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Seasonal and spatial distribution of noctuid moths (Lepidoptera: Noctuidae) in the northern and central Arava Valley, Israel

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ABSTRACT

Little is known about the biology of deserticolous noctuids compared to noctuids from temperate regions. To address this disparity, a three-year survey was conducted during which 141 noctuid species were collected using automatic light traps at six different sites representing three kinds of habitats (referred to in this paper as extreme desert, oases, and settlements) in the Arava Valley desert in southern Israel. Most of the collected species were highly specific to either extreme desert or oases, and displayed different seasonal specificity. The oases fauna was generally comprised of bivoltine or multivoltine polyphagous species of Palearctic or tropical origin. Most of these species were on the wing in oases and settlements in May and October. Some oases species were on the wing during the hottest months, from June to September, though none showed peak occurrence during that period. The extreme-desert noctuids were on the wing generally once a year (monovoltine) in March or in November. The March-flying species were predominantly monophagous, whereas the November-flying species were polyphagous. These two different types of lifecycle adaptation to extreme desert conditions are discussed.

KEY WORDS: Lepidoptera, Noctuidae, seasonal adaptation, phenology, light traps, Arava, desert, Israel.

INTRODUCTION

The life cycles of most phytophagous insects, including moths and butterflies (Lepidoptera), are synchronized with the life cycles of their host plants (Brian et al., 2001). Even in temperate climates with long vegetative periods, most caterpillars are found during a relatively short time that coincides with the period of highest nutritional value of their host plants (Alonso and Herrera, 2000; Jones, 2001). Therefore, the time of flight (i.e., time of mating and egg-laying) has to precede the period of highest nutritional value of the host plants, thus becoming an important component of the seasonal reproductive strategy of Lepidoptera. In the Mediterranean subregion, the highest species diversity of butterflies is found in spring and autumn, avoiding the hot and dry summer in which food for both adults and larvae is scarce. The spring and autumn fauna comprises both multivoltine and univoltine species. A great number of univoltine species aestivate during the dry period, showing a bimodal phenology with two clearly separated peaks (Stefanescu, 2000).

The life cycle of many Lepidoptera pests is well known, but little data exist on non-pest species. Light-trapping is the main tool enabling us to study the seasonal patterns of adult flight. Yathom (1975) categorized four seasonal patterns of lepidopteran flight for species of Noctuidae inhabiting the Mediterranean regions: (1) pests and other multivoltine and polyphagous species, common in wet or irrigated locations, whose populations increase towards the end of summer, and which pass the winter in larval or pupal quiescence, resuming their development when temperatures allow; (2) species flying at the beginning and end of summer, aestivating during the midsummer hottest period; (3) univoltine species, flying during a single short period of the year, mostly in spring or autumn; and (4) species flying in late autumn (October–November), whose populations dwindle during winter and peak again in early spring (March–April), but which do not fly during the summer.

The Arava Valley is a harsh desert in the southern part of Israel (receiving less than 70 mm average annual rainfall and characterized by riverbed vegetation only — online at: http://www.botanic.co.il/english/research/desertad.htm), extending from the northern tip of the Red Sea to the southern tip of the Dead Sea. Geomorphologically, this alluvial valley lies in the northern part of the great African rift valley. Most of the area is below sea level, ranging from 400 m below sea level up to approximately 200 m above sea level. For approximately 180 days/year the maximal daily temperature exceeds 35 °C. The annual number of rainy days per year ranges from 0 to 10, with a maximum of 50 mm of annual rainfall (Ashbel, 1951; Jaffe, 1988). Biogeographically, the rift valley is an important link between the Afrotropical and the Palaearctic regions, featuring a unique mixture of these faunas (Furth, 1975; Por, 1975).

Worldwide there are about 35,000 species of noctuids, making them the largest known family of Lepidoptera. (online at: http://en.wikipedia.org/wiki/Noctuidae). Many noctuid species are well adapted to desert conditions, comprising a dominant group of Lepidoptera in deserts (Falkovich, 1979; Aly, 1996).

Some ecological notes on the bionomics of noctuids of the Middle East have been published by Bytinsky-Salz (1936, 1937); Wiltshire (1948, 1949, 1957, 1964, 1990), Hacker (1989, 1999, 2001), and Ronkay and Ronkay (1994, 1995). The flight periods and distribution of Noctuidae in Israel were studied by Amsel (1933), Rivnay (1964), Rivnay and Yatom (1964), and Halperin and Sauter (1991). Recently, a checklist of species collected in the Arava by the present authors was published by Hacker et al. (2001). Surveys on distribution, flight period, and host plants of Israeli noctuids were published recently by Kravchenko et al. (2007a,b).

This study focuses on the differences in species assemblages and the seasonal distribution of noctuids at six different sites representing three general kinds of habitat (extreme desert, oases, and settlements) in the northern part of the Arava Valley, southern Israel.

MATERIAL AND METHODS

Collection Sites

Extreme desert sites

(1) The Shezaf Nature Reserve (Shezaf hereafter) is an alluvial stony desert featuring *Acacia raddiana* Savi and *A. tortilis* (Forskk.) Hayne trees, and bushes of *Retama raetam* (Forssk.) Webb and *Anabasis* sp. with no or very sparse undergrowth. Annuals, such as *Anthemis maris-mortui* Eig., *Aaronsohnia factorovskyi* Warb. and Eig., *Erucaria pinnata* (Viv.) Tackholm and Boulos, are only found for a short period after rains. The reserve is approximately 40 km^2 and about 100 m below sea level.

(2) Naẖal Neqarot (Neqarot hereafter) occupies the lowest part of one of the canyons draining the Central Negev (including Machtech (crater) Ramon) into the Arava Valley. The area is a stony clay desert, approximately at sea level, with groups of *Tamarix* spp. and *Acacia* spp. trees and *Ochradenus baccatus* Delile bushes.

Oases

(3) The ‘En Z̲in oasis is situated in the lower part of the Naẖal Z̲in gorge, approximately 100 m above sea level. This valley, with its stony clay soil, drains the Central Negev (Sede Boqer–Avdat area) and is regularly flooded by winter rains. During the summer numerous water pools appear, primarily with thickets of *Phragmites australis* (Cav.) and *Typha domingensis* Pers. There are also areas of dense thickets of *Tamarix* sp. trees, as well as *Atriplex halimus* L., *Suaeda fruticosa* Forssk., and *Hammada* sp.

(4) Ne’ot Ha’Kikkar is the largest oasis on the southern shore of the Dead Sea (approximately 25 km^2; 350 m below sea level). It includes marshland, numerous springs, and areas flooded in winter. The vegetation is diverse, and includes a mixture of *Tamarix nilotica* (Ehrenb.), *Prosopis farcta* (Banks & Soland.) J.F. Macbr., *O. baccatus*, *Nitraria retusa* (Forssk.), *Acacia* trees, and *Saccharum ravennae* (L.), *P. australis*, *Arundo donax* L., and *T. domingensis*.

Settlements

(5) ‘Iddan is an agricultural settlement with tomato, melon, and other crop fields with sandy and stony desert soil with *Acacia* spp. and *Haloxylon persicum* Bge. The area is approximately 150 m below sea level.

(6) H̲az̲eva Field School (H̲az̲eva hereafter) — a settlement in alluvial, stony desert soil with *Tamarix* spp. and garden vegetation situated at approximately 150 m below sea level.

Method of light trapping

The sites were visited once a month on consecutive nights, and three modified black-light traps were operated at each site from November 1998 to May 2001 (Müller et al., 2005). The light source in each trap was a pair of black-light tubes (TLD 18W/80). Trapping nights were typically with neither strong wind nor rain and with less than a quarter-moon. Traps were operated overnight, from sunset to sunrise, in permanent positions in a straight line at 50 m intervals. On the following morning, the catch was recovered, mostly determined to species, and counted. Voucher specimens and specimens that could not be readily determined were pinned. Most of the specimens are deposited in the National Collection of Insects, Tel Aviv University (TAUI).

Calculations

Similarity of species assemblages was evaluated using the Jaccard coefficient of similarity. The coefficient ranges from 0 (no similarity), to 1 (complete similarity) (Southwood, 1978). The number of collected specimens of each species per month and location were considered as binary data (presence = 1; absence = 0) for index calculation. Samples from one location (from three traps) with less than four species or less than 20 specimens were not included in the index calculations.

RESULTS

Preference of species for either extreme desert or oasis sites

A total of 27,203 specimens belonging to 141 species of noctuids were collected during 154 trapping nights from October 1998 to October 2001. Seasonal and habitat preferences and host plant specialization are shown in Table 1. Most of the species showed a clear preference (e.g., reached the threshold of more than 80% individuals collected) either for oases (58 species), or for dry localities (64 species). Only 19 species did not reach the 80% threshold and were considered ubiquitous. Some species were collected exclusively at oases, e.g., *Lacanobia softa*, *Eremobastis judaica*, *Heterographa puengeleri*, *Hadula trifolii*, *Clytie delunaris*, *Sesamia cretica*, *Arenostola deserticola*, *Mythimna languida*, *Rhabdophera arefacta*, *Catamecia minima*; or only at the extreme desert sites, e.g., *Scythocentropus eberti*, *Odontelia daphnadeparisae*, *Diadochia stigmatica*, *Anydrophila stuebeli*, and *Paradrina kravchenkoi* (Table 1). No species was collected from human-modified habitats (‘Iddan and H̲az̲eva) only.

Different types of seasonal distribution

We have distinguished between three main patterns of seasonal flight: uni-, bi-, and trimodal, and a fourth modality that is locality-dependent.

1) Unimodal species

Each species showed a consistent pattern of peak occurrence throughout the study period. The unimodal species (Table 2), i.e., species peaking only once per year, comprised about 40% of the total species collected (58 of 141). Most of them (47 of 58) inhabited extreme desert sites, flying in March or November, with six winter

Table 1
Seasonal and habitat preferences and host plant specialization of Noctuidae of the Arava Valley

Species	Type of seasonal distribution	Month(s) of highest occurrence	Preferable biotope	Host plant specialization
1. *Acontia biskrensis* (Oberthür, 1887)	Sp	iii	desert	unknown
2. *Acontia lucida* (Hüfnagel, 1766)	Sp–Aut	v, x	oases	polyph
3. *Coccidiphaga scitula* (Rambur, 1833)	Sp	iii	desert	monoph
4. *Eublemma albina* (Staudinger, 1898)	Sp	iv	oases	unknown
5. *Eublemma apicipunctalis* (Brandt, 1939)	Sp–Aut	v, x	desert	unknown
6. *Eublemma cochylioides* (Guenée, 1852)	Sp–Aut	iv, x	oases	unknown
7. *Eublemma kruegeri* (Wiltshire, 1970)	Sp–Aut	v, x	desert	unknown
8. *Eublemma ostrina* (Hübner, 1808)	Sp–Su	iii, v, x	oases	polyph
9. *Eublemma parva* (Hübner, 1808)	Sp–Su	iii, v, x	oases	polyph
10. *Eublemma polygramma* (Duponchel, 1836)	Sp–Aut	v, x	oases	polyph
11. *Metachrostis velocior* Staudinger, 1892	Sp–Aut	v, x	oases	unknown
12. *Metachrostis velox* (Hübner, 1813)	Sp–Aut	v, x	oases	unknown
13. *Ozarba sancta* (Staudinger, 1900)	Sp	iii	desert	unknown
14. *Pseudozarba mesozona* (Hampson, 1896)	Aut	xi	ubiquitous	unknown
15. *Thalerastria diaphora* (Staudinger, 1879)	Sp–Su	iii, v, x	ubiquitous	unknown
16. *Boursinia deceptrix* (Staudinger, 1900)	Aut	xi	desert	polyph
17. *Arenostola deserticola* (Staudinger, 1900)	Sp–Su	ii, v, viii	oases	monoph
18. *Catamecia minima* (Swinhoe, 1889)	Sp–Su	iii, v, x	oases	unknown
19. *Condica viscosa* (Freyer, 1831)	Sp–Aut	iv, xi	ubiquitous	polyph
20. *Diadochia stigmatica* Wiltshire, 1984	Aut	xi	desert	unknown
21. *Eremobastis judaica* (Staudinger, 1898)	Aut	xi	oases	unknown
22. *Eremodrina alfierii* (Boursin, 1937)	Aut	xi	desert	polyph
23. *Eremodrina bodenheimeri* (Draudt, 1934)	Aut–Sp	xi, iii	ubiquitous	polyph
24. *Eremodrina distigma* (Chretién, 1913)	Aut	xi	desert	polyph
25. *Eremodrina melanurina* (Staudinger, 1901)	Aut	xi	desert	polyph
26. *Eremodrina casearia* (Staudinger, 1900)	Aut	xi	desert	polyph
27. *Eremodrina flava* (Oberthür, 1876)	Sp–Aut	iv, x	ubiquitous	polyph
28. *Paradrina amseli* (Boursin, 1936)	Sp–Aut	v, x	oases	polyph
29. *Paradrina atriluna* (Guenée, 1852)	Aut–Sp	xi, iii	oases	polyph
30. *Paradrina clavipalpis* (Scopoli, 1763)	Sp–Aut	iv, x	ubiquitous	polyph
31. *Paradrina mairei* (Draudt, 1909)	Aut	xi	desert	polyph
32. *Paradrina scotoptera* (Püngeler, 1914)	Sp–Aut	v, x	ubiquitous	polyph
33. *Paradrina kravchenkoi* (Hacker, 2004)	Aut	xi	desert	unknown
34. *Platyperigea oberthuri* (Rothschild, 1913)	Sp–Aut	iv, x	ubiquitous	polyph

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Sp — spring; Aut — autumn; W — winter; Sp–Aut — from spring via summer to autumn; Aut–Sp — from autumn via winter to spring; Sp–Su — from spring along summer.
monoph — monophagous; oligo — oligophagous; polyph — polyphagous.

Species	Type of seasonal distribution	Month(s) of highest occurrence	Preferable biotope	Host plant specialization
35. *Hoplodrina ambigua* (Denis & Schiffermüller, 1775)	Sp-Aut	V, X	oases	polyph
36. *Heterographa puengeleri* Bartel, 1904	Aut-Sp	X, III	desert	unknown
37. *Mniotype johanna* (Staudinger, 1898)	Aut	XI	oases	unknown
38. *Eremotrachea bacheri* (Püngeler, 1902)	Sp	III	desert	unknown
39. *Polymixis epiphlebs* (Turati & Krüger, 1936)	W	XII	desert	polyph
40. *Polymixis juditha* (Staudinger, 1898)	W	I	desert	polyph
41. *Polymixis trisignata* (Ménétriés, 1847)	Aut	XI	oases	polyph
42. *Scythocentropus eberti* Hacker, 2001	Aut	XI	desert	unknown
43. *Scythocentropus inquinata* (Mabille, 1888)	Aut	XI	desert	unknown
44. *Sesamia cretica* Lederer, 1857	Sp-Aut	VI, X	oases	polyph
45. *Sesamia nonagrioides* (Lefebvre, 1827)	Sp-Aut	V, X	oases	polyph
46. *Spodoptera cilium* (Guenée, 1852)	Sp-Aut	IV, X	ubiquitous	polyph
47. *Spodoptera exigua* (Hübner, 1808)	Sp-Aut	V, X	ubiquitous	polyph
48. *Spodoptera littoralis* (Boisduval, 1833)	Sp-Aut	V, X	oases	polyph
49. *Cryphia paulina* (Staudinger, 1892)	Sp	IV	ubiquitous	unknown
50. *Africalpe intrusa* Krüger, 1939	Sp-Su	III, VI, X	desert	unknown
51. *Anumeta arabiae* Wiltshire, 1961	Sp-Su	I, IV	desert	monoph
52. *Anumeta asiatica* Wiltshire, 1961	Sp-Su	IV, VI, VIII	desert	monoph
53. *Anumeta atrosignata* (Walker, 1858)	Sp-Su	III, V, VIII	desert	monoph
54. *Anumeta spilota harterti* Rothschild, 1913	Sp-Su	III, V, IX	desert	monoph
55. *Anumeta straminea* (Bang-Haas, 1906)	W	I	desert	monoph
56. *Anydrophila stuebeli* (Calberla, 1891)	Sp	III	desert	monoph
57. *Armada panaceorum* (Ménétriés, 1849)	Sp	III	desert	monoph
58. *Autophila cerealis* (Staudinger, 1871)	Sp-Su	I, V, XI	desert	oligo
59. *Autophila pauli* Boursin, 1940	Sp-Su	III, V, VIII	desert	oligo
60. *Catocala puerpera* (Giorna, 1791)	Sp	V	oases	monoph
61. *Cerocala sana* Staudinger, 1901	Sp-Aut	IV, X	desert	monoph
62. *Clytie infrequens* (Swinhoe, 1884)	Sp-Su	III, V, X	oases	monoph
63. *Clytie illunaris* (Hübner, 1813)	Sp-Aut	V, X	oases	monoph
64. *Clytie sancta* (Staudinger, 1898)	Sp-Aut	IV, VIII	oases	monoph
65. *Clytie scotorrhiza* Hampson, 1913	Aut-Sp	XI, III	oases	monoph
66. *Drasteria flexuosa* (Ménétriés, 1847)	Sp-Aut	V, X	oases	monoph
67. *Drasteria herzi* (Alphéraky, 1895)	Aut-Sp	XI, III	oases	unknown
68. *Drasteria kabylaria* (Bang-Haas, 1906)	Sp-Aut	IV, X	desert	monoph
69. *Gnamptonyx innexa* (Walker, 1858)	Sp-Su	III, V, X	desert	monoph
70. *Heteropalpia acrosticta* (Püngeler, 1904)	Sp-Aut	V, XI	desert	monoph
71. *Heteropalpia profesta* (Christoph, 1887)	Sp-Aut	VI, X	oases	monoph
72. *Ophiusa tirhaca* (Cramer, 1777)	Sp-Su	III, V, X	ubiquitous	polyph
73. *Pandesma robusta* Walker, (1858)	Sp-Su	II, VII, X	ubiquitous	polyph
74. *Pericyma albidentaria* (Freyer, 1842)	Sp-Aut	VI, X	oases	monoph
75. *Pericyma squalens* Lederer, 1855	Sp-Aut	VI, X	oases	monoph

Species	Type of seasonal distribution	Month(s) of highest occurrence	Preferable biotope	Host plant specialization
76. *Prodotis boisdeffrii* (Oberthür, 1867)	Sp-Aut	V, X	oases	oligo
77. *Prodotis stolida* (Fabricius, 1775)	Sp-Aut	V, X	oases	polyph
78. *Rhabdophera arefacta* (Swinhoe, 1884)	Sp-Aut	V, X	oases	oligo
79. *Scodionyx mysticus* Staudinger, 1900	Aut-Sp	XI, III	desert	monoph
80. *Tathorhynchus exsiccata* (Lederer, 1855)	Sp-Aut	IV, X	ubiquitous	oligo
81. *Tytroca dispar* (Püngeler, 1904)	Sp-Aut	V, X	desert	monoph
82. *Ulotrichopus tinctipennis* (Hampson, 1902)	W	I	desert	unknown
83. *Earias chlorophyllana* Staudingr, 1892	Sp-Aut	V, XI	oases	oligo
84. *Earias insulana* (Boisduval, 1833)	Sp-Aut	IV, X	oases	oligo
85. *Brachygalea albolineata* (Blachier, 1905)	Sp	III	desert	unknown
86. *Pamparama sinaica* (Wiltshire, 1948)	W	I	desert	monoph
87. *Cleonymia chabordis* (Oberthür, 1876)	Sp	III	desert	monoph
88. *Cleonymia jubata* (Oberthür, 1890)	Sp	III	desert	monoph
89. *Cucullia syrtana* (Mabille, 1888)	W	I	desert	monoph
90. *Metopoceras kneuckeri* (Rebel, 1903)	Sp	III	desert	monoph
91. *Metopoceras omar* (Oberthür, 1887)	Sp	III	desert	monoph
92. *Metopoceras philbyi* Wiltshire, 1980	Sp	III	desert	monoph
93. *Metopoceras solituda* (Brandt, 1938)	Sp	III	desert	monoph
94. *Acantholeucania loreyi* (Duponchel, 1827)	Sp-Aut	IV, X	oases	polyph
95. *Mythimna languida* (Walker, 1858)	Sp-Aut	IV, X	oases	polyph
96. *Mythimna sicula* (Treitschke, 1835)	Sp-Aut	V, X	ubiquitous	polyph
97. *Cardepia affinis* Rothschild, 1913	Sp-Aut	IV, X	oases	oligo
98. *Cardepia sociabilis* (de Graslln, 1850)	Sp-Aut	IV, X	oases	oligo
99. *Hadena silenides* (Staudinger, 1895)	Sp	III	desert	polyph
100. *Hadula sabulorum* (Alphéraky, 1882)	Sp	III	desert	polyph
101. *Hadula trifolii* (Hüfnagel, 1766)	Sp-Aut	IV, X	oases	polyph
102. *Hecatera weissi* (Boursin, 1952)	Sp	III	desert	unknown
103. *Lacanobia softa* (Staudinger, 1898)	Aut-Sp	XI, IV	oases	unknown
104. *Leucania palaestinae* Staudinger, 1897	Sp-Su	III, VI, X	oases	polyph
105. *Leucania putrescens* (Hübner, 1824)	Aut	XI	desert	polyph
106. *Mythimna alopecuri* (Boisduval, 1840)	Aut	XI	ubiquitous	polyph
107. *Mythimna riparia* (Rambur, 1829)	Sp	IV	oases	polyph
108. *Mythimna vitellina* (Hübner, 1808)	Sp-Aut	V, X	oases	polyph
109. *Odontelia daphnadeparisae* Müller et al, 2007	Sp	III	desert	monoph
110. *Polytela cliens* (Felder & Rogenhofer, 1874)	Sp	III	desert	monoph
111. *Pseudaletia unipuncta* (Haworth, 1809)	Sp-Aut	IV, X	oases	polyph
112. *Thargelia gigantea* Rebel, 1909	Sp	III	desert	monoph
113. *Helicoverpa armigera* (Hübner, 1808)	Sp-Aut	VI, X	oases	polyph
114. *Chazaria incarnata* (Freyer, 1838)	Sp	III	desert	monoph
115. *Heliothis nubigera* Herrich-Schäffer, 1851	Sp-Aut	IV, X	ubiquitous	polyph

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Species	Type of seasonal distribution	Month(s) of highest occurrence	Preferable biotope	Host plant specialization
116. *Heliothis peltigera* (Denis & Schiffermüller, 1775)	Sp-Aut	V, X	oases	polyph
117. *Masalia albida* (Hampson, 1905)	Sp	III	desert	unknown
118. *Zekelita ravalis* (Herrich-Schäffer, 1851)	Sp-Aut	VI, X	ubiquitous	oligo
119. *Agrotis spinifera* (Hübner, 1808)	Sp-Su	III, V, X	oases	polyph
120. *Agrotis haifae* Staudinger, 1897	Aut	XI	desert	polyph
121. *Agrotis herzogi* Rebel, 1911	Aut-Sp	XI, III	ubiquitous	polyph
122. *Agrotis ipsilon* (Hufnagel, 1766)	Sp-Aut	V, X	oases	polyph
123. *Agrotis pierreti* (Bugnion, 1837)	Aut	XI	desert	polyph
124. *Agrotis puta* (Hübner, 1803)	Aut-Sp	XI, III	oases	polyph
125. *Agrotis sardzeana* Brandt, 1941	Aut	XI	desert	polyph
126. *Agrotis segetum* (Denis & Schiffermüller, 1775)	Sp-Su	III, V, X	oases	polyph
127. *Agrotis trux* (Hübner, 1824)	Aut	XI	ubiquitous	polyph
128. *Dichagyris imperator* (Bang-Haas, 1912)	Sp	III	desert	monoph
129. *Dichagyris singularis* (Staudinger, 1892)	Aut	XI	desert	polyph
130. *Euxoa anarmodia* (Staudinger, 1897)	Aut	XI	desert	polyph
131. *Euxoa canariensis* (Rebel, 1902)	Sp	III	desert	polyph
132. *Euxoa oranaria* (Bang-Haas, 1906)	Aut	XI	desert	polyph
133. *Euxoa temera* (Hübner, 1808)	Aut	XI	ubiquitous	polyph
134. *Noctua pronuba* (Linnaeus, 1758)	Sp-Aut	V, X	oases	polyph
135. *Peridroma saucia* (Hübner, 1808)	Sp-Su	III, V, X	oases	polyph
136. *Powellinia lasserei* (Oberthür, 1881)	Aut	XI	desert	unknown
137. *Autographa gamma* (Linnaeus, 1758)	Sp-Aut	V, X,	oases	polyph
138. *Chrysodeixis chalcites* (Esper, 1789)	Sp-Su	III, V, X	oases	polyph
139. *Cornutiplusia circumflexa* (Linnaeus, 1767)	Sp-Aut	V, X	oases	polyph
140. *Trichoplusia ni* (Hübner, 1803)	Sp-Aut	V, X	oases	polyph
141. *Thysanoplusia daubei* (Boisduval, 1840)	Sp-Aut	IV, X	oases	oligo

species flying only in December and January. None of the species were found during the summer. The majority (46 of 58) were eremic elements, 10 being Palearctic and two being tropical species.

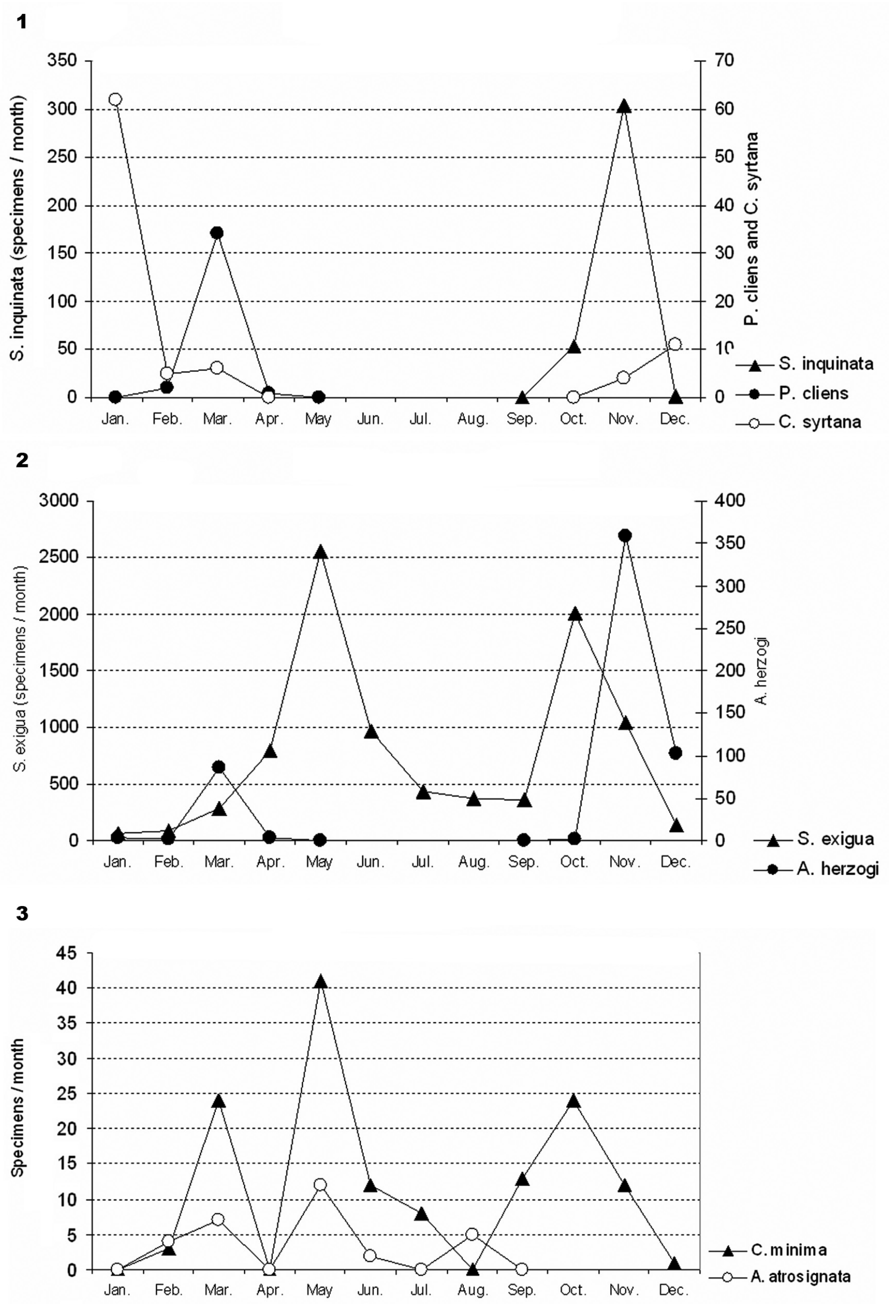
a) Autumnal species flying around November (Table 2) with dynamics as in *Scythocentropus inquinata* (Fig. 1). Most of the species (18 of 25) inhabited extreme desert localities, although *Eremobastis judaica*, *Mniotype johanna*, and *Polymixis trisignata* were restricted to oases. None of the autumnal species are known to be monophagous, although for nine species the host plants are unknown; the other 16 are polyphagous, including the well-known root-feeding pest species of the genera *Agrotis* and *Euxoa*, as well as species generally polyphagous on low plants, such as species of the *Caradrina* group (genera *Eremodrina*, *Paradrina*, *Holpodrina* (Table 1).

Table 2

Number of species per habitat and rate of similarity between species assemblages

Months	Unimodal				Bimodal				Trimodal				Total per all sites	Rate of similarity between species assemblages	
	Extreme desert	Oases	Settlements	Total	Extreme desert	Oases	Settlements	Total	Extreme dessert	Oases	Settlements	Total		Similarities <0.5	Localities sharing similar fauna
Jan	5			5	1			1	1			1	7		
Feb										1	1	2	2	0	
Mar	23			23	2	4	2	8	5	9	2	16	47	1	Zin / Sh
Apr		2	1	3	3	11	6	20	1			1	24	1	Zin / Haz
May		1		1	4	21	3	28	2	12	2	16	45	10	Zin / Haz / Id / Sh / Kik
Jun						5	1	6	2	1		3	9	1	Zin / Kik
Jul						1		1			1	1	2	1	Zin / Kik
Aug									3	1		4	4	1	Zin / Kik
Sep									1				1	1	Zin / Kik
Oct					7	34	10	51	3	9	3	15	66	8	Zin / Haz / Id / Sh / Kik
Nov	19	2	4	25	2	5	4	11				1	37	8	Haz / Id / Sh / Neq
Dec	1			1									1		
Total:	47	6	5	58	9	41	13	63	7	10	3	20			

Legend: Zin — En-Zin, Kik — Ne‘ot-HaKikkar, Neq — Nahal Neqarot, Sh — Shezaf, Haz — Hazeva, Id — ‘Iddan.



Figs. 1–3. Different types of seasonal distribution. 1. Unimodal dynamics of flight. 2. Bimodal dynamics of flight. 3. Trimodal dynamics of flight.

b) Spring species flying around March (Table 2), with dynamics as in *Polytela cliens* (Fig. 1). These include 23 exclusively "extreme desert" species flying in March, and three "oases" species, *Eublemma albina*, *Catocala puerpera*, and *Mythimna riparia*, flying in April and May. All of the species with known host plants (17 species) are monophagous on ephemerous desert plants. The most common species were: *Hadula sabulorum*, *Cleonymia chabordis*, *Metopoceras omar*, and *Polytela cliens*. One species, *Odontelia daphnadeparisae*, was only collected on sand dune habitats.

c) Winter species (6), flying around December and January (Table 2), with dynamics as in *Cucullia syrtana* (Fig. 1). All winter species were restricted to the dry sites, with five of them being eremic and one being an Afrotropical element. The most common species was *Cucullia syrtana*. The host plants for all of them are unknown.

2) Bimodal species

Species flying twice a year (bimodal) comprised about 45% of the total (63 of 141), mostly with two periods of highest occurrence, one in April–May, and another in October (Table 2). Two groups are included here. The spring–autumn species were common in May, rare during the summer, reappeared in high numbers in October and did not occur during winter. The autumn–spring species appeared in November together with the autumn species. In March they re-occurred in a second peak together with the spring species. During the winter they were uncommon except on mild nights, but they never occurred during summer.

d) The spring–autumn group comprises 53 species. The most common of them in the Arava was *Spodoptera exigua*, which is multivoltine (Avidov and Harpaz, 1969) and was found almost all year round except December and January, although with only two short peaks, in May and October (Fig. 2). Such noctuids are largely restricted to oases and settlements (41 of 53), with only nine species occurring in dry sites. Most of the species are polyphagous (43 of 53) with a Palaearctic or tropical distribution. Some of them, such as *Agrotis ipsilon*, *Agrotis segetum*, and *Trichoplusia ni*, are also known as agricultural pests.

e) The autumn–spring group comprises nine species. One of the most common of these species was the "extreme desert" species, *Agrotis herzogi* (Fig. 2), which is univoltine (Hacker, 2001), and regularly found from October to April but peaked in November and March, when almost 80% of the specimens were collected. The bulk of species (7/9) are of eremic origin and polyphagous on annual grasses. Only one species, *Scodionyx mysticus*, is monophagous on Acacia.

3) Trimodal species

Trimodal species included 20 multivoltine species, flying in three consecutive peaks (Table 2), with the highest rate of occurrence in March, May, and October. In oases and extreme desert sites they were represented by different species with different times of flight, respectively.

f) The trimodal oasis species, such as *Catamecia minima* (Fig. 3), peaked in March, May, and October. They are mainly of tropical origin (*Arenostola deserticola*, *Agrotis spinifera*, *Sesamia cretica*) or Mediterranean polyphagous species (*Sesamia nonagrioides*).

g) The trimodal extreme desert species typically fly in March, May, and August. Most of them are Catocalinae, such as the psammophilous species of the genus *Anumeta* that develop on *Calligonum* sp. (Hacker, 2001), with larvae adapted to living in sand dunes, such as *Anumeta atrosignata* (Fig. 3) or Catocalinae species that develop on *Acacia*, such as *Tytroca dispar* and *Gnamptonyx innexa*.

4) Species with locality-dependent modality

h) Some species of Catocalinae showed plasticity in their patterns of flight, depending on their biome. For example, in the extreme desert sites, *Prodotis boisdeffrii* and *Drasteria flexuosa* were scarce but regularly seen in March and April, whereas in oases they were common from March to August.

Seasonal changes in species diversity and differences between the sites

To compare seasonal changes in species assemblages, the Jaccard coefficients of similarity among sites were calculated for each month, resulting in a 6 × 6 matrix with 15 coefficients of similarity. The number of coefficients per matrix that are higher than 0.5 (more than 50% of species in common for any two localities compared) is considered an indicator of faunal resemblance between sites. The coefficients of winter catches (December and January) and summer catches (June–September for desert localities) were not calculated due to the small number of species.

The fauna of February was extremely poor, with only two trimodal species flying in oases and settlements. In March the total number of species "peaking" rose to 47 (Table 2) with almost half of them (23 species) being unimodal species of extreme desert. Most of the Jaccard coefficients for this month were below 0.5, showing generally a very distinct faunal composition between all sites; the only coefficient slightly higher than 0.5 was calculated between 'En Z̲in and Shezaf. In April the unimodal species of the extreme desert sites disappeared and the total number of species fell to 24. The following month was characterized by another jump in the number of species, totalling 45. These are mostly multivoltine (bimodal and trimodal) species flying in oases. The number of the Jaccard coefficients with value higher than 0.5 reached 10, showing that this species assemblage occupied all habitats with the exception of an extreme desert site – Neqarot, which was more species-poor. From June to September the number of species flying in the desert dropped to two species each of the genera *Tytroca* and *Heteropalpia* (Catocalinae) that are monophagous on acacia trees, whereas in oases eight polyphagous species (developing on herbs) were on the wing during the same period.

October was characterized by a peak in appearance of 66 species (Table 2) in oases and settlements, occurring generally throughout all the habitats with the exception of Neqarot, i.e., the same picture as in May. In November another species assemblage appeared, represented mostly by unimodal species. These occupied all the extreme desert sites and settlements, while the number of species flying in oases became negligible.

DISCUSSION

This study has shown that in the Arava Valley the noctuid fauna of extreme desert sites, on the one hand, and of the oases and settlements, on the other hand, differs in species composition and in the periods of highest species occurrence. The oases and settlements fauna is generally represented by bivoltine or multivoltine polyphagous species of Palearctic and tropical origin, most of them flying in May and October. In the oases, some species extend their flight periods through the hottest months, from June to September, though none of them showed a peak during this period. It was also observed that "extreme desert" noctuids generally fly only once a year (monovoltine), in March or November. The species that fly in March are predominantly monophagous, while the species that fly in November are polyphagous. These two groups probably represent two different types of lifecycle adaptation to extreme desert conditions.

Diapause, obligatory or facultative, and aestivation are specific adaptations of insects to survive harsh conditions (Tauber et al., 1986). Depending on the bio-geographical zone, different survival strategies have developed. In the Arctic most insects are monovoltine and typically emerge early in order to use the short summers as efficiently as possible (Danks, 2004). Likewise, in extreme desert sites, a common survival strategy is to limit offspring to a single generation per year and to abbreviate the duration of larval development. In this case, the insects spend the unfavourable hot summer droughts in diapause.

Reproductive success of phytophagous insects living in extreme deserts depends on the ability to synchronize the period of larval development with the period of highest nutritional value of their host plants. For species developing on trees, the larval food is available most of the year, which enables them to be multivoltine even in extreme deserts, such as species of the noctuid genera *Heteropalpia*, *Tytroca*, and *Gnamptonyx*, that are monophagous on acacia, or species of *Clytie*, that are monophagous on tamarisk. For species developing on ephemeral desert plants, the larval food is available only during a short period, because these plants also exhibit short life cycles, but without resistance to drought. Their reproductive success depends on the ability to synchronize germination with favourable environmental conditions (Leopold and Kriedemann, 1975).

Because of irregular rainfall vegetative periods in the desert are short and unpredictable (Zohary and Orshansky, 1949). In the Arava desert, different univoltine *Lepidoptera* species living in extreme desert sites peak either in March or November (Hacker et all. 2001). The noctuid species that fly in March are oligophagous or monophagous, developing mainly on annuals (Wiltshire, 1948, 1949, 1957, 1964, 1990; Schetkin, 1965; Falkovich, 1979). The mating and egg-laying period of these species, therefore, must coincide with the first growth of the desert vegetation in order to allow oviposition. Any further delay in egg-laying or a long duration of egg development would increase the risk of larval mortality due to the short vegetative period.

The species flying in November use a different strategy to cope with this problem. Many of them are predominantly polyphagous, often on roots and other subterranean parts of plants (Zolotarenko, 1970; Falkovich, 1979; Fibiger, 1990, 1993). Because they are able to utilize a large variety of host plants, they can lay their eggs in autumn before the rains and plant development. After the first winter rain, the larvae hatch and develop synchronously with their host plants. These species oviposit on the soil, the lower parts of stems or, with specialized ovipositors, deep into the soil, similar to some desert *Agrotis* (Kozhantshikov, 1937). Some *Euxoa* larvae remain inside their eggs over long drought periods, awaiting suitable conditions after the first rain (Zolotarenko, 1970).

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