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The rôle of migration for the population dynamics of the larch bud moth, *Zeiraphera diniana* Gn. (Lep. Tortricidae)^{1,2}

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The rôle of migration for the population dynamics of the larch bud moth, Zeiraphera diniana Gn. (Lep., Tortricidae) - Moth flight of *Z. diniana* was monitored during the last population cycle by means of pheromone and light traps in an area of approx. 20000 km². The relationship between larval density and male moth catch is quantified by means of the power function $y = ax^b$. It is postulated that long range migration over several 100 km may contribute to the remarkable synchronization of outbreaks along the alpine arch, but that this stochastic form of migration cannot influence the regularity of the cycles. Rather, this regularity appears to stem from regional migration phenomena; i.e. moths immigrate annually by positive anemotactic behaviour from lower altitudes into the upper region of alpine mountain valleys. A verbal model of migration is outlined in view of simulation studies in the future.

Population dynamics has to be looked upon in a holistic view. There are no single processes or factors responsible for its outcome, even when we have to deal with the apparently most simple ecological situation: the cyclic population fluctuation. This statement, however, should not divert from careful evaluation of single processes as only their relative impacts defined in time and space provide the necessary base for a general understanding of a species' population dynamics. The recent verbal model of the larch bud moth system (BALTENSWEILER, 1977) is presented to provide the necessary background for the discussion of the rôle of moth migration and the formulation of a new enlarged model.

The larch bud moth (*Zeiraphera diniana* Gn., Lep., Tortricidae), is the most serious forest defoliator of the larch stands in the European Alps. Since 1850 it devastated the Engadine area in south-eastern Switzerland 15 times. Its population dynamics has been investigated in details by the Department of Entomology, Swiss Federal Institute of Technology, Zürich, since 1949 throughout the Alps and especially in the Engadine valley. *Z. diniana* exhibits in the subalpine region between 1700 m and 2000 m a cyclic fluctuation of great regularity and amplitude (AUER, 1977; BALTENSWEILER, 1978). Larval density increases on the average from 1 to 30000 per larch tree within 4 generations, then defoliation occurs. Outbreaks last 1 to 3 years and occur at intervals of 8.64 ± 0.29 years (5% confidence interval). They may cause economic losses (reduction of larch growth, tree mortality) and are locally detrimental to the recreational use of the forests.

The cyclic fluctuation of the bud moth results from the interaction of the bud moth and its host, the larch tree, within an abiotic environment which in general favours population growth continuously. Defoliation of the larch induces a

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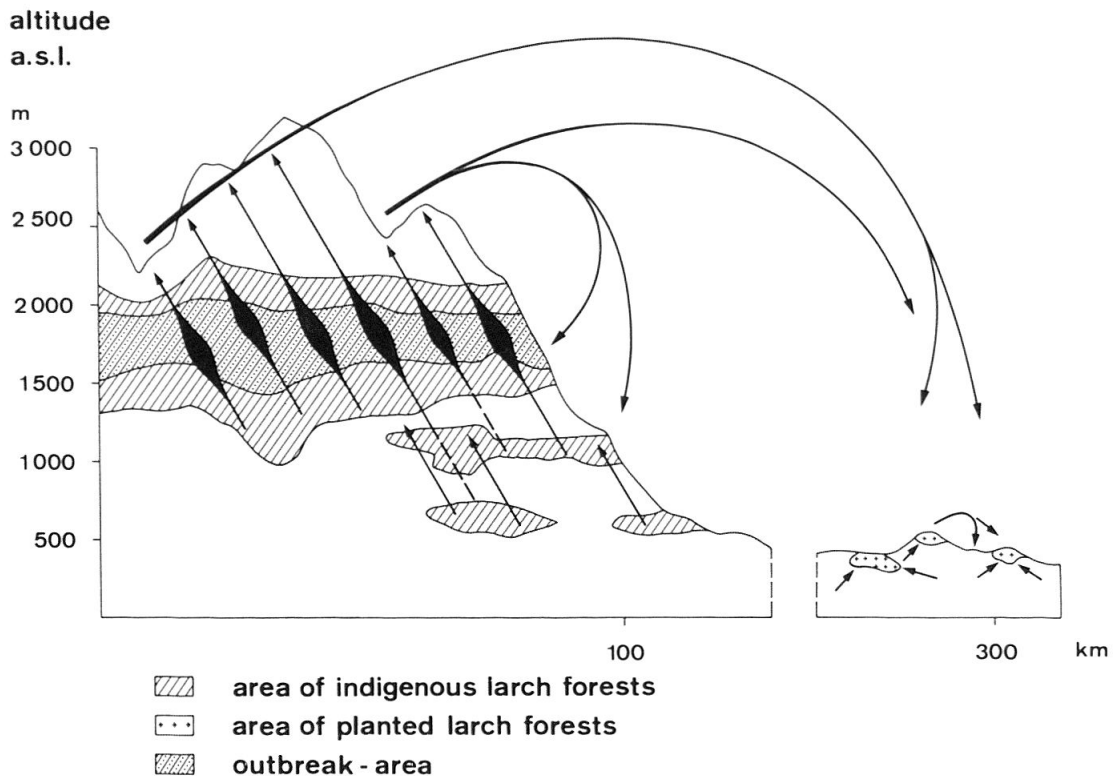


Fig. 1: Migration pattern of *Zeiraphera diniana* in the European Alps.

deterioration of the food quality and a decrease in food quantity, which in turn causes a decline in population density and selects for a more resistant ecotype. Thus a remarkable resilience is conferred to the system by the recovery of the host plant and directional selection processes through their time lags and the fixed carrying capacity of the biotope.

Accounts of migrating masses of larch bud moth are quite frequent (ANDRINSHEV, 1947; BURMANN, 1965; ESCHERICH & BÄR, 1909; SCHABUNEVITSCH, 1967); invariably they are mentioned in relation to outbreaks with their large tracts of defoliated larch stands. Thus they were considered as anecdotal phenomena. Concern about migration arose only when the magnitude of moths which swamped the extensive area of the latent fluctuation type outside the Alps at low altitude was recognized (GRAF, 1974; BALTENSWEILER & VON SALIS, 1975). The probability of influx in anyone area by long range dispersal would depend on the predominant weather pattern and the relative geographic position with respect to the exodus area. Because weather patterns vary with regards to locations rather stochastically the impact of long range dispersal on a specific area is not predictable.

From this it was deduced that long range dispersal may contribute to the conspicuous time sequence of defoliating densities throughout the Alps, but would not determine the regularity of regional cycles. Rather, this regularity of cycles appears to be partly the result of migration on a regional scale. This hypothesis is discussed in the following and supplemented with a verbal model which displays our approach to test this conception.

MOTH FLIGHT IN MOUNTAINOUS AREAS

The following definitions as formulated by BAKER (1978) are used throughout this paper. Migration is defined as the act moving from one spatial unit to another. In this context dispersal means to increase the distance between the individual members of a group whereas convergence describes the opposite process.

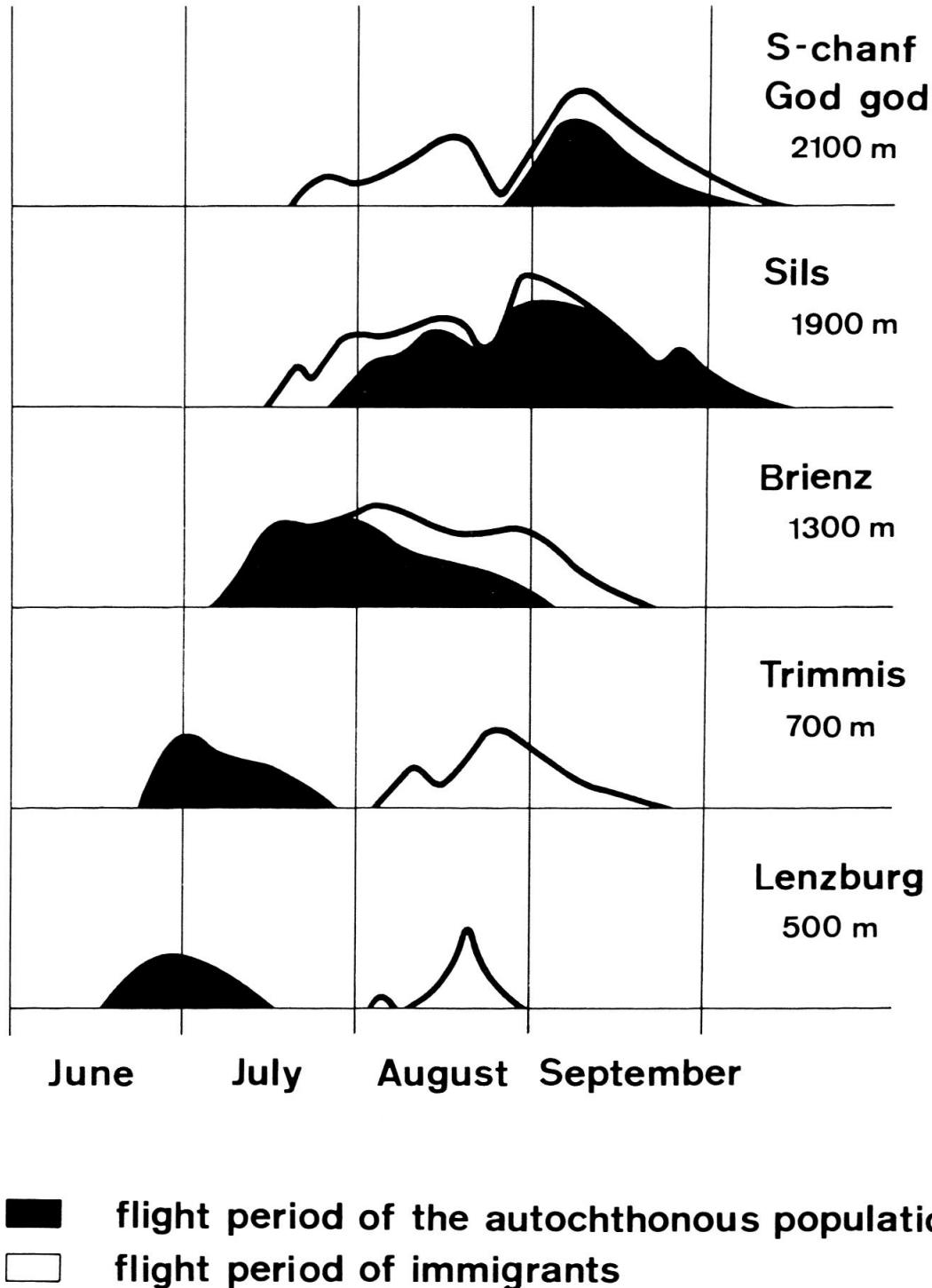


Fig. 2: Flight periods of *Zeiraphera diniana* at various sites in Switzerland.

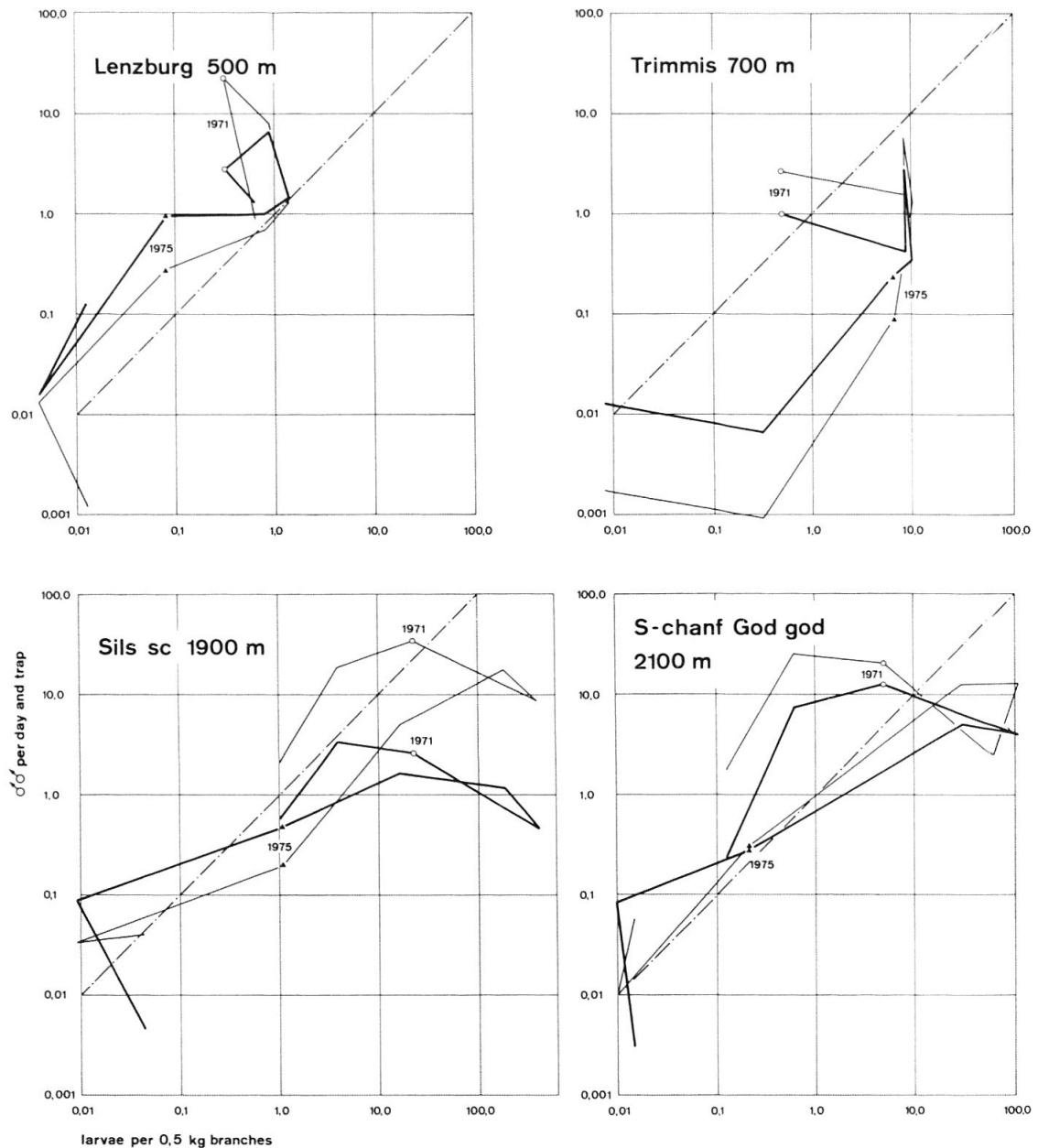


Fig. 3: Relationship between larval density per 0.5 kg larch branches and male moth catch per day and trap during the period 1970–1977 at 4 sites. Thick line: first flight per season; thin line: second flight per season.

Long range migration for most airborne organisms is generally downwind orientated; in contrast to this, local and regional flight of the larch bud moth is upwind. GREEN'S (1962) analysis of the flight behaviour of the European pine shoot moth, *Rhyacionia buoliana* (SCHIFF.), was the first showing that upwind flight turned into downwind flight at windspeeds in the range of 2.7 to 3.6 m/sec. This phenomenon, at that time appreciated only in terms of energetics, gained a biological aspect when knowledge about pheromone communication between the sexes added a new dimension to ecological studies since the late 1960's. From carefully controlled laboratory experiments, KENNEDY (1974) reports on phero-

monotaxic anemotaxis in day-flying moth, whereby the anemotactic angle is considered to be a function of the odor stimulation: odour causes positive anemotaxis whereas clean wind induced a typical searching or casting behaviour at right angles to the wind direction. With a discontinuous odour plume, the typical flight

Table 1: Population densities of the grey larch bud moth in the larval and moth stage in non-outbreak areas during the last population cycle, 1969-1978. Larval density N: Data 1969-1974 from AUER, 1975: Data Sils Maria, S-chanf unpublished; 0: number of kg branches sampled; 1: $\frac{1}{2}N$ = number of larvae per 1 kg branches corrected for sex-ratio 0.5; 2,5,8: number of traps x days; 3,6,9: number of $\sigma\sigma$ captured per trap and day; 4,7,10: number of $\sigma\sigma$ captured per trap and day in unbaited traps in % of columns 3,6 and 9 respectively.

locality	year	Larval density N		Moth densities								
				First flight period			Second flight period			Total flight period		
		0	1	2	3	4	5	6	7	8	9	10
Lenzburg	1970	40	0.640	176	1.057		224	0.893		400	0.965	
	1971	30	0.320	30	2.707		77	21.262		107	16.060	
	1972	40	0.870	270	6.300		819	7.781		1089	7.414	
	1973	30	1.316	283	1.428		632	1.236		915	1.300	
	1974	30	0.784	562	1.012		871	0.685		1433	0.814	
	1975	30	0.070	355	0.972		871	0.028		1226	0.301	
	1976	39.5	0.006	189	0.016		593	0.014		782	0.014	
	1977	48	0.011	280	0.125		846	0.001		1126	0.031	
	1978	60	0.017									
Trimmis	1971	40	0.512	128	0.992		421	2.634		549	2.251	
	1972	30	8.916	148	0.419		749	1.534		897	1.350	
	1973	30	8.666	136	2.698		336	5.631		472	4.786	
	1974	30	10.666	599	0.354		1044	1.301		1643	0.956	
	1975	30	6.700	229	0.227		456	0.086		685	0.133	
	1976	18.5	0.324	616	0.006		2156	0.001		2772	0.002	
	1977	30	0.008	320	0.012		602	0.002		922	0.005	
	1978	60	0.008									
	Sils sc	1969	63	1.000	221	0.557		704	2.094		925	1.726
1970		63	3.913	364	3.382		500	18.448		864	12.101	
1971		63	22.659	442	2.568		704	34.152		1146	21.970	
1972		42	399.243	252	0.429	16.7	866	8.426	63.7	1118	6.623	75.4
1973		22	185.728	266	1.128	1.2	441	17.095	0.9	707	11.088	0.9
1974		22	16.455	273	1.634	1.6	339	5.060	0.2	672	3.668	0.4
1975		22	1.091	110	0.473		278	0.194		388	0.273	
1976		15	0.009	210	0.086		240	0.033		450	0.058	
1977		60	0.043	226	0.004		125	0.040		351	0.017	
Sils Maria	1972	15	22.450	206	5.262		140	1.686	7.3	346	3.815	-
	1973	15	106.750	280	2.911	1.7	413	9.460	5.6	693	6.814	4.0
	1974	15	245.400	284	0.507	6.7	358	5.448	3.1	652	3.300	3.3
	1975	15	4.170	305	0.157		380	0.087		685	0.118	
	1976	15	0.016	304	0.030		112	0.018		416	0.026	
	1977	30	0.008	290	0.002		110	0.009		400	0.002	
S-chanf	1969	90	0.128	294	0.235		667	1.756		961	1.290	
	1970	7.5	0.619	418	7.187		652	25.534		1070	18.367	
	1971	7.5	5.075	214	12.145		357	20.535		571	17.390	
	1972	7.5	70.850	845	4.895	52.3	698	2.481	56.2	1543	3.803	54.0
	1973	7.5	106.650	185	4.005	1.7	300	13.017	2.8	485	9.580	2.6
	1974	7.5	31.350	218	5.005	0.0	212	12.533	0.3	430	8.716	
	1975	6	0.208	349	0.278		612	0.291		961	0.286	
	1976	24	0.010	560	0.082		504	0.010		1064	0.048	
	1977	90	0.015	644	0.003		434	0.058		1078	0.025	

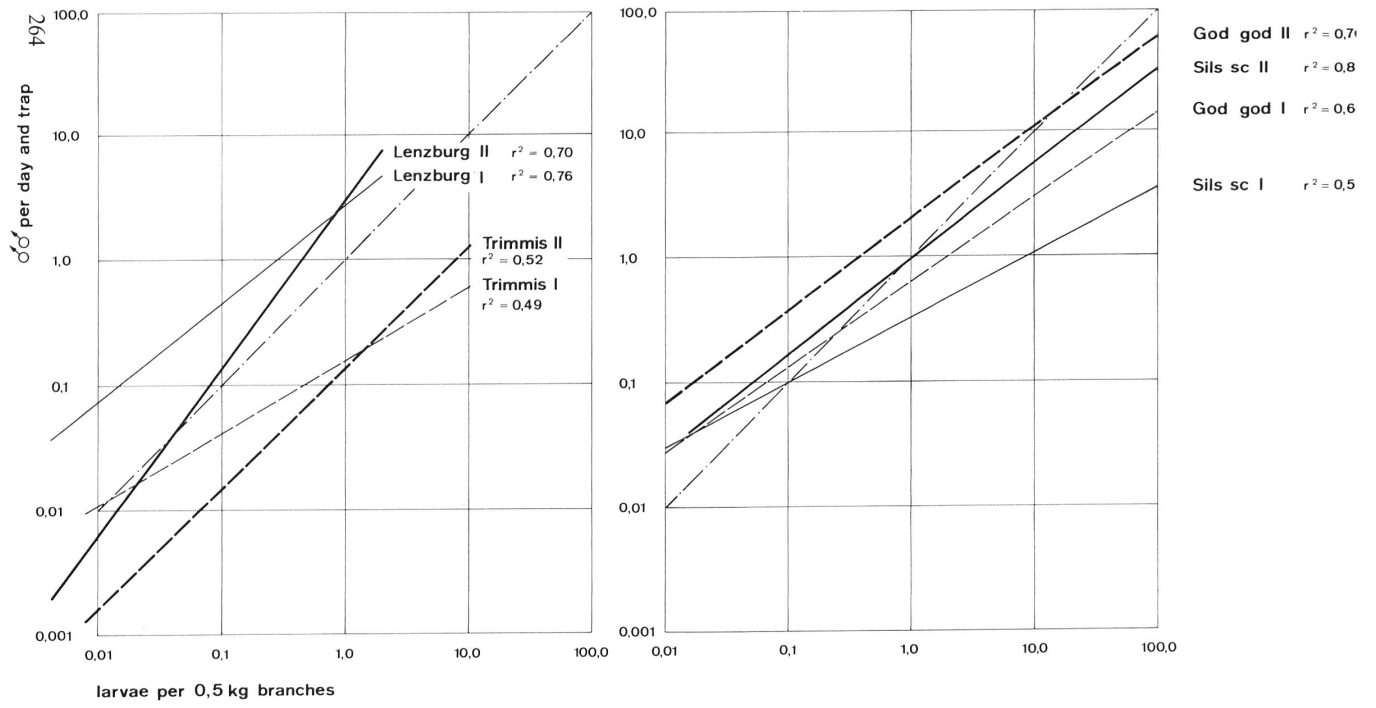


Fig. 4: Relationship between larval density (x) and male moth catch (y). The thin lines depict the regression of the densities of the first flight on larval density, the thick lines those of the second flight. Regression formula: $\ln \hat{y} = b \ln x + \ln a$.

track consists of irregular zigzags obliquely upwind along the plume. Outdoors, and especially in forests, wind turbulence tends to interrupt the pheromone plume irregularly which brings about a forward movement of the moth at various rates.

In its subalpine habitat the larch bud moth is most active during the first half of the night in July and August at temperatures above 7 °C (VAČLENA & BALTENSWEILER, 1978). At this time cold air drainage from the upper regions of the mountains occurs. These laminar winds rarely exceed velocities of 3 m/sec and they are characterized by a surprisingly high degree of periodicity (BUETTNER & THYER, 1965; GERIG, 1978; URFER-HENNEBERGER, 1964) This is due to either temperature conditions, i.e. the mutual fluctuation of temperature gradients and inversions, and the accentuated orography. These conditions may lead to very different windsystems at local or regional scales; in its most extreme forms, we may find either a very steady down-slope or down-valley wind from high ridges or mountain-passes or wind-convergence zones with increased turbulence in places where lateral down-slope winds and valley-bottom winds impinge on each other.

Positive anemotactic behaviour leads moths against down-slope and down-valley winds to the upper regions of mountain valleys. This is easily monitored by pheromone traps spread out along the altitudinal profile. Pheromone traps fixed parallel to the contour-lines catch in general considerably more moths on the valley oriented lee-side of the trap than on the upper luv-side. The fact that moths are caught at the upper timber line at 2100 m just when the local population enters the pupal stage, supports this reasoning. Although we are still ignorant about the mechanisms which cause the moths to continue their flight after having passed the timberline, informations from light traps show that males and females reach mountain ridges and passes by active flight. At these places conditions are optimal for windborne moths to be taken up into the gradient wind and then long-range migration starts (fig. 1).

Larch stands at the upper timber line which gain moths from lower source areas but lose moths to higher regions due to a steady down slope windfield are called transition sites (fig. 5: e.g. site 10). In contrast to this type of sites larch stands in areas with high wind turbulence are termed convergence sites since the males are trapped within the site by odour plumes changing continuously in their direction (fig. 5: e.g. site 1).

RELATIVE EVALUATION OF MOTH CATCH

It is generally known that pheromone trapping of males is not very well suited to measure population density as the mutual competition between traps and females varies in relation to the density of the females. However by relating male counts to larval density over the entire density range at a given site, moth catch can be interpreted in a relative sense. In addition important phenological differences between sites at different altitudes allow to separate immigrants from the autochthonous moths (fig. 2). The following discussion relies on census data collected at four sites in Switzerland: Lenzburg near Zürich and Trimmis in the Rhine river valley near Chur lie both in the area of latent fluctuation below 1000 m altitude. The localities Sils sc and S-chanf God god in the Engadine valley belong to the cyclic fluctuation area, they lie in site 1 and 10 resp. (fig. 5).

In the area of latent fluctuation the flight curve is bimodal, the two maxima are separated by nearly one month. The first flight represents the flight of the

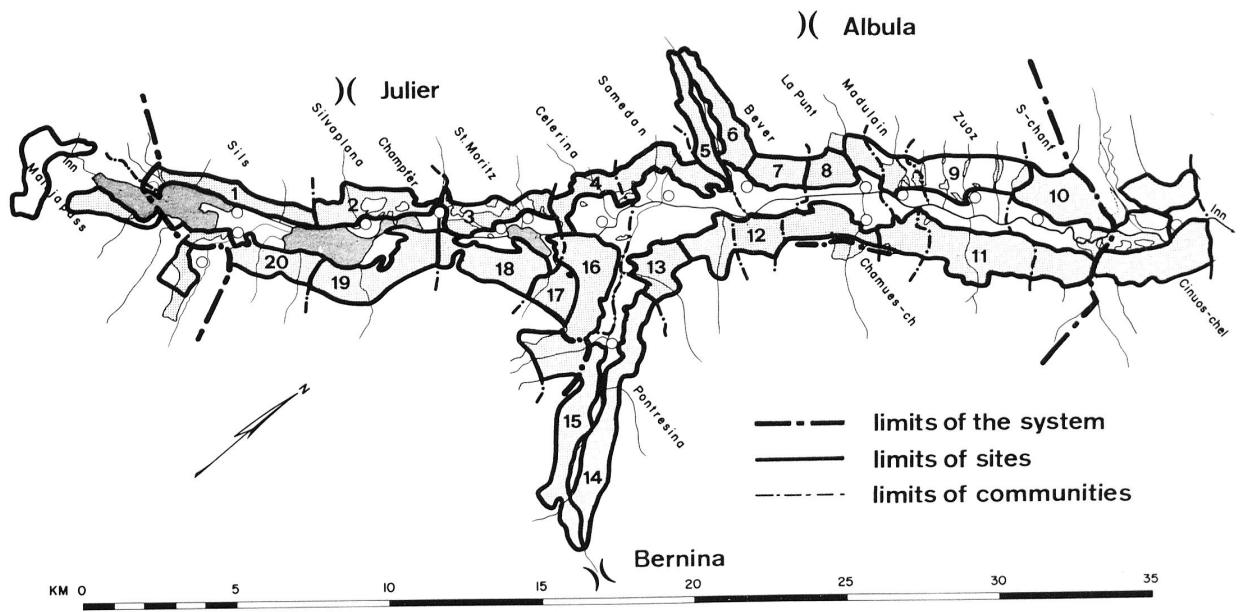


Fig. 5: Map of the upper Engadine with the outline of the sites 1-20.

Table 2. Relationship between densities of bud moth larvae and male moths catch at various sites expressed by the function $y = ax^b$.

Regression calculus for the function $\ln \hat{y} = b \ln x + \ln a$:

n: number of samples, a: intercept, b: slope,

r^2 : coefficient of determination.

I: Male moth density of the first flight regressed on larval density

II: Male moth density of the second flight regressed on larval density.

Relationship		Area of latent fluctuation		Area of cyclic fluctuation		
		Lenzburg	Trimmis	Sils sc	Sils Maria	S-chanf God god
I	n	8	7	8	5	8
	a	2.698	0.156	0.330	0.165	0.627
	b	0.781	0.581	0.513	0.710	0.739
	r^2	0.758	0.487	0.592	0.874	0.677
II	n	8	7	8	4	8
	a	3.060	3.060	0.967	0.125	1.999
	b	1.350	1.350	0.956	0.563	0.732
	r^2	0.700	0.523	0.810	0.920	0.695

resident population, whereas the second flight curve displays the flight of immigrants. The seasonal timing and the magnitude of this second flight depend on the large scale synoptic weather pattern and the defoliation status in the cyclic fluctuation area.

For sites in the cyclic fluctuation area above 1700 m the reverse is true: moth emerging at altitudes between 1200 m to 1600 m reach by regional migration sites at higher altitudes some time before the autochthonous flight begins. As long as moth emerge and fly at lower altitudes regional migration towards higher altitudes will occur. Later in the season, moths immigrating into forests at higher altitude cannot be distinguished from flying residents. For this analysis we defined as the flight of immigrants the particular portion of the seasonal flight curve which occurred before the mean temperature sum for 50% emergence is reached in a particular site and season. Immigration occurring at a later date was neglected.

The mean number of males caught per trap and season in relation to larval density is shown on double logarithmic scale (fig. 3; tab. 1). For Lenzburg and Trimmis moth- and larval-densities are presented for each year since 1970 and 1971 respectively until 1977. It is evident that at equal larval densities significantly more moths were caught at Lenzburg than at Trimmis. At both sites however, more males were caught during the autochthonous flight than in the second flight, except for peak densities from 1971 to 1973 when defoliation occurred in the Alps. The most striking feature in the two graphs Sils and God god is the fact that at highest larval densities the moth catch is considerably reduced. As the density threshold for the defoliation lies at a density of 50 ♂ larvae, this reduction is a quantitative measure of desorientation.

For ease of comparison of the relationship below the defoliation threshold the data were expressed by the power function $y = ax^b$, which, after transfor-

The outline of the recursive formula is depicted in fig. 5. The flight period and the processes which stimulate or constraint flight behaviour are defined as follows:

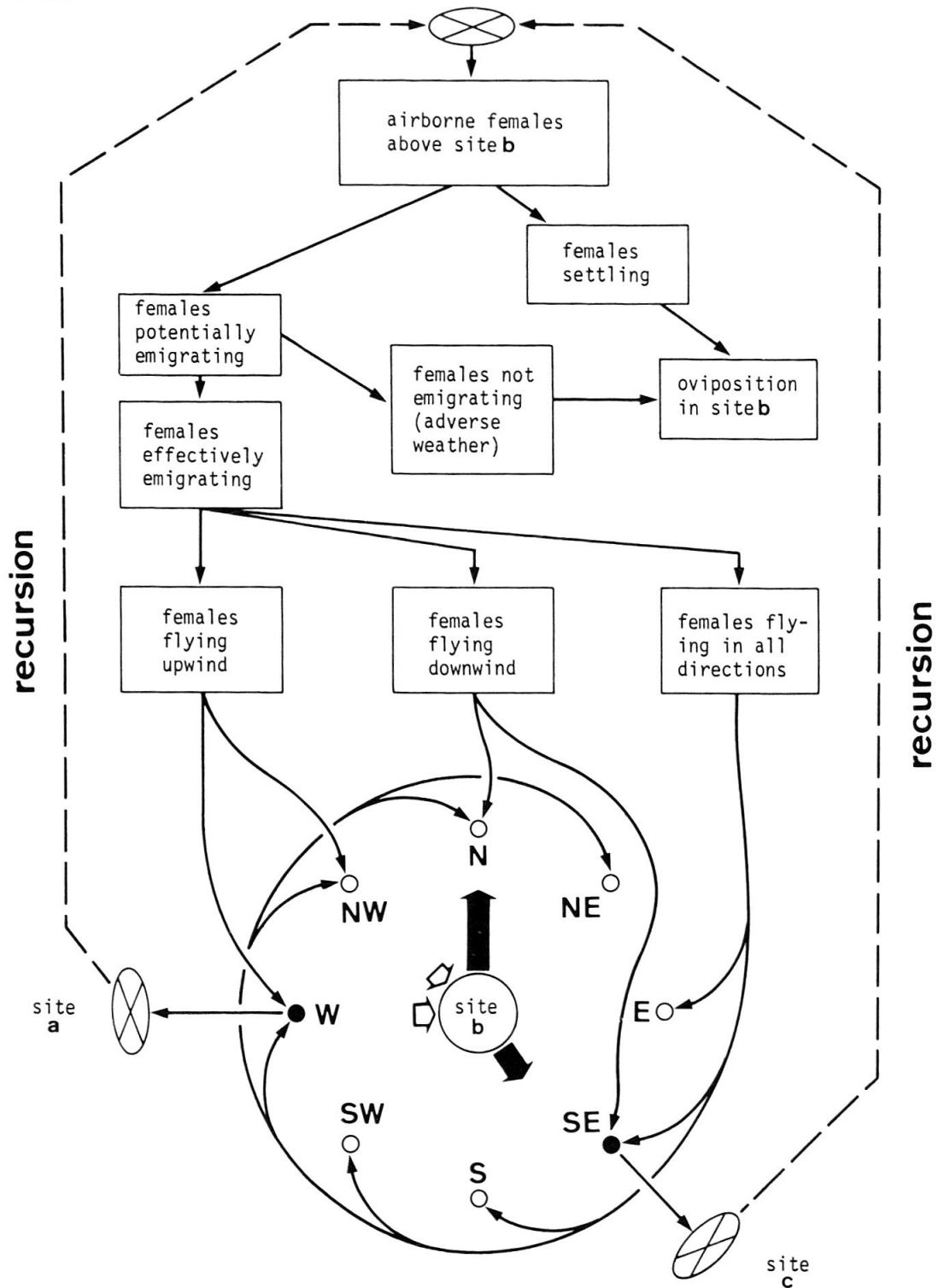


Fig. 6: Recursive formula for the migration applicable to any site. Here site b is depicted with two neighbouring sites to the west and southeast. Wind vectors: length proportional to average velocity during cyclonic (\blackrightarrow), resp. anticyclonic (\rightarrow) weather. o: sinks for females lost to the system.

mation in logarithms, may be solved by linear regression (fig. 3, tab. 2). At low densities moth catch is generally higher in the Engadine area than at the Lenzburg and Trimmis sites. It was not investigated whether the regression lines for the Engadine area differ significantly from each other; however the fact that moth catch at the God god site is highest at all larval densities, is in agreement with the idea of continuous moth immigration from lower altitudes (fig. 4).

By similar reasoning we may explain the discrepancy of moth catch for the autochthonous flight at Lenzburg (LZ I) and Trimmis (TR I). The traps at the Lenzburg site are located near the top of NE-facing slope which is covered by 100 ha of mature larch trees. Since on the Swiss Plateau westerly winds prevail, the high catch may be conceived as the result of a convergence-mechanism in a regional windsystem. In contrast to this, the traps at the Trimmis site sample the moths in a fringe of larch trees of about 200 m width at the lower end of an extensive pine-spruce forest and above an extensive range land. In the light of the proposed forms of migration, the Trimmis site cannot gain moths from lower altitudes, but loses constantly autochthonous moths to higher regions.

From this verbal model, supported by quantitative information, it is postulated that continuous moth immigration from source areas at 1200-1600 m contributes to switch the regression phase of the gradation cycle over to the progression phase. Thus regional moth immigration could represent an important prerequisite for the longterm regularity of the cyclic fluctuation.

VERBAL OUTLINE OF THE MODEL FOR SPATIAL DYNAMICS: THE MIGRATION MODEL

The long term studies of the population dynamics of the larch bud moth in the Upper Engadine have revealed consistent differences in local dynamics. Therefore the Engadine has been subdivided into 20 spatial units (fig. 5) by considering various ecological relevant aspects such as topographical features, exposure, forest stand composition and also the structure of the basic field data in relation to space. These spatial units are called sites. The dynamics of larch bud moth numbers within a site, the local dynamics, is described by FISCHLIN & BALTENSWEILER (1979).

This model yields for each site and each generation (year) a qualified number of mated females, which in turn provides the quantitative base to start the model of spatial dynamics, the migration-model. This migration model is conceived as a recursive process, i.e. the behaviour of all female moths in a site, either residents or immigrants, is defined by the recursive formula (fig. 6) relative to the specific site conditions. The recursive formula calculates the proportions of females which either lay their eggs in that particular site or leave it. Recursion is established as some of these emigrating females are accounted for as immigrants in neighbouring sites in just the same way as in the previous site until all of them are either ovipositing or lost to areas outside the system. The recursion is limited by the number of females and by the rule that no female may deposit eggs in more than three sites. Because it is assumed that only mated females become airborne, no interference between moths has to be considered, therefore this recursive formula may be repeated for the females of all sites in sequence. With this approach the two models for the local dynamics and migration are intimately linked and form a new system at a superior level.

(1) The flight period is bound exclusively to the time of seasonal occurrence of the moth from July 15 to September 30 and within this period to diurnal moth activity from dusk to midnight (1800–2400).

(2) VAČLENA & BALTENSWEILER (1978) have shown that the defoliation status of a larch forest determines whether moths are attracted to stay and oviposit in the particular stand (site) or whether they avoid it.

(3) Weather affects flight behaviour by various parameters:

- the temperature of 7 °C determines the lower activity threshold (VAČLENA & BALTENSWEILER, 1978)
- Winds determine moth flight and its orientation by their intensity and direction.

Anticyclonic weather induces a stable and very predictable nightly windfield and subsequent up wind flights of the moths. Cyclonic weather with its turbulent and strong winds often prohibit any flight. Indifferent pressure areas, characterized by warm airmasses and thunderstorms intensify moths activity and lead frequently to long range downwind migration. The local wind conditions are classified and quantified according to the synoptic weather pattern by adding up the duration of the various weather types.

Because weather types are assumed to determine by means of wind direction and intensity subsequent direction of moth migration as well, airborne females above a specific site can be allocated as immigrants to neighbouring sites. This allocation is assumed to be proportional to the duration of relevant weather types and the surface of neighbouring sites in any one of the 8 cardinal points. For the time being we assume that females flying in directions where no sites occur, will be lost to the system.

This approach which considers migration as recursive process offers many advantages, the most important is without doubt the profit in lucidity by reducing the migration process to what happens to females in a spatial unit, the site. This verbal model has been tested quantitatively with encouraging results (FISCHLIN, in prep.).

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