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# Flight year of the alternate-year *Xestia* moths (Lepidoptera, Noctuidae) in north-eastern Siberia – A character from the Ice Ages (<sup>1</sup>)?

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#### Summary

A total of 1848 noctuid moths of 39 species were collected with light traps in the Upper Kolyma River area, north-eastern Siberia, U.S.S.R. (62°N 149°40'E) in the summer of 1987. Twelve *Xestia* species ( $\frac{1}{3}$  of all species) known to fly only every second year constituted 79.2% of the catch in the taiga biotopes, 53.2% on mountain tundra and 14.3% on a steppe slope ; catches from the same areas in previous years show that the moths fly almost exclusively in odd-numbered years.

It is concluded that the strategy is peculiar for the taiga, owing to the short season and relatively predictable environmental conditions. The distribution of the flight years in North America is consistent with the hypothesis that flight year correlates with Ice Age refugia, with different flight years on different sides of the Continental Ice Sheet. If the odd-year area extends from NE Siberia all the way to the Kola Peninsula, from where it is again known, the situation would be similar to North America. The contact zones of the populations with different flight years would be situated in the west in Finland and in the east at Hudson Bay, Canada. According to this model, the age of the flight year areas would exceed 10 000 years.

As an addition to an earlier hypothesis that suggested that parasitoids and predators eliminated the intervening-year population, it is suggested that the defence strategy of the host plants may be a synergistic factor : the plants would invest less on chemical defence when they are free of the *Xestia* herbivores every second year.

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## INTRODUCTION

A fascinating ecological and zoogeographical phenomenon in the subarctic and boreal lepidopterous fauna is the alternating-year occurrence of many butterflies and moths. The flight-years in Fennoscandia of *Erebia* and *Oeneis* species (Satyridae) were mapped by Douwes (1980) and those of *Xestia* species by MIKKOLA (1976). For the *Xestia*, some additions from Sweden were published by IMBY & PALMQVIST (1978). Recently, the flight-year pattern of *Xestia* species in North America was described briefly by LAFON-TAINE et al. (1987), and PULLIAINEN & ITÄMIES (1988) analyzed habitat preferences of *Xestia* species in eastern Finnish Lapland.

The phenomenon is most pronounced in the predominantly taiga subgenera *Anomogyna* and *Pachnobia* of the genus *Xestia*. A total of nearly 20 species occur in the subarctic and boreal areas, and in any one area, where two or more of these fly together, they do so synchronously. *Xestia sincera* (H.-S.) has been noted to show the most loose contact with the other species (MIKKOLA, 1976) and in some areas *X. alpicola* (ZETT.) seems to fly asynchronously with *X. speciosa* (HB.) (MIKKOLA, 1976; IMBY & PALMQVIST, 1978).

The alternating-year rhythm of *Xestia* species is known from the British Isles through Fennoscandia to the western part of the Kola Peninsula, USSR, and again from North America, from Alaska to Newfoundland, but the situation in Siberia has not been studied. Recently we were able to make observations on the noctuid community during a flight year of *Xestia* species in the Upper Kolyma River area in northeastern Siberia. Here we describe the phenomenon in relation to other night-flying noctuids and discuss its ecological significance in the subarctic biota and its zoogeographic character.

## MATERIAL AND METHODS

Most of the material was collected during the period July 8 to August 3, 1987 at or near the Aborigen Biological Station, the Upper Kolyma River, Magadanskaya oblast', USSR ( $62^{\circ}N$  149°40'E) (Fig. 1). Each night when the weather was reasonable, two light traps (Jalas model) were run using a Honda generator for 4-5 h/night. They operated for 13 nights in different biotopes of the taiga at elevations of 500-600 m a.s.l. : 6 nights in a larch (*Larix gmelinii*) bog, 2 nights in a larch forest in a small mountain stream valley, 1 night on an aspen (*Populus tremula*) slope with scattered larches and 4 nights on an open scree slope with sparse larch stand. In mountain tundra habitats, at elevations of 1250 to 1450 m (the timber line at about 900 m), the traps were operated for 9 nights. The main biotope was dry stony



Fig. 1. The Aborigen Biological Station near Kolyma River in north-eastern Siberia in August 1987. All coniferous trees are larches (*Larix gmelinii*), in the foreground as dense stand along a small stream, to the right small trees scattered in a natural bog. Two meter thick ice still covers the stream in the background.

tundra with Dryas, Rhododendron redowskianum, Anemone sibirica, etc. ; the traps were positioned in the upper parts of steep slopes. In addition, we had one trapping night on a steppe slope near the shore of the Kolyma River.

Only the trap material is treated in this article, i.e. the catches from daytime netting or night catches from bait traps or from a lamp and sheet combination are not included. The results from the two traps were compared with light catches (no traps used) as well as with netting results from the Magadanskaya oblast' (mainly from the biological station of Aborigen and Kulu, but also from NE Chukotka) from the years 1979 (L. MARCHENKO), 1980 (KONO-NENKO), 1981, (MIKKOLA), 1982, (KONONENKO), 1983. Yu. A. CHISTYAKOV) and 1986 (KONONENKO) (Table 3).

#### RESULTS

The results from the year 1987 are presented in Tables 1 and 2. The average catches of the traps from the taiga and tundra were not very different, 86.4 moths/trap/night from the former and 62.7 moths/trap/night from the latter. The variation was huge, from 1 species/5 specimens with two traps on a bright, cool night on July 9, to 14 species/139 specimens on a dark, warm night on July 29. The total of the material was 1848 noctuid moths of 39 species of which 1213 (65.6%) were alternating-year *Xestia*. In the taiga habitats, nearly 80% of individuals belonged to these species; in the tundra habitats the proportion would probably have been lower if the margin of the taiga forest would have been situated further away than about one kilometre.

Table 1.	The proportion	on of altern	ating-year	Xestia at	t the U	Jpper H	Kolyma	area, N	IE S	iberia,
from July	8 to August	3, 1987, as	revealed b	y light ti	raps. S	pp. : sp	pecies; i	ind. : in	divi	duals;
% : % tot	al individuals									

	Taiga 500-600 m			Tundra 1250-1450 m			Steppe slope 450 m			
	Spp.	ind.	%	Spp.	ind.	%	Spp.	ind.	%	
Altyear Xestia Other	11	889	79.2	7	300	53.2	4	24	14.3	
noctuids Total	16 27	234 1123	20.8 100.0	14 21	264 564	46.8 100.0	9 13	137 161	85.7 100.0	

#### DISCUSSION

A general hypothesis and deterministic model explaining the phenomenon of alternating-year flight was offered by MIKKOLA (1976). In the northern areas the species are unable to reach maturity in a single year, and, probably influenced by the advantage of the alternating-year flight, the evolution has lead to a two-year life cycle (the larvae have two diapauses, as young and as a full-grown larva). During a numerical imbalance between the successive populations which are genetically more or less isolated from each other, the predators and/or parasitoids developed by the larger larval population begin to control the smaller one. In many areas, the smaller population is entirely wiped out, but in others, the smaller population is regularly occurring in low numbers. This shows the dynamic nature of the phenomenon.

Species	Taiga	Tundra	Steppe slope	Total
Subgenus Pachnobia			-	
Xestia tecta (HB.)	155	62	6	223
X. kolymae (HERZ)	-	-	1	1
X. ursae (McD.)	15	13	2	30
X. atrata (MORR.)	30	19	-	49
Subgenus Anomogyna				
X. rhaetica (STGR.)	7	1	-	8
X. rhaetica ssp.				
fuscogrisea (Kon.) (1)	91	-	-	91
X. sp. n. nr. rhaetica	19	-	-	19
X. speciosa (HB.)	129	-	-	129
X. brunneopicta (MATS.)	57	1	-	58
X. gelida (SPSCH.)	41	-	-	41
X. laetabilis (ZETT.)	24	1	-	25
X. albuncula (Ev.)	321	203	15	539

Table 2. The occurrence of different alternating-year *Xestia* species in different biotopes in the Upper Kolyma area in the year 1987

(1) This taxon may be a distinct species and will be treated in a future revision.

Table 3. Species of *Xestia* subgenera *Anomogyna* and *Pachnobia* caught in different years in the Magadanskaya oblast, NE Siberia. A = Aborigen Biological Station, K = Kulu Biological Station and CH = Chukotka (see text)

Year	Area	Species caught
1979	K	12
1980	A + K	0
1981	A	3
1982	CH	1 (X. tecta 5-8 ind.)
1983	K	6
1984	-	-
1985	-	-
1986	CH	1 (X. tecta 2-3 ind.)
1987	A	12

The regulating system in the 13- or 17-year cicadas (Magicicada) seems to be relatively similar to that in Xestia (LLOYD & DYBAS, 1966a; KARBAN, 1966b, 1982). Similarly, in the Xestia species a side effect of the parasitoid/ predator control might be that during high population densities the relative efficiency of parasitization/predation may remain lower because of the inability of the enemies to use the prey effectively when it is very abundant. The population mathematical model proposed by HANSKI (1988) does not explain the dynamic, self-regulating character of the phenomenon, but the effect may have had significance in the initial phase of the evolution of the alternating-year strategy. HELIÖVAARA & VÄISÄNEN (1984) presented a misleading criticism against the parasitoid/predator hypothesis because it was based on the alternate-year occurrence of the bug Aradus cinnamomeus (PANZ.) (Heteroptera). In the bug, food competition between larval and adult populations causes periodicity (Heliövaara & Väisänen, 1986) which is not the case in Xestia. The Xestia larval populations of succeeding years would overlap, but the young and old larvae hardly need to compete for food because (1) according to ex ovo rearings, the larvae are quite polyphagous (except X. sincera (H.-S.)) and may even change foodplants, some of which are very abundant in nature, and (2) the main feeding periods of the larval populations would occur in different years : in the first year the young larvae eat very little before overwintering in the 1st instar, and after the second overwintering they feed only for a short period (M. AHOLA, pers. comm.; BERGMANN, 1954). The larvae have not been observed to have any cannibalistic behaviour (M. AHOLA, K. & J. SILVONEN, pers. comm.).

Do the *Xestia* species in question just happen to live predominantly in taiga habitats, or does the ecological strategy of alternate-year flight restrict them to taiga? We propose both. The strategy probably only works on taiga because of the short growing season which necessitates a biennial life cycle and because of the relatively predictable environmental conditions. On the other hand, the strategy may have contributed to the success and wide speciation of these moths.

Here we present an additional hypothesis about a mechanism which may work synergistically with parasitoid/predator mechanism : the food plants of the larvae may invest less on the defence strategy against herbivores when they are free of herbivores every second year. The plants may even show an alternating-year rhythm in their defence, presumably to the advantage of the *Xestia* larvae. The poor edaphic conditions in a boggy northern area may promote such interactions : "Resource limitation selects for inherently slow growth rates [in plants], which in turn favor large investments in defense" (COLEY et al., 1985). The present material is important because, due to the light nights in northern areas, effective light catching of these species is difficult, particularly in open biotopes. Thus, in Lapland at 67°40'N the light trap catches from tundra of *Xestia tecta* and *X. alpicola* (ZETT.) were roughly 1/10 of the traps in the forest (PULLIAINEN & ITÄMIES, 1988) while in NE Siberia, at 62°N, these species (the latter represented by the closely related *X. albuncula*) were more abundant on the tundra, the catches being about 1/3 and 2/3, respectively, of the forest catches. The difference is certainly caused by the different light conditions.

Several of the alternate-year *Xestia* also occur in southern montane areas but do not, as far as is known, show a similar biennial rhythm (possibly they secondarily have an annual life cycle).

In North America, the pattern of flight years (LAFONTAINE *et al.*, 1987) seems to reflect the history of the Beringian refuge (KONONENKO *et al.*, 1988). The odd-year flight area from Alaska westward to the Hudson Bay would represent the flight-year of the *Xestia* populations which survived the Ice Ages in the Beringia. The even-year area of eastern Canada would show the flight-year of the populations which survived south-east of the Continental Ice Sheet. Some subspecific differences may reflect interaction between the geographical isolation described and the isolation caused by the flight years. Thus, there is a clear border between *X. t. tecta* and *X. t. tectoides* (CORTI), and between *X. o. okakensis* (PACK.) and *X. o. morandi* (BENJ.) in the Hudson Bay area which would possibly not exist without the latter kind of isolation.

For Eurasia it is known that an even-year area extends from the British Isles (only *X. alpicola* occurs there) to Scandinavia and western parts of Finland (MIKKOLA, 1976), and an odd-year area exists in eastern Finland and western parts of the Kola Peninsula. Now we know that north-eastern Siberia also has an odd-year flight (the observed rhythm is probably typical of a wide area). If the odd-year area extends all the way through northernmost Siberia to the Kola Peninsula, we would have a pattern similar to North America. This would clearly point towards the postglacial distribution of the flight year from Beringia to the east and to the west.

The complicated borderline in Finland would actually be the postglacial contact zone of the two populations, corresponding to that in the Hudson Bay area. It is not known how stable this kind of borderline may be. In fact, there exists some indication of a westward movement of the borderline in South Varanger, Norway, during the past hundred years (MIKKOLA, 1976). The zoogeography of the flight-years should be kept separate from the distribution histories of moth populations, though these may sometimes

coincide, as probably in the case of X. tecta and X. okakensis in North America.

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#### Kommunikation

Für eine faunistische Bearbeitung der Microlepidoptera des Monte Baldo-Gebietes (Italien) ersuchen wir alle Kollegen um Überlassung von Sammellisten aus dem betreffenden Gebiet. Eventuell nötige Determinationen werden gerne durchgeführt.

Meldungen erbeten an : Dr. h.c. K. BURMANN und Dr. P. HUEMER Tiroler Landesmuseum Ferdinandeum Museumstr. 15, A-6020 Innsbruck.

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