

Weather-induced changes in moth activity bias measurement of long-term population dynamics from light trap samples

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Abstract

Interpretation of light trap catches of moths is complicated by daily variation in weather that alters flight activity and numbers caught. Light trap efficiency is also modified by wind and fog, and daily weather may effect absolute abundance (numbers actually present). However, actograph experiments and other sampling methods suggest that changes in daily activity are large by comparison to changes in absolute abundance. Daily variation in weather (other than wind and fog) is therefore a form of sampling error in absolute abundance estimates. We investigated the extent of this sampling bias in 26 years of population dynamics from 133 moth species. In a subset of 20 noctuid and geometrid species, daily numbers caught were positively correlated with temperature in 14 species, and negatively correlated with rainfall in 11 species. The strength of correlations varied between species, making it difficult to standardize catches to constant conditions. We overcame this by establishing how weather variation changed with time and duration of the flight period. Species flying later in the summer and for shorter periods experienced more variable temperatures, making sampling error greater for these species. Of the 133 moth species, those with shorter flight periods had greater population variability and more showed significant temporal density dependence. However, these effects were weak, which is encouraging because it suggests that population analyses of light trap data largely reflect factors other than sampling error.

Introduction

Density dependence is central to understanding population persistence and fluctuations (Ginzburg et al., 1990; Royama, 1992; Murdoch, 1994). Temporal population variability is also a potentially useful measure of population stability (Connell & Sousa, 1983). However, measured population variability is difficult to interpret because time series of animal abundances usually contain both sampling error and variation in population size due to real changes in abundance (Gaston & McArdle, 1994; Link & Nichols, 1994). This problem also extends to measurement of density dependence (Bulmer, 1975); if population level is constant, but is recorded as varying because of sampling error, any analyses of density dependence would be nonsense

because changes in recorded abundance are not due to population dynamics. We estimated the size of a predictable form of sampling error in light trap catches of moths and assessed how it affects population variability and detection of density dependence in 26 years of annual abundances.

Light traps have been used widely in studies of abundance of agricultural pest species, community structure, population variability, incidence of density dependence and spatial synchrony (Wolda, 1978; Hanski & Woiwod, 1991, 1993a, b; Holyoak, 1993a; Yela & Herrera, 1993). Numbers of moths caught in light traps are higher on warmer nights and lower on windy or wet nights (Williams, 1940, 1961; Persson, 1976; Bowden, 1982; Dent & Pawar, 1988). Daily changes in moth captures are more representative of

changes in flight activity than changes in abundance (Muirhead-Thomson, 1991). This is supported by: (1) Actograph experiments with tethered moths (Lance et al., 1988). (2) Comparisons of activity of captive moths with light trap catches (Riley et al., 1992). (3) Comparisons between direct censuses of moths and light trap catches (Riley et al., 1992; Quiring, 1994). The last two forms of evidence also suggest that daily changes in moth abundance are usually small by comparison to changes in numbers flying. Environmental conditions are also likely to influence light trap catches by altering trap efficiency. For example, winds might blow moths approaching a trap off course, and background illumination could reduce trap efficiency (e.g., Hardwick, 1972).

Changes in flight activity and trap efficiency in response to weather also cause light trap catches to vary with weather conditions. In studies of moth behaviour, number of active moths may be our best measure of population size. For example, mating opportunities are likely to be influenced by numbers of active moths rather than by actual numbers present. However, in investigations of population dynamics, the actual number of moths present (which we term 'absolute' population size) is likely to be more important; measured changes in moth abundance caused by changes in trap efficiency and flight activity would lead to misleading estimates of population growth and decline. Morton et al. (1981) interpret the effects of weather on light trap catches as sampling error that could be corrected for by estimating the size of weather effects on abundances and adjusting to constant conditions. In the present investigation of population dynamics we also treat the effects of weather on light trap catches as a form of sampling error. We cannot separate meteorological effects on flight activity from those on trap efficiency without independent evidence. However, variation in both flight activity and trap efficiency represent forms of sampling error in absolute abundance estimates. No studies of population dynamics have included the effects of weather on catches, possibly because effects vary between species (Morton et al., 1981; Gaydecki, 1984; Muirhead-Thomson, 1991). We investigated the consequences of variation in light trap catches caused by daily weather using analyses of 26 years of annual abundance for 133 moth species in the Czech Republic. Our aim is to measure the extent to which long-term measures of population variability and detection of temporal density dependence from light trap data are biased by this form of sampling error.

First we report analyses of effects of day-to-day temperature and rainfall on numbers of individuals caught in light traps in a subset of 20 species. The 20 species were selected to have flight periods representative of the 133 species; ten were noctuids and ten were geometrids. We used these species to investigate the effects of weather on trap catches, and whether these varied between species. We then sought a general relationship between daily temperature and population variability measured using annual abundance over 26 years. This was done by identifying periods with high or low variability in daily temperature and testing if moths flying during these periods differed in their long-term population variability. Finally, we tested whether temporal density dependence is likely to be detected in moth species flying during periods with different variability in daily temperature.

Materials and methods

Moth and weather data. Moths were sampled using a light trap at Prague-Ruzyně (14°15'E., 50°06'N) in the Czech Republic, which was 1 km from the airport that provided meteorological data. The sampling methodology and trap are described by Novák (1983). We used one time series for each of 133 univoltine species with a mean abundance of at least 5 individuals per year; this minimum abundance avoids excluding species with low abundances (Woiwod & Hanski, 1992), and eliminates series containing an excessive number of zero values, that are problematic in analyses of population variability (Gaston & McArdle, 1994). Of the 133 species, 94 belong to the Noctuidae, 32 to the Geometridae, five to the Arctiidae, and one each to the Thyatiridae and Sphingidae.

We obtained daily records of average and minimum temperature (in °C), and precipitation (in mm) for 5 selected years (Table 1), collected at the Prague-Ruzyně airport meteorological station, which was 1 km from the trap. Because the trap was situated on the side of a building, no attempt was made to analyze the effects of wind speed on trap catch.

Effects of daily temperature and rainfall on light trap catches. To obtain a manageable data set we selected 10 noctuid and 10 geometrid species with a range of flight periods, and also considered only 5 randomly selected years from the 23 years when all species were sampled (Table 1). A subset of species was analyzed because only annual abundance data was computerized

Table 1. Multiple regressions of daily temperature and precipitation on catches of each of 10 species of noctuids and geometrids in 5 years. Counts were Ln-transformed and weather variables were standardized to have zero mean and unit variance. Flight period is defined in the materials and methods. n is the total number of days used and comes from 1973, 74, 80, 82, and 90. A Poisson distribution of sampling error was assumed. Only significant regressions are given ($P \leq 0.05$ in a χ^2 -test using a maximum likelihood model)

Species	flight period (days)	n (days)	Temperature		Rainfall	
			r^2	Slope \pm s.e.	r^2	Slope \pm s.e.
Noctuidae						
<i>Charanyca trigrammica</i>	57	177	0.067	0.121 \pm 0.034	–	–
<i>Noctua janthina</i>	60	184	0.261	0.264 \pm 0.034	0.078	–0.048 \pm 0.016
<i>Mythimna comma</i>	63	226			0.027	–0.012 \pm 0.006
<i>Apamea anceps</i>	68	210	0.051	0.091 \pm 0.027	–	–
<i>Mythimna ferrago</i>	82	264	0.126	0.146 \pm 0.025	0.034	–0.011 \pm 0.004
<i>Hoplodrina alsines</i>	94	299	0.096	0.128 \pm 0.023		
<i>Amphipoea fucosa</i>	96	291	0.041	0.089 \pm 0.030	0.040	–0.018 \pm 0.007
<i>Apamea monoglypha</i>	105	329	0.106	0.134 \pm 0.022	0.011	–0.006 \pm 0.003
<i>Noctua pronuba</i>	116	327	0.046	0.082 \pm 0.022	0.016	–0.007 \pm 0.003
<i>Agrotis exclamationis</i>	126	388	0.038	0.075 \pm 0.019	–	–
Geometridae						
<i>Cleora cinctaria</i>	34	70	–	–	–	–
<i>Eulithis pyraliata</i>	35	121	0.046	0.087 \pm 0.040	0.040	–0.018 \pm 0.008
<i>Epirrita dilutata</i>	38	132	–	–	–	–
<i>Xanthorhoe quadrifasiata</i>	46	156	–	–	0.048	–0.024 \pm 0.008
<i>Ourapteryx sambucaria</i>	46	152	0.093	0.166 \pm 0.042	–	–
<i>Opisthographis luteolata</i>	55	163	–	–	–	–
<i>Perizoma alchemillatum</i>	59	188	0.080	0.133 \pm 0.038	0.029	–0.015 \pm 0.007
<i>Semiothisa wauaria</i>	63	205	0.150	0.192 \pm 0.038	0.098	–0.073 \pm 0.025
<i>Eulithis prunata</i>	67	207	0.122	0.187 \pm 0.039	0.018	–0.013 \pm 0.008
<i>Biston betularius</i>	84	263	–	–	–	–

for all species; daily abundance indices were extracted from paper records for the 20 species. For each species, the effects of mean daily temperature and rainfall on trap catch were examined using a multiple regression analysis (Table 1). Minimum daily temperature was rejected as an explanatory variable because it explained less of the variation in trap catch than mean daily temperature, and mean and minimum daily temperature were strongly correlated causing colinearity.

Effects of temperature and rainfall on measured population variability and detection of density dependence. Tests for temporal density dependence assume that abundances were sampled continuously, and zero abundance values must be absent because we cannot take the logarithm of zero. However, only seven moth species were identified and counted every year (1967–1992). Yearly abundance values were not recorded

between 1977 and 1979 for the remaining 126 species, and differ from recorded zero values. In testing for density dependence we replaced any zero abundance values by 0.1 times the species' minimum recorded annual abundance. The proportion (0.1) is an arbitrary value, however preliminary analyses showed that the exact value did not effect the results (Andrews, 1991).

We tested for density dependence using the test of Pollard et al. (1987), which is amongst the most reliable methods available (Holyoak, 1993b). The form of the test is described in Holyoak (1993b), with the exception that we excluded the three missing years of data (1977–1979 in 126 species) from the test statistic, and performed randomizations only between years where abundances were recorded. Density dependence was considered to be detected if $P \leq 0.05$ was obtained from 10 000 randomizations. Likelihood of detection of density dependence was -1 times the logit-

transformed P-value from the test of density dependence. The logit transformation was used to normalize the distribution of likelihoods and the value was multiplied by -1 to give larger values when P-values were smaller.

Variation in daily weather conditions was compared with population variability and likelihood of detection of density dependence from time series of abundances from the light trap. The nature of weather effects were investigated for the 20 species in Table 1 and the reliability of results was checked using all 133 species. Population variability, s , was the standard deviation of the $\text{Ln}(1 + \text{annual abundance})$ from all years sampled. In the moth series adding one to abundances is not a serious form of bias in variability because of the small number of zero values present (Gaston & McArdle, 1994). We assumed that temperature is the most important component of weather influencing light trap catches (Table 1), and measured variability in weather as the standard deviation of daily temperature. Regression analyses and Spearman's rank correlations related variability in daily temperature to population variability or likelihood of detection of density dependence.

We investigated whether variability in temperature was correlated with the length, and time of start of flight periods. We then tested if population variability and detection of density dependence varied during periods with different variability in temperatures. For the 20 species in Table 1 the length of the flight period was the number of days between the average first and last day of capture in the 5 randomly selected years (Brakefield, 1987). For investigations using all 133 species the flight period was measured to the nearest month and averaged over all 26 years. Preliminary analyses showed that for the 10 geometrid species, lengths of flight period calculated for days and months were highly correlated ($r=0.97$), and were related by a regression slope similar to unity ($t_8=0.14$, $0.5 < P < 0.9$); however, the figures using average annual date were on average 12 days (s.e.=3 days) shorter than the earliest and latest recorded flight dates rounded to the nearest month. Similarly, the start of the flight period was measured to the nearest day (from 5 years of data) for the 20 species in Table 1 and the nearest month (from all 26 years) for all species.

Results

Effects of daily temperature and rainfall on light trap catches. For the noctuid species, light trap catches were greater on warmer nights in 9 of the 10 species, and were lower on rainy nights for 6 of the 10 species (Table 1). For the geometrid species, light trap catches were also greater on warmer nights for 5 of the 10 species and lower on rainy nights for 5 of the 10 species. Although these results are consistent with light trap catches of geometrids being less frequently influenced by weather than noctuids, the number of species is too small for this to be statistically analyzed. However, we can test for differences in the strengths of effects of temperature and rainfall where regressions were significant. None of the 20 species showed negative effects of temperature on numbers caught or positive effects of rainfall. The effect of temperature on numbers caught explained 3.8–26.1% of deviance, depending on species, whereas rainfall explained only 1.1–9.8% of deviance. The mean slope for $\text{ln}(\text{trap catch})$ against temperature (Table 1) was 0.126 (s.e.=0.080) for noctuids and 0.153 (s.e.=0.093) for geometrids, which do not differ in a student's t -test ($t_{12} = 0.22$, $P > 0.05$). Similarly, the mean slope for rainfall was -0.017 (s.e.=0.051) in noctuids and -0.029 (s.e.=0.071) in geometrids, which do not differ ($t_8=0.14$, $P > 0.05$). Slopes for both temperature and rainfall differed widely across species (Table 1). To check whether this was because of species differences, or arbitrary differences resulting from the years selected, we repeated the multiple regressions within years; comparison of within-year regressions within and between species (where significant) suggest that responses to temperature and rainfall were species characteristics.

Effects of temperature and rainfall on measured population variability and detection of density dependence. Variability in daily temperature was greater when measurements were made over a longer period (Figure 1, linear regression: $P < 0.025$, $t_9 = 2.84$, $r^2 = 0.50$). This was not a sample size effect, as sample sizes were standardized in Figure 1. Variability in temperature was also greater if the period of measurement was later in the year and this effect was of larger magnitude than the effect of length of period of measurement on variability in temperature (Figure 2). Similar effects were found if variation in temperature was measured using the coefficient of variation rather than the standard deviation.

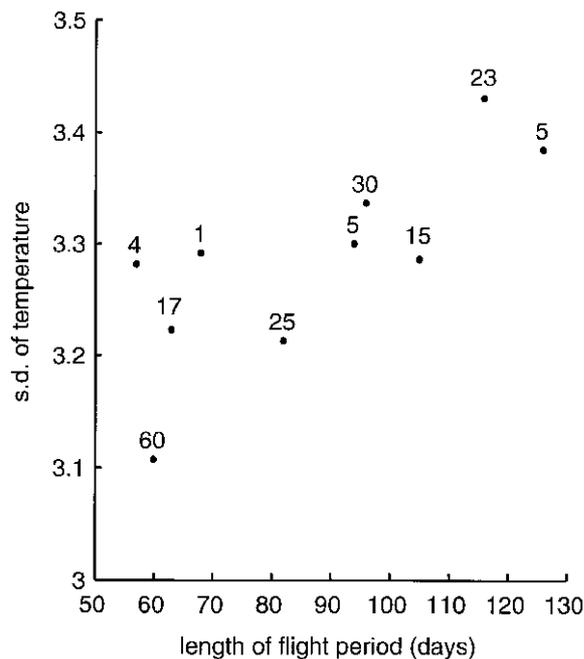


Figure 1. The effect of the duration of flight period on variability in daily temperatures. Each point represents 150 randomly selected days from the 5 years of data used in Table 1. Figures above points give the beginning of the flight period, measured in days after 13 May.

Variation in daily temperatures has a greater range of possible values when the flight period is shorter (Figure 2). To fit a long flight period into a summer, this period must start early in the year, whereas shorter flight periods can start later in the year. Summer temperatures are more variable than spring temperatures, causing species with short flight periods in summer (e.g., days 60–120) to experience greater daily temperature variation than species with similar flight periods during spring (e.g., days 0–45 in Figure 2). Additionally, species with long flight periods are constrained to start flying during spring, so that on average they experience less variable temperatures than some species with short flight periods (Figure 2).

Of the 133 species, those with longer annual flight periods had lower population variability than species with shorter flight periods (Figure 3). Population variability of an average species with a 2-month flight period was 2.4 times that of an average species with a 6-month flight period (Figure 3). However, the effect of length of the flight period on population variability explained only 9% of the variance in the regression (Figure 3). Figure 3 also shows that species with shorter flight periods (<4 months) have a greater range of observed values of population variability than those

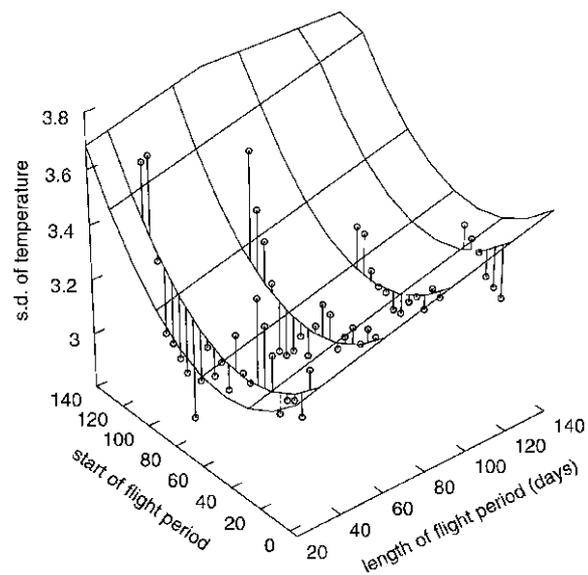


Figure 2. The effect of duration and time of start of flight period on variability in daily temperatures. Each point indicates the standard deviation of temperature (*sd*) averaged from 100 groups of 80 days with flight periods of length $l=30, 60, 90$ or 120 days, over the same 5 years as Table 1. The start of the flight period is given by the number of days after 13 May. The surface (indicated by non-vertical lines) comes from a step-wise multiple regression: $sd=3.2+0.002l+0.001l^2-0.006d$, where d is the first day of flight. Student's t -values for the slope terms were 3.06 ($P<0.005$), 3.19 ($P<0.005$) and -2.62 ($P<0.02$), respectively, and $r^2 = 0.26$. Vertical lines indicate whether points on the graph lie above or below the fitted surface, with longer lines representing greater differences between the point and surface.

with longer flight periods (≥ 4 months). Hence both population variability (Figure 3) and variability in temperature during the flight period (Figure 2) were more variable in species with shorter flight periods.

Density dependence was detected more often from species with longer flight periods (Figure 4). The average P -value from Pollard et al.'s test was 0.009 for a species with a flight period of 2 months and 0.046 for a species with an 8-month flight period (figures are back transformed from the regression in Figure 4). Ninety-two percent of species showed significant ($P\leq 0.05$) density dependence. The regression between flight period and P -values from Pollard et al.'s test accounted for only 7% of the variance (Figure 4).

Conclusion

Numbers of moths caught in light traps were influenced by daily weather variation, which is a form of sampling

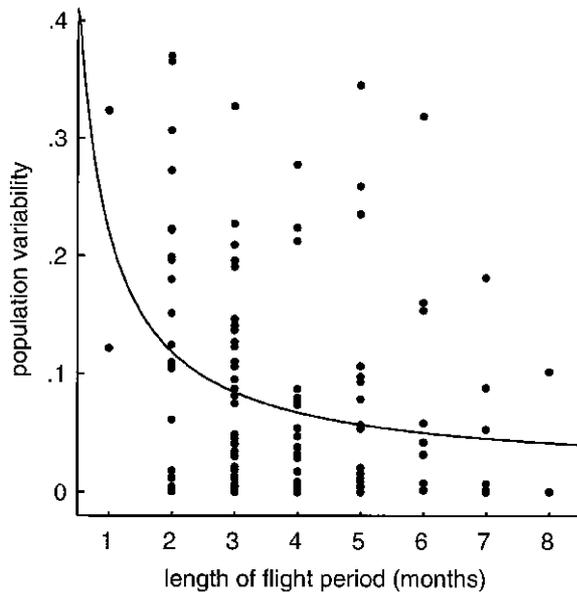


Figure 3. The effect of length of flight period on population variability of moth species from 23 or 26 year abundance series. Population variability was the standard deviation of $\text{Ln}(1+\text{abundance})$. A linear regression of population variability, s , against $1/\text{length}$ of the flight period gave a significant ($t_{131} = 3.54$, $P < 0.001$) positive slope, with $r^2 = 0.089$. The regression equation was $s = 0.016 + 0.205/\text{months}$.

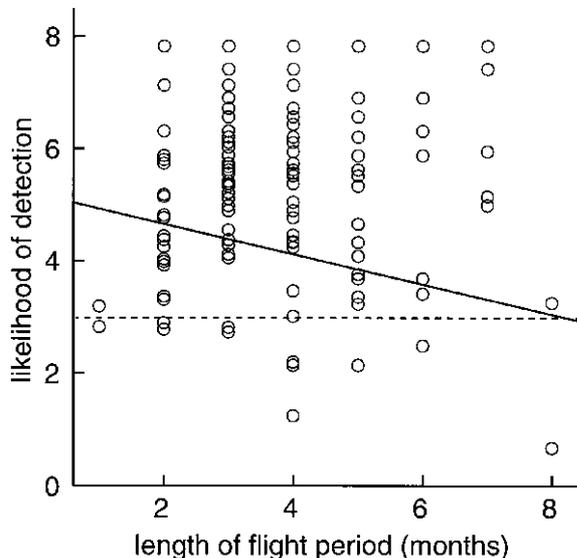


Figure 4. The effect of length of flight period on detection of density dependence from moth time series of 23 or 26 years. The likelihood of detection of density dependence, π is defined in the materials and methods. Density dependence was detected at $P \leq 0.05$ for all points on or above the dashed line. Logistic regression gave $\pi = 5.20 + 0.27m$, where m is the length of flight period in months ($\chi^2_{1} = 10.05$, $P < 0.005$, $r^2 = 0.07$). The regression is shown by the solid line. The regression was still significant ($\chi^2_{1} = 6.83$, $P < 0.01$) without the two outlying points on the extreme right.

error in absolute abundance. Conversely the number of moths flying would be better represented by light trap catches, which depend on both flight activity and trap efficiency. The effects of temperature and rainfall on numbers caught varied between species (Table 1, also Morton et al., 1981; Gaydecki, 1984; Muirhead-Thomson, 1991). Absolute abundances could only be obtained from light trap catches if we knew the strength of the effect of different meteorological factors for particular species. However, temperature and rainfall accounted for less than 26% of the variance in light trap catches, so that correction for these effects might lead to large errors in absolute abundance estimates. Additionally, this is a prohibitively large task for large numbers of species (e.g., Woiwod & Hanski, 1992, or the present study). We therefore do not recommend correcting for the effects of weather on trap catches without having more detailed knowledge of how weather effects flight activity and trap efficiency. In the present analysis, we used differences in variability of daily temperature to indirectly assess the importance of temperature for measurement of population variability and detection of density dependence.

Daily temperature experienced was, on average, more variable if the flight period was shorter (Figures 1 and 2). Since daily temperature effects light trap catch, we expect species with shorter flight periods to have greater population variability. This was shown to be true for the 133 moth species investigated in this study (Figure 3). Additionally, measuring temperatures over a shorter period gave a greater range of values of temperature variation. Moth species with shorter flight periods also have a greater range of values of annual population variability (Figure 3). Consequently, we are more likely to obtain biased abundance estimates for species with shorter flight periods. Whether these are general effects, that apply to other countries and taxonomic groups remains to be determined.

Wolda (1978) found that of 32 homopteran species caught in light traps in Panama those with short seasons (<25 week flight periods) had 3 times greater population variability than those with long seasons (>50 weeks). Wolda repeated his analysis whilst excluding species with less than 50 days of abundances and found no significant effect of season length. From this he concluded that the effect of flight period on population variability was a sample size effect. However, the lack of significance in the second analysis may be due to small sample sizes. In the present study we ruled out sample size effects by holding sample size constant (Figure 2). In Wolda's (1978) study variability of short

season species was 3.0 times that of long season species, compared to the equivalent figure of 2.4 times in the present study.

There is a great deal of scatter in the relationship between population variability and flight period (Figure 3, $r^2 = 0.09$), and likelihood of detection of density dependence and flight period (Figure 4, $r^2 = 0.07$). This shows that other factors have a greater effect on population variability and detection of density dependence than sampling error caused by weather variation. This study, like that of Woiwod & Hanski (1992), suggests that non-delayed density dependence occurs in the majority of the moth populations analyzed.

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