Effects of Moonlight and Meteorological Factors on Light and Bait Trap Catches of Noctuid Moths (Lepidoptera: Noctuidae)

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ABSTRACT The effects of moon-phase and meteorological factors on activity of adult noctuid moths were investigated using light and bait traps in southern Spain for 170 nights (2 sampling years). The number of individuals caught in the light trap increased with temperature and decreased with the fullness of the moon. The effect of temperature on flight activity was similar between light and bait traps. The total number of individuals recorded in the bait trap was not affected by fullness of the moon. Increased cloud cover increased catches in light traps, but not bait traps. Bait trap records were lower on windy nights. Average light trap catch varied 6- to 9-fold because of changes in temperature. Moonlight and cloud cover caused light trap captures to vary ≈2-fold. Bait trap records were at least as strongly affected by meteorological factors. No significant differences in effects of moonlight and meteorological factors on trap catch were detected between years. The strength of environmental effects on trap catch make it difficult to obtain an accurate record of both community composition and the abundance of individual species.

KEY WORDS bait traps, flight activity, light traps, meteorological factors, moonlight, noctuid moth assemblage

LIGHT TRAPS ARE commonly used to sample night-flying noctuid moths (Lepidoptera: Noctuidae) and are the most efficient way of capturing large numbers of individuals (Williams 1936, Löbel 1982, Muirhead-Thomson 1991). Noctuids are the most species-rich family in the Lepidoptera (Fibiger 1990, Gaston 1991, Scoble 1992), and usually comprise a larger proportion of captures in light and bait traps than any other family (Janzen 1988, Barlow and Woiwod 1989, White 1991). Data from light traps have been used for a variety of purposes, such as sampling populations of pest species (Zalucki 1991, Luttrell et al. 1994), studies of population dynamics (Rejmánek and Spitzer 1982; White 1988, 1991; Hanski and Woiwod 1993; Tucker 1994), community ecology (Wolda 1978, Butler and Kondo 1991, Yela and Herrera 1993), migration (Showers et al. 1989, 1993; Gregg et al. 1993, 1994), and flight behavior (Persson 1971, Sappington et al. 1994). Meteorological factors affect the number of specimens caught in light traps as does moonlight (e.g., Williams 1940, 1961; Hardwick 1972; Persson 1976; Gaydecki 1984; Dent and Pawar 1988). The effect of moonlight on light trap catch is intriguing because it is unclear whether moonlight modifies flight activity or whether it merely affects the efficiency of light traps by modifying brightness of the trap relative to background illumination (Muirhead-Thomson 1991). Changes in flight activity in response to moonlight have previously been reported for other taxa, including mosquitoes, delphacids, cicadellids, and certain neuropterans (Provost 1959, Bidlingmayer 1964, Bowden 1981, Perfect and Cook 1982) and for some individual noctuid species (Persson 1971). For noctuid moth communities, moonlight alters the number of specimens caught in light traps (Williams 1936, 1940; Persson 1976; Morton et al. 1981; Poltawski and Schintlmeister 1988), but it is still unclear whether these changes are the result of altered flight activity or light trap efficiency.

According to previous studies, the most important environmental effect on the number of individuals caught in light traps is that of temperature. Williams (1940) reported that the number of individuals caught doubled for each 2.8°C rise, and similar results were obtained by Williams (1951, 1961), Harling (1968), Hardwick (1972), Persson (1976), Gaydecki (1984), Camps (1986), and McGeachie (1987). However, Harstack (1979) and Morton et al. (1981) found nonlinear relationships between temperature and catch, and Verma et al. (1982), Tucker (1983), and Mizutani (1984) found no relationship. Although effects of temperature on trap catches have been shown in 9 of 12 studies of noctuids, they have been ignored in almost all studies that use trap data to measure abundance and species composition. After temperature, the next most important effect was that wind reduced the numbers of individuals caught in light traps (Williams 1940, Harling 1968, Douthwaite 1978, Harstack 1979, Járfás and Viola 1981, Gaydecki 1984, Mizutani 1984, Camps 1986, McGeachie 1987). Williams (1940, 1961) also

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reported both positive and negative effects of rainfall on the number of individuals caught in light traps. The effect of moonlight on the numbers of moths caught is generally negative (Williams 1936, Nemec 1971, Bowden and Church 1973, Persson 1976, Vaishampayan and Shrivastava 1978, Harstack 1979, Nowinsky et al. 1979, Morton et al. 1981, Vaishampayan and Verma 1982, Mizutani 1984, Taylor 1986, McGeachie 1987, Nag and Nath 1991). However, 2 studies of moths found positive correlations (Bowden and Morris 1975, Harstack 1979) and 5 found no correlation (Williams 1951, 1961; Williams et al. 1956; Hardwick 1972; Morton et al. 1981). McGeachie (1987) reported that many of these studies had small sample sizes, failed to use appropriate statistical methods, and only Persson (1976) correctly calculated incident moonlight. We avoided these shortcomings by using 170 nights of simultaneous light and bait trap catches recorded during 1991 (131 sampling nights) and 1992 (39 sampling nights) in southern Spain. Because bait traps do not use illumination to attract moths, the effect of moonlight on moth activity and light trap efficiency can be separated.

In this study we examined the magnitude of the effects of moonlight and weather variables on both light trap and bait trap catches of an assemblage of noctuid moths; assessed whether trap catches can be corrected for sampling biases caused by moonlight and environmental effects; and analyzed whether moonlight modifies flight activity of noctuids (at the community level) or if light traps are less efficient on brightly moonlit nights.

Materials and Methods

Field work was conducted in a mountain valley at 1,300 m a.s.l. at Roblehondo in the Sierra de Cazorla (natural reserve of Navahondona-Guadahornillos, Jaén province, southeastern Spain). The main climatic features and vegetation are described in Herrera (1984) and Yela and Herrera (1993). The site is in a valley with no sources of artificial light other than the light trap. During 2 consecutive years, April–November 1991 and March–November 1992 (totalling 170 sampling nights), noctuid moths were sampled using a light trap and a bait trap run simultaneously. This period covers 14 moon cycles (7 in 1991 plus 7 in 1992).

The light trap consisted of a blacklight, Heath trap (Heath 1965), as modified by Fernández-Rubio (1992); further details are given in Yela and Herrera (1993). The light trap was in a clearing within *Pinus nigra* Arnold and *Quercus rotundifolia* Lam. mixed forest ≈50 m from the biological station (which lacks exterior lights). The light trap was run all night, specimens were anaesthetized, identified, and released (except for a few examples of species that were difficult to identify). The bait trap consisted of 5 ropes (each 2 m long) soaked in a red wine and sugar mixture (a standard mixture of 4 liters of red wine and 2 kg of sugar) in a covered bucket during the daytime. Ropes were suspended horizontally in trees (always in the same positions) at ≈1.7 m above ground with ≈12 m between each rope. Because previous observations showed that most individuals arrived within the first 2 h after sunset (Yela 1992), sugar ropes were inspected with a head torch at 0.5-h intervals during the first 2 h of the night (totalling 5 visits). Light intensity of the torch did not disturb moths when viewed at a distance of 0.5 m, which was sufficiently close to allow specific identification and sexing of most specimens. Moths generally settled quickly to feed and then remained feeding in the same position for a few hours, provided they were not disturbed and winds were not strong. Specimens were identified and sexed in situ and positions were noted to avoid recounting them. Specimens that were difficult to identify were captured with a killing bottle and stored for dissection when necessary. No captures were made until all other individuals had been identified and sexed. Results of the 5 ropes were pooled.

Environmental variables were checked twice nightly, at dusk and 2 h later. Air temperature and relative humidity were measured using a portable meteorological station situated at the same height as the sugar ropes. For these 2 variables, the arithmetic mean of the 2 measurements was used in analyses. Wind speed, cloud cover, rain, and fog were ranked visually. Although visual ranking is not the best way of measure these factors, wind, rain, and fog were rarely present, therefore this method should not affect the results in a significant way. Wind was categorized into 5 categories: no wind, slight breeze, light wind, moderate wind, and strong wind. Rain was also categorized into 5 categories: no rain, a few drops, continuous light rain, heavy intermittent rain, and continuous heavy rain. Cloud cover was ranked as <10, 10–50, 50–90, and >90%. We quantified moonlight as the percentage of the moon's surface that was illuminated (as described in Bowden 1973), because the angle of inclination has only minor effects on illumination (Austin et al. 1976). Attempts to include the amount of time that the moon was in the sky had less explanatory power than simply using the percentage of the moon illuminated, and therefore were disregarded.

Trap catches were analyzed using univariate analyses of covariance (ANCOVAs) with number of specimens caught as the dependent variable, temperature, humidity, and percentage of the moon's surface as covariates and wind, rain and cloud cover as factors. Analyses were carried out using GLIM (Nelder and Wedderburn 1972, Crawley 1993) and models were simplified in a step-wise fashion, removing least significant (lowest mean square) variables first. Models were weighted for sample size and corrected for over-dispersion, using a scaling factor that was calculated as the residual deviance (when each full model was fitted) divided by the residual degrees of freedom. Changes in deviance then follow a chi-square distribution (Crawley 1993). All temporal autocorrelation coefficients in a catch

Table 1. ANCOVA tables for the effect of environmental factors and moonlight on light trap catches of noctuid moths, for all species and for the species that were caught in both light traps and came to sugar ropes, in 1991 and 1992

Factor	1991			1992		
	χ^2 (df)	P	R^2	χ^2 (df)	P	R^2
			All species			
Wind	0.25 (4)	NS		3.83 (4)	NS	
Humidity	1.34 (1)	NS		0.01 (1)	NS	
Temp	37.18 (1)	<0.001	0.202	13.15 (1)	<0.001	0.181
Moon	11.46 (1)	<0.001	0.062	12.83 (1)	<0.001	0.176
Cloud cover	17.26 (3)	<0.001	0.094	8.94 (3)	<0.05	0.123
Cloud cover*temp	0.32 (3)	NS		3.51 (3)	NS	
Cloud cover*moon	0.68 (3)	NS		6.13 (3)	NS	
Total			0.321			0.432
			Only species caught in both traps			
Wind	1.49 (4)	NS		2.05 (4)	NS	
Humidity	2.67 (1)	NS		3.47 (1)	NS	
Temp	46.94 (1)	<0.001	0.239	10.52 (1)	<0.005	0.122
Moon	11.43 (1)	<0.001	0.058	22.57 (1)	<0.001	0.262
Cloud cover	17.38 (3)	<0.001	0.089	12.81 (3)	<0.01	0.149
Cloud cover*temp	0.10 (3)	NS		4.34 (3)	NS	
Cloud cover*moon	0.20 (3)	NS		3.92 (3)	NS	
Total			0.354			0.516

NS, not significant.

were not significant at $P < 0.05$, so that a repeated measures analysis was not required. Because the ANCOVAs are unbalanced, the interaction terms may be unreliable (Shaw and Mitchell-Olds 1993). However, in our analyses all interaction terms were far from being significant, and the current analyses are therefore considered adequate. Analyses were carried out both on all species and on those species that were caught in both kinds of trap, thereby avoiding differences in effects of environmental factors that could be a result of species composition. All nights, including those when no specimens were caught, were included in the analyses; therefore, a logarithmic link function of number of individuals was used. We conducted 8 ANCOVAs: 2 types of trap (light and bait), multiplied by 2 types of sample (total, and species common to both traps), multiplied by 2 sampling years.

Results

In total, 2,472 individuals (1,669 in 1991, 803 in 1992) of 142 (1991) and 100 (1992) species of noctuids were collected in the light trap. The bait trap yielded 1,840 individuals (1,188 in 1991, 652 in 1992) from 121 (1991) and 89 (1992) noctuid species. In 1991, 87 species (49% of all species) were recorded in both traps, with 1,349 specimens from the light trap and 1,042 from the bait trap. In 1992, 57 species (43% of all species) visited both traps, with 803 specimens from the light trap and 464 from the bait trap. The light and bait traps recorded 81 and 69%, respectively, of the species recorded in either type of trap in 1991; in 1992, the same figures were 75% (for the light trap) and 56% (for the bait trap).

Temperature was the dominant environmental factor influencing numbers recorded in both type of trap. The natural logarithm of number of individuals caught and temperature were positively related ($0.101 < R^2 < 0.439$ and $P < 0.01$ in all cases; Tables 1 and 2). Moonlight was the next most important effect on light trap catch. The number of individuals caught was negatively related to percentage of the moon's surface that was illuminated (Table 1). The amount of variance in catch explained by moonlight was small in 1991 for all species and species caught in both type of trap ($R^2 = 0.062$ and 0.058, respectively). In 1992 it was higher ($R^2 = 0.176$ and 0.262, respectively), and moonlight was the most influential factor for species common to both traps (Table 1). However, there were no significant differences between years in the effect of temperature or moonlight for all species ($t = 0.84$, df = 1, $P < 0.05$) or species caught in both traps ($t = -0.08$, df = 1, $P < 0.05$) (Table 3). For the bait trap, there was a small, positive effect of moonlight on total number of individuals in 1991 for all species (Table 2). This effect was nonsignificant ($P > 0.05$) for the species that were caught in both traps (Table 2) and for the 1992 data sets.

Cloud cover affected the number of individuals caught in the light trap, but not the bait trap (Tables 1 and 2). Also, in 1991, bait trap catches were reduced on windy nights, but this relationship depended on 3 nights with winds strong enough to disturb moths, and explained <4% of the variance in the logarithm of catch (Table 2). No effect of wind was found on light trap catches (Table 1). This finding agrees with the observation that moths were disturbed when feeding at sugar ropes on windy nights.

The magnitude of the reported effects are highlighted by the regression equations from the ANCOVAs (Tables 3 and 4). In 1991, temperature varied between 3 and 26°C. For the analysis including all species, this leads to predicted average light trap catches (with no moon) of 4.4–30.4 individuals per night on clearer nights and 6.7–58.2 individuals

Table 2. ANCOVA tables for the effect of environmental factors and moonlight on bait trap catches of noctuid moths, for all species and for the species that were caught in both light traps and came to sugar ropes in 1991 and 1992

Factor	1991			1992		
	χ^2 (df)	P	R^2	χ^2 (df)	P	R^2
		All species				
Wind	10.98 (4)	<0.05	0.039	0.07 (4)	NS	
Humidity	2.46 (1)	NS		2.04 (1)	NS	
Temp	122.6 (1)	<0.001	0.439	6.79 (1)	<0.01	0.101
Moon	4.64 (1)	<0.05	0.017	1.86 (1)	NS	
Cloud cover	6.33 (3)	NS		6.64 (3)	NS	
Cloud cover*temp	6.79 (3)	NS		5.38 (3)	NS	
Cloud cover*moon	3.86 (3)	NS		3.82 (3)	NS	
Total			0.474			0.101
		Only species caught in both traps				
Wind	9.82 (4)	<0.05	0.036	1.55 (4)	NS	
Humidity	2.91 (1)	NS		3.63 (1)	NS	
Temp	99.8 (1)	<0.001	0.372	9.98 (1)	<0.005	0.122
Moon	3.56 (1)	NS		1.17 (1)	NS	
Cloud cover	5.41 (3)	NS		6.40 (3)	NS	
Cloud cover*temp	0.10 (3)	NS		3.70 (3)	NS	
Cloud cover*moon	0.20 (2)	NS		3.12 (3)	NS	
Total			0.482			0.122

NS, not significant.

on cloudier nights. Hence, temperature alone caused a variation in light trap catch of 6.9- to 8.7 times. Equivalent figures for nights with a full moon were 1.9–13.5 individuals per night on clearer nights and 3.0–25.9 individuals per night on cloudier nights; temperature caused a variation in light trap catch of 7.1- to 8.6-times on nights with a full moon. Average catches on nights with no moon were 2.2–2.3 times those on nights with a full moon, and average catches on cloudy nights were 1.5–1.9 times those on clearer nights. In 1992, temperature ranged between 4 and 21°C; predicted average light trap catches were 9.1 and 55.9 individuals per night on clearer nights and 20.6–127.0 individuals on cloudier nights (with no moon). Hence, in 1992, temperature caused a variation of 6.1- to 6.2-times in light trap catch on nights with no moon. For nights with full moon, similar figures were 2.3–14.5 specimens per night on clearer nights and 5.3–32.9 specimens on cloudier nights, causing average catches on nights with no moon to be 3.8–3.9 times those on nights with a full moon and average catches on cloudy nights to be 2.3 times those on clearer nights. Thus, in 1992, temperature alone caused a variation in light trap catch of 6.2- to 6.3-times on more moonlit nights. For the data sets containing species recorded at both traps, values were slightly different, but the differences were not statistically significant (Table 3).

Average numbers of individuals coming to the bait trap in 1991 were between 0.9 and 17.1 individuals per night with no moon (on less windy nights) and 0.2 and 3.8 individuals per night on more windy nights, depending on temperature. Equivalent figures with a full moon were 1.5–27.9 and 0.3–6.3 individuals per night, respectively; hence, average numbers recorded on the warmest nights (26°C) were 19 times those on the coldest nights (3°C) when no moon was present, and 18.6–21 times when full moon. Numbers at full moon were 1.5–1.6 times greater than those with no moon; on less windy nights, numbers of records were 4.4–5.7 times greater than those on more windy nights. For the data set containing only species caught in both traps, the effect of moonlight on bait trap catch was not significant, but the effects of temperature and wind speed were generally similar to those found with all species (Tables 2 and 4). In 1992, only temperature

Table 3. Comparison of equations showing the effect of meteorological factors and moonlight on number of specimens caught in the light trap in 1991 and 1992 and for either all species or just for those caught in both light trap and recorded at sugar ropes

Analysis	c_i (SE) i	b_1 (SE)	b_2 (SE)
1991, all species	1.23 (0.29) i = 1 or 3	0.084	−0.0081
	1.88 (0.20) i = 2 or 4	(0.014)	(0.0024)
1991, species in both traps	0.69 (0.32) i = 1 or 3	0.103	−0.0086
	1.38 (0.24) i = 2 or 4	(0.016)	(0.0026)
1992, all species	1.63 (0.56) i = 1, 2 or 3	0.114	−0.0135
	2.45 (0.47) i = 4	(0.033)	(0.0039)
1992, species in both traps	1.72 (0.53) i = 1, 2 or 3	0.100	−0.0184
	2.48 (0.45) i = 4	(0.032)	(0.0041)

Equation is $y_i = c_i + b_1 t + b_2 m$, where y_i = ln (number of moths captured), t = mean nightly temperature (in °C), m percentage of full moon, and c_i = level of cloud cover, where i = 1, 2, 3, and 4 correspond to <10, 10–50, 50–90, and >50 cloud cover.

Table 4. Comparison of equations showing the effect of meteorological factors and moonlight on number of specimens coming to sugar ropes in 1991 and 1992, and for either all species or just for those caught in both light trap and recorded at sugar ropes

Analysis	w_j(SE)j	b_1(SE)	b_2(SE)
1991, all species	−0.49 (0.34) j = 1 to 4 −1.98 (0.95) j = 5	0.128 (0.014)	0.0049 (0.0020)
1991, species in both traps	−0.48 (0.35) j = 1 to 4 −2.18 (1.13) j = 5	0.113 (0.015)	NS
1992, all species	1.69 (0.49) j = 1 to 5	0.074 (0.030)	NS
1992, species in both traps	0.89 (0.59) j = 1 to 5	0.103 (0.035)	NS

Equation is $z_j = w_j + b_1t + b_2m$, where z_j = ln (number of moths recorded), t = mean nightly temperature (in °C), m = percentage of full moon, and w_j = level of wind, where j = 1, 2, 3, 4, and 5 correspond to no wind, slight breeze, light wind, moderate wind, and strong wind. NS, not significant.

exerted a significant effect on numbers of records; for all species, average bait trap record was 7.3–25.6 individuals over the observed temperature range (3.5 times larger at 26°C), and for species caught in both traps it was 3.7–21.2 individuals (5.7 times larger at 26°C).

Numbers of individuals caught in light and bait traps (for simplicity considering only the full species sample) were positively correlated ($R = 0.296$, $n = 131$, $P < 0.001$ for 1991; $R = 0.717$, $n = 39$, $P < 0.001$ for 1992). However, when the effects of temperature on catch were partitioned out, this correlation was no longer significant ($R = 0.080$, $n = 130$, $P = 0.43$ for 1991; $R = -0.055$, $n = 38$, $P = 0.74$ for 1992). This indicates that the relationship between catches in the 2 types of traps was mediated by a common dependence on temperature.

Discussion

Despite having first been reported in 1940 (Williams 1940), temperature effects have been largely ignored in ecological and pest management studies that use light trap data. In our analyses, the number of individuals caught in both light and bait traps is strongly dependent on temperature. This is similar to the findings of Williams (1940, 1951, 1961), Harling (1968), Hardwick (1972), Persson (1976), Seldon (1976), Morton et al. (1981), Gaydecki (1984), Camps (1986), and McGeachie (1987), who used light traps. Two of the more thorough studies, Persson (1976) and McGeachie (1987), give slopes for ln(catch) versus temperature that do not differ from our results for either light or bait traps. This suggests that the effect of temperature on number of individuals caught is general and also of large magnitude.

Number of individuals caught in the light trap decreased as fullness of the moon increased (Table 1). This effect is similar to that recorded by Persson (1976) and McGeachie (1987). In the current study, total catches were 2.2–3.9 times greater with no moon than with a full moon. Previous studies of noctuids have speculated whether the moon has a direct effect on flight activity or whether increased ambient light at night time merely decreases the efficiency of light traps (see review in Muirhead-Thomson 1991). However, these studies did not use an independent source of information to test whether flight activity increased or not (Muirhead-Thomson 1991). Our bait trap does not use illumination to attract insects and is therefore suitable for testing these propositions. For the 1991 data set including all species (but only for that), number of individuals at bait trap increased with increasing fullness of the moon; this was a barely significant effect explaining only 1.7% of the variance (Table 2). We consider this extremely weak effect to be spurious and not important biologically. In the rest of the analyses, including species recorded at both traps in 1991 (Table 2), the effect of moonlight on bait trap records was not significant. The prevailing flight activity of the noctuid moth assemblage therefore did not change with fullness of the moon. Because light trap catches decreased with increased moonlight, moonlight must have a negative effect on light trap efficiency by modifying background illumination (as suggested, but not demonstrated, by Robinson and Robinson 1950, Dufay 1964, Mikkola 1972, Bowden and Church 1973, Bowden and Morris 1975, and Bowden 1982). The observation that ambient moonlight competes with light traps is supported by the effect of cloud cover on the number of individuals caught; we found that 1.5–2.3 times more noctuid moths were caught in the light trap on cloudier nights than on clearer nights. Cloudier nights tend to be darker, so there would have been less ambient light to compete with the light trap.

In this study, no effect of wind speed on light trap catches was found, but the effect of wind reported for bait trap records relied on only 3 nights with strong winds. This is in contrast to the findings of Williams (1940), Harling (1968), Douthwaite (1978), Harstack (1979), Járfás and Viola (1981), Gaydecki (1984), Mizutani (1984), Camps (1986), and McGeachie (1987), who found that stronger winds reduced light trap catches. This difference can be explained thus: the sampling locality was in a sheltered valley. The lack of effects of rainfall was probably caused by low summer rainfall in southern Spain and exceptionally dry conditions of the years 1991 and 1992. In any case, the overwhelming majority of nights sampled were without wind, or with only a slight breeze, and without rain.

A record of moonlight and environmental factors at the time of trapping is required to standardize catches to constant conditions. Although Camps (1986) and others suggested this, few studies using light trap data have attempted to do it. The short-term effects that we report here for noctuids might also be expected to translate into error in the long-term measurement of abundance (Wolda 1978), but long-term abundance estimates could be corrected for environmental variation in catches if environmental factors were monitored at the time of trapping.

Light and bait traps, respectively, recorded 81 and 69% in 1991, and 75 and 56% in 1992 of the species that were recorded in either type of trap. Only 49% (1991) and 43% (1992) of all species were caught in both kinds of traps. Once the effect of temperature on catches was removed, light and bait trap catches were also uncorrelated, which is consistent with light and bait trap sampling a different range of species (because different assemblages might be expected to differ in abundance more at a given time than any single species). If light or bait traps tend to favor the capture of certain species, then a biased sample of species present in a given area will be obtained. This is of concern for biodiversity studies, but would be of less concern if one wished to compare populations through time or between sites. The light trap gives a more reliable picture of the noctuid assemblage than the bait trap because more species are attracted to it, which was also noted by other authors (Cleve 1971, Löbel 1982, Ylla 1990). Behavioral responses of individual noctuid species regarding both types of traps will be reported elsewhere.

Caution should be used in biodiversity and synecological studies of noctuids using light and bait trap data. The effects of environmental factors on activity, trap efficiency, and trap catch can easily be corrected by using analyses of the type conducted here. This will enable a more accurate record of both short term and long term abundance.

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