habitats are less affected by species declines. These include primarily beech forests, but also large-scale agricultural land, fallow and ruderal sites as well as habitats in settlements and gardens (except orchards).

Lost and new species in the study region

Based upon their last documented observation year, we found an accelerating speed of species loss during the

last 100 years (Fig. 5 and Supplement, spreadsheet ‘lost species’). Between 1920 and 1980, about one species was lost every 2 years. From 1980 to 2010, we lost more than one species per year. Today, about 14% of evaluated moth species (66 of 488) can be considered as ‘lost’ (not observed for at least 10 years) and the number of formerly native butterflies declined by 29% (14 of 49). For the period 2009–2019 there are already 34 additional species of the trend category ‘decreasing’ in the abundance class 1 (very rare), this means, close to lost. In contrast, we observe ‘new’ species that are entering the study region while spreading from southwest to northeast. Starting from 1970, this process is accelerating: 7 out of 13 of these species entered the study region within the last decade, i.e.

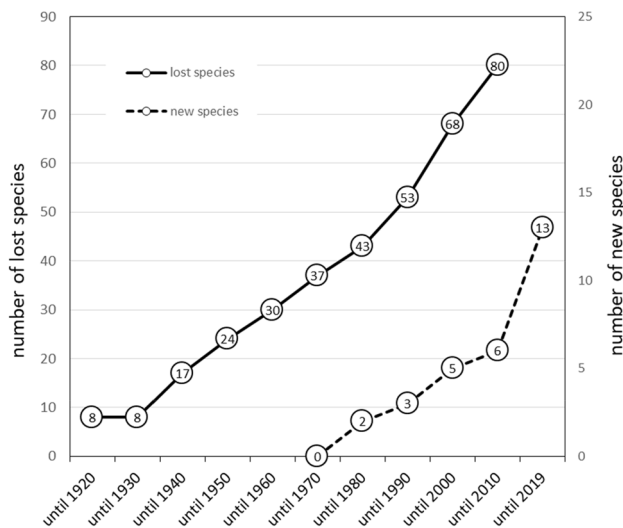


Fig. 5 Lost and found macrolepidoptera in Wuppertal. Cumulated numbers of lost (or extinct on a regional scale) macrolepidoptera species and the period of their last documented observation and cumulated numbers of new spreading macrolepidoptera species and the period of their first documented observation

during the last 6 years (Fig. 5 and Supplement, spreadsheet ‘new species’).

Correlation between population trend and climate change

For the correlation of changes in butterfly species trends and climate change, we used the CLIMBER dataset provided in Platania et al. (2020). Actually, we did not find a significant correlation between the species temperature index or the species precipitation index to the trend categories (see Supplement, spreadsheet ‘CLIMBER eval.’). However, we see that the species temperature index of the two species that lately (re)appeared in the study region (i.e. *Cupido argiades* and *Pieris manni*) show a remarkable higher species temperature than the mean species temperature index of the butterflies that are constantly common. Regarding moths, we have 46 mountainous macrolepidoptera species (according to Retzlaff and Seliger 2007) in our dataset. Twenty-nine of those are found in the trend categories 2–5 and can be evaluated. Eighteen of these species (62%) are in category ‘decreasing’, eight in category ‘consistently rare’ (28%) and only two in category ‘constantly common’. One species was newly found in the study region (*Puengeleria capreolaria*). Thus, the mountainous moth species are vanishing from the study region. In contrast, 12 moth species spread from the southern and western climatic zone (see Fig. 5 and Supplement,

spreadsheet ‘new species’). Two of these, *Agrotis puta* and *Omphaloscelis lunosa* are common species in the study region today.

Discussion

Lepidopterists have observed and documented moths and butterflies in the study region for the last 160 years. In times of dramatic landscape and climate change, we are now able to comment on the trend of species facing these environmental conditions. The authors have observed butterflies and moths in Wuppertal and its surroundings since the 1980s. Local senior lepidopterists [Helmut Kinkler, Friedhelm Nippel (*1944–1993), Günter Swoboda and Willibald Schmitz] introduced us into observation techniques for moths and butterflies. At that time, our predecessors were already of the opinion that the decline was mainly due to the modern agricultural use of open land. Especially the land consolidation measures in the 1950s and 1960s led to habitat destruction.

Taking all the data together, we get a quite clear picture of the consequences of industrialization, urbanization, intensive agriculture and forestry for species richness of macrolepidoptera. In particular, we see which species used to be common and have now disappeared for decades. However, the data cannot be as precise as we wish because there are some factors that we are not able to assess: e.g. observation techniques, especially for moths, changed from collecting caterpillars or observing moths attracted by gas mantle lights (Petromax lantern) to modern methods with UV fluorescent lights or even LED equipment. The impact of this on species counts is unknown. Our idea of a ‘translation table’ from textual descriptions to relative numbers for species abundances is an approximation since the estimation of species abundances depends on personal perception of observers. When interpreting the data, we wish to remind that today about 50% of the study region consists of settlements and infrastructure. Thus, if we talk about abundances, we only talk about places that are still lepidoptera habitats. Since these habitats are shrinking, the total amount of butterflies and moths (their total biomass) in the whole study region is likely to be decreasing as well. Pähler et al. (2019) demonstrated this decline for a number of common species in the west of Germany, including our observation area. Some species occur only at one or a few special habitats in the study region. Therefore, one can discuss if a species observed in high abundance at only one or a few places (e.g. *Ematurga atomaria*, *Adscita staites* and *Zygaena trifolii*) is common or not. Further impacts on moth observations e.g. increased light pollution are very plausible but are not easily separated from other factors (Merckx and Slade 2014; Altermatt and Ebert 2016;

Macgregor et al. 2017; Langevelde et al. 2017). Keeping this in mind, we come to the following interpretation:

What influence does the change of the landscape have on the butterfly fauna?

It is striking that Kinkler et al. (1971) already write about many butterfly species: ‘in the last ten years no observations’ or ‘until 1960 quite frequent’. Thus, the environmental changes that were decisive for species decline must have started by the 1950s and 1960s. Habel et al. (2019a) came to a similar result and, compared to our findings, Maes and van Swaay (1997) described a similar decline in butterfly species (24–29%) for Flanders and The Netherlands already at the end of the twentieth century. Obviously, observers initially recognised a reduced abundance in diurnal species. This is not only the case in Wuppertal, but in neighbouring regions like Düsseldorf, the Rhine-Erft region and Cologne (Lenz and Schulten 2005; Jelinek 2006; Hanisch 2009) as well. The authors think that the loss of species is mainly due to intensive agriculture.

At the time Weymer was living (1833–1914), the study region was an open landscape (Pogt 1998; see Lausmann et al. 2010 for historical and current images of the landscape). Since we see a massive loss of specialist species typically found in open landscapes, we speculate that the main cause of the species decline is the land consolidation in the late 1950s followed by intensive agriculture and afforestation. This development led to the destruction of many edge and fringe structures as well as scrub areas, which had to make way for large agricultural land cultivated by machinery. Hills were afforested mainly with monocultures of common beech (*Fagus sylvatica*) or spruce species (*Picea spec.*). Thus, only ‘forest species’ that rarely visit flowering plants and rather euryoecious species are less affected by species decline.

Especially, many butterfly and moth species typical for low-nutrient grassland and shrubbery are under pressure. With the loss of meagre, flower-rich fringes and meadows, some well-known butterflies were lost. *Boloria euphrosyne*, *Boloria selene*, *Euphydryas aurinia*, *Melitaea athalia* and *Melanargia galathea*, which were formerly frequently observed or very common completely disappeared already in the second half of the twentieth century. In particular, the loss of the rather euryoecious *M. galathea* is alarming. Obviously, there is a lack of flowering plants such as knapweeds (*Centaurea*), widow flowers (*Knautia*) and thistles (*Carduus*). Missing nectar resources have an enormous impact on the survival of butterflies (Lebeau et al. 2016). The loss of butterfly species typically found on open grassland and heath is a widespread phenomenon (Fartmann 2017; van Swaay et al. 2019). Recently, the negative impact of intensive farming has been documented by analysis of long-term

observations for south-western Germany as well (Schmitt and Habel 2018; Habel et al. 2019a, 2019b; Seibold et al. 2019). In the UK the decline of grassland butterflies is quite similar (Fox et al. 2015) and concerning Mediterranean habitat specialists, a negative effect of increasing temperature and positive effect of grassland availability on butterfly species richness has been reported (Stefanescu et al. 2011). Similarly, Fox et al. (2014) wrote that monophagous moths that feed on plant species on high light intensity and low-fertility soils decrease most strongly.

Typical coppice and shrub species are missing today. These include, in particular, *Satyrrium ilicis*, *Callophrys rubi*, *Eriogaster lanestris*, *Malacosoma neustria*, *Lasiocampa quercus*, *Gastropacha quercifolia*, *Euproctis chrysoorrhoea* and *Apeira syringaria*. Even species spread in the ‘cultural landscape’ such as *Clostera pigra*, *Cerura vinula* and *Furcula bifida* disappeared. This may be partly due to the loss of hedgerows along small agricultural parcels. In the past, heath and bogland species such as *E. atomaria*, *Bupalus piniaria*, *Eulithis populata*, *Hada plebeja* and *Lycophotia porphyrea* were very common. These species are now rare, reduced to few remaining areas or already lost.

Additionally, private gardens changed as well: for many decades, the trend is away from the self-supply garden with fruit trees, currant or gooseberry bushes and vegetable beds to the easy-care garden with mostly exotic plants, which provide no nectar for native insects and no feed for their larvae. In recent years, there is additionally a trend to stone gardens without any plants. Thus, butterfly and moth species typical for orchards largely disappeared (e.g. *M. neustria*, *Odonestis pruni*, *Nymphalis polychloros*, *Abraxas grossulariata*, *Eulithis prunata*, *Eulithis mellinata*, *Diloba caeruleocephala*).

Today, there are some new brownfield site habitats. In particular, due to shutdown of railways, quarries and landfills xerothermic places have emerged. In these areas, some species find a habitat that can serve as a substitute for lost xerothermic places in open landscape. The populations of the following species are stable or developed positively: *Calophasia lunula* (on *Linaria vulgaris*), *Hadena bicurris* and *Hadena perplexa* (both on *Silene vulgaris*) and *Aetheria dysodea* (on *Lactuca serriola*). Particularly noteworthy is the high abundance of *A. dysodea* in the recent two decades. Larvae of this species were, according to Weymer (1878), formerly a pest and frequently found on *Lactuca sativa* (lettuce) in gardens in the nineteenth century. For the twentieth century Kinkler et al. (1992) mention only one single observation of this species in 1990. Today, we find *A. dysodea* as larvae at many places, even in the middle of the city, on compass plant (*L. serriola*) thriving on narrow bark strips besides streets. Interestingly, according to Schmidt (1887) and Müller (1925), this plant did not occur in the study region, whereas Stieglitz (1987, 1991) described it as ‘fairly widespread’. Although this species might always

have used *L. serriola* as a hostplant, this is an example for a ‘hostplant switch’ from *L. sativa* to *L. serriola* in the study region, leading to a massive population increase. A switch in hostplant preference leading to an expansion of the colonised area has been shown for *A. agestis* (Thomas et al. 2001) and *Polygonia c-album* (Braschler and Hill 2007) as well. Thus, hostplant switch might be an underestimated potential of species to react on changing environmental conditions.

Finally yet importantly, some species of moths and butterflies, which thrive in or in proximity of humid forests, benefit from increased forested areas. Character species of beech forests show stable or increasing populations (i.e. *Pararge aegeria*, *Aglia tau*, *Watsonalla cultraria*, *Cyclophora linearia*, *Hydriomena impluviata*, *Asthena albulata*, *Stauropus fagi*, *Herminia grisealis*, *Xanthia aurago*, *Calliteara pudibunda*, *Pseudoips prasinana*, *Drymonia obliterata* and *Agrochola macilenta*). Increasing species thrive as larvae on Impatiens species, i.e. *Xanthorhoe biriviata*, *Ecliptopera silaceata*, on Clematis species, i.e. *Horisme tersata*, *Melanthis procollata* and *Axyliia putris*, on eagle fern (*Pteridium aquilinum*), i.e. *Petrophora chlorosata* or on tree lichens, i.e. *Cryphia algae*, *Laspeyria flexula*, *Atolmis rubricollis*, *Eilema depressa*, *Eilema griseola* and *Eilema sororcula*. Groenendijk and Ellis (2011), Fox et al. (2011) and Boyes et al. (2019) describe an increase in moth species depending on tree lichens in The Netherlands and the UK as well. Strikingly, the list of 51 Anthropocene winners among British moths supplied by Boyes et al. (2019) is largely consistent with our findings (22 of these species appear in our category ‘increasing’). Furthermore, two butterfly species appeared at the beginning of the twentieth century: *Araschnia levana* and *Brenthis ino*, both associated with humid forest glades. Weymer (1878) described *P. c-album*, which is a woodland species, as ‘not common’. Today this species is ubiquitous in the study region.

What role does climate change play?

Species that are prevalent today mainly in hilly and mountainous landscapes of North-Rhine Westphalia are in retreat in Wuppertal. However, we do not see that this phenomenon is exclusively due to climate change. Many of these mountainous species inhabit bogland and heath landscapes, which are missing today in the study region. Thus, habitat destruction and climate change work together and we cannot consider both separately. However, especially in the last decade, we observe more and more ‘new’ species spreading from the south and west into the study region (see Fig. 5). During the last 6 years, seven species entered the study region. Three of these species (*P. manni*, *Caradrina kadenii* and *Lithophane leautieri*) have not been recorded in Germany before the beginning of the twenty first century. The species temperature index (Platania et al. 2020) of the

two butterfly species that recently (re)appeared (*C. argiades* and *P. manni*) is a remarkable higher than the mean species temperature index of the butterflies that have always been present in the study region. Fox et al. (2011) found a northward shift of moth species in the United Kingdom as well. Some of these species typically inhabit urban climate (i.e. *C. kadenii*, *Caradrina gilva*, *Eilema caniola*). Additionally, we see increasing counts of typical late autumn, winter and early spring species (i.e. *Apocheima hispidaria*, *Agriopsis aurantiaria*, *Asteroscopus sphinx*, *Agrochola circellaris*, *Agrochola lota*, *Agrochola macilenta*, *Eupsilia transversa*, *Conistra ligula*, *Conistra rubiginosa*, *Conistra erythrocephala*, *Orthosia cruda* and *Orthosia munda*). We think that this is due to increasingly milder winter half-years and therefore better observation days with higher counts. Furthermore, we see extended flight seasons and more generations for a number of species (Laussmann et al. 2010). Altermatt (2010) reported an increase in voltinism in European butterflies and moths as well.

Unexpected trends

Some species like *Aglais urticae*, *Coenonympha pamphilus*, *Pararge aegeria* and *Catocala sponsa* show long- or medium-term fluctuations in the study region that are not easily interpreted (Laussmann et al. 2010). *Cupido argiades* was found ‘once in Juli 1858’ (Weymer 1878). Surprisingly, after about 80 years of absence, this species managed to populate North Rhine-Westphalia again in 2011. First observations in Wuppertal were in 2012 (Dahl and Radtke 2012). Now, we observe this species widespread throughout the whole region. Whether or not climate change is a reason for the spreading of *C. argiades* remains to be seen (Filz and Schmitt 2012).

Conclusions

In recent years, scientists appeal to draw political attention to the loss of insects (e.g. Klausnitzer and Seegerer 2019; Cardoso et al. 2020). If we intend to increase species richness and biodiversity of butterflies and moths again, the focus must be on protecting, restoring and promoting open landscapes and shrubbery rather than forests. The forestry sector should consider opening up clearings and gaps in commercial forests. If we recognise species richness and biodiversity as a value, it must be worth investing money. For example, willing and committed farmers could be paid for ‘producing’ insects on flowering meadows. These meadows must be kept out of intensive farming for decades as stable habitats. Actually, these ideas are not new at all and there is no time to postpone the necessary countermeasures against insect species loss (e.g. Krogmann et al. 2018; Samways et al. 2020).

Since butterflies, moths and their corresponding larvae are important prey for e.g. birds and bats, a loss of biomass would be fatal for these species placed higher in the trophic pyramid. With regard to the study region, a renaturation of the steep Wupper slopes facing south and west in the sense of an open landscape would be ideal. At present, these are predominantly forested. Actually, after massive landscape change, another decisive factor increasingly contributes to species turnover: climate change. Therefore, we continue in spending time and money on what we do best: observe.

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Author contributions TL formulated the idea to correlate historical and actual observations. TL and AR reviewed historical data and wrote the manuscript. AD and AR did most of the fieldwork. TL performed data evaluation. AD cared for the database, carried out data quality assurance, extracted the data for the study region and collected recent data from other observers.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Statement of Human and Animal Rights For this type of study formal consent is not required.

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