Polymorphism in *Noctua pronuba* (Lepidoptera, Noctuidae) in southern Norway

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Forty-five light trap samples of *Noctua pronuba* (Linnaeus, 1758), consisting of nearly 11 000 individuals, from 38 localities in western and southeastern Norway, were scored for three morphs, *rufous*, *ochre* and *silver*, according to the forewing colouration. *Rufous* constituted 37% to 62% of the samples from western Norway, and 50% to 73% of the samples from southeastern Norway. Males constituted 93% of the specimens. In 12 samples, with a sufficient number of females (n>25), no sex difference in the frequency of *rufous* was established. The seasonal variation in the frequency of *rufous* was considered negligible and no annual variation was apparent. No geographic variation in the frequency of *rufous* was demonstrated in western Norway. In southeastern Norway one sample differed significantly from all the others. When samples from adjacent localities were lumped, significant differences in the frequency of *rufous* were found between three regions in western Norway, and between southeastern Norway and all the regions in western Norway. In southeastern Norway, regression analyses showed a significant increase in the frequency of *rufous* towards the east.

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1. Introduction

The Large Yellow Underwing, *Noctua pronuba* (Linnaeus, 1758) is polymorphic for forewing colouration. Several phenotypes have been described (see e. g. Heath & Emmet 1979). The polymorphism is considered to have a genotypic basis, the morphs being controlled by several alleles at one or more loci (Cook & Sarsam 1981).

Geographic variation in the distribution of the three most common phenotypes, *rufous*, *ochre* and *silver*, has been studied on the British Isles and in France. On the British Isles the frequencies have been found to be fairly constant throughout the country (Cook & Sarsam 1981), while geographic variation in morph frequencies was demonstrated in France (Poitout & Bues 1976). A single sample analysed from Finland (Mikkola & Jalas 1977) showed 67% *rufous*, a somewhat higher value than those obtained from the British Isles and France.

The reason for the lack of geographic variation in morph frequencies has been sought in the mobility of the adults. In the British Isles, Cook & Sarsam (1981) reported that *N. pronuba* is highly mobile, but in France Poitout & Bues (1976) considered *N. pronuba* to be a moderately mobile species.

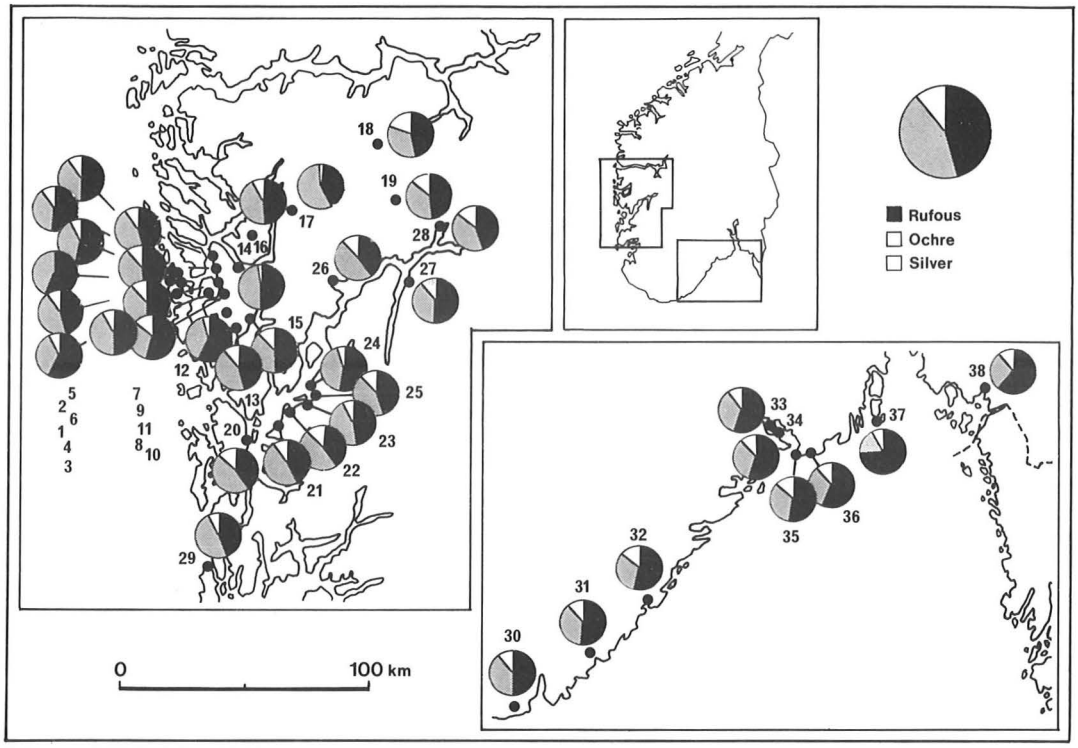

Fig. 1. The frequency of the three morphs of *Noctua pronuba* at 38 localities in southern Norway. The numbers refer to the localities in Table 1.

N. pronuba is common and widely distributed in the coastal areas of southern Norway (Nordström et al. 1969), and large samples are readily obtained with light traps. In Grenland, southeastern Norway, the duration of the flight period was estimated at 74 days, the median day for males being 13 August (Søli 1987), and in Sotra, western Norway, at about 65 days, with the median day for males on 12 August (Andersen 1982).

The present study of *N. pronuba* outlines the sexual differences, and temporal, annual and geographical variation in the morph frequencies in southern Norway. As adult mobility reduces geographic variation, a higher degree of variation may be expected in western Norway, where geographic barriers, such as high mountains and fjords, are likely to reduce dispersion. In southeastern Norway, where the topography is less interrupted, the morphs ought to be more evenly distributed.

2. Study area

The material comprises samples from 38 localities, of which 29 are situated in western Norway, and 9 in southeastern Norway (Fig. 1; Table 1). The samples from western Norway have been grouped in five regions:

Sotra: Eight samples (localities 1–6) collected in the northern part of the island of Sotra, where the landscape is rather flat and the sampling sites are not separated by more than 7 km.

Bergen: Eleven samples (localities 7–15) collected in Bergen and its surroundings, from Saudalskleivane in the north to Lundatræ in the south.

Central Hordaland: Four samples (localities 16–19) collected from different localities in the central, mountainous regions of northern Hordaland.

Table 1. Samples of *Noctua pronuba* from 38 localities in southern Norway, scored for the three morphs *rufous*, *ochre* and *silver*.

			Males				Females			
	Locality	Year	*ruf*	*och*	*sil*	% *ruf*	*ruf*	*och*	*sil*	% *ruf*
1	Landro	1978	17	13	0	57	1	2	1	
2	Austre Loftmyra	1978	34	35	8	44	4	4	1	
3	Eidesvåg	1975	43	31	8	52	1	3	1	
		1976	56	30	5	62	4	6	0	
4	Ongeltveit	1976	361	368	80	45	28	35	9	39
5	Austervågen	1977	228	186	38	50	23	24	10	40
		1978	38	34	8	48	6	5	0	
6	Geitneset	1978	14	10	2	54	0	1	0	
7	Saudalskleivane	1976	99	102	21	45	11	18	5	32
8	Straume	1975	271	239	50	48	15	16	6	41
		1976	129	126	20	47	6	8	0	
		1980	14	18	3	40	0	0	0	
9	Ervik	1976	212	192	49	47	22	10	8	55
10	Paradis	1977	26	16	6	54	4	4	1	
11	Ole Irgensvei	1976	176	148	37	49	12	4	1	
12	Kalandseid	1976	101	104	24	44	11	19	2	34
13	Lundatræ	1975	41	27	3	58	2	5	0	
14	Garnes	1979	19	17	1	51	1	1	1	
15	Lii	1976	96	81	22	48	10	12	3	40
16	Kleppe	1975	112	105	19	48	15	15	0	50
17	Dale	1979	15	21	1	41	0	0	0	
18	Ekse	1976	13	11	5	45	6	7	0	
19	Møn	1979	53	46	14	47	14	22	2	37
20	Rommetveit	1975	40	50	13	39	6	8	1	
21	Husnes	1977	40	48	9	41	5	6	2	
22	Uskedalen	1977	47	63	16	37	1	3	1	
23	Dimmelsvik	1975	97	99	15	46	10	8	1	
24	Nes	1977	42	34	4	53	4	6	4	
25	Rosendal	1975	63	77	13	41	7	6	0	
		1976	234	237	58	44	12	19	0	39
		1977	187	198	53	43	16	12	4	50
26	Øystese	1979	56	75	16	38	5	2	1	
27	Ystanes	1977	40	31	8	51	1	4	0	
28	Hjeltnes	1979	94	96	28	43	8	9	7	
29	Haugesund	1977	17	20	3	43	2	0	0	
30	Kvernhusvannet	1980	55	44	11	50	2	1	0	
31	Grimenes	1985	67	41	16	54	5	8	4	
32	Hasselåsen	1980	227	161	44	53	10	12	4	39
		1981	68	50	16	51	4	3	0	
33	Gravastranda	1983	496	314	85	55	7	5	1	
34	Sandøya	1986	60	37	11	56	2	3	2	
35	Mølen	1984	90	61	21	52	3	3	1	
36	Nevlunghavn	1984	79	46	15	56	1	0	0	
37	Mostranda	1980	38	10	4	73	0	0	1	
38	Ullerøy	1980	23	11	4	61	0	0	0	

Outer Hardanger: Eight samples (localities 20–25) collected along the southern side of the Hardangerfjord and on the island of Stord, from Rommetveit in the southwest to Rosendal in the northeast.

Inner Hardanger: Three samples (localities 26–28) collected along the inner part of the Hardangerfjord; in addition one sample from Haugesund (loc. 29).

In southeastern Norway the 9 localities range from Kvernhusvannet (loc. 30) in the southwest to Ullerøy (loc. 38) in the northeast (Fig. 1). One locality, Mostranda (loc. 37), was situated on the island of Tjøme.

3. Material and methods

The material was collected with modified Robinson traps, fitted with mercury vapour bulbs, during the period from 1975 to 1986. The material consisted of 45 samples and 10 623 individuals; only samples with at least 25 males were included. Males constituted 93% of the specimens. Sex differences were tested only in samples with at least 25 females, i.e. in 12 samples; geographical variation was studied in males only.

The specimens were sexed, and scored for three morphs according to their forewing colour (see e.g. Heath & Emmet 1979). The three morphs are characterized by

1) a fairly even brownish/ reddish colour on the forewings;
2) a more mottled ochreous colour, or
3) a grayish/silverish colour.

Each morph has a different expression in the two sexes, the females always being paler, and for the ochreous and grayish morphs also less mottled than the males. The nomenclature used by Cook & Sarsam (1981) is adopted, the darkest morph being named *rufous*, the paler morph *ochre*, and the third morph *silver*. *Silver* was identified by the presence of scales, which give the moth its silverish appearance. These scales seem to be poorly pigmented, and are most distinct along the costal and distal parts of the wing. They can easily be recognized in a stereo-microscope with a magnification of 30×. According to Robinson (1973), this whiteness/silverness may be due to air-filled cavities within the scales.

The variation in morph frequencies was tested for independence using G statistics on R×C tables, and applying Williams' correction to the estimated G values. As *rufous* was by far the most abundant morph, the tests were focused on the distribution of *rufous* vs. non-*rufous*. Regression analysis was used for testing the clinality of the geographic variation, and t statistics for testing the significance of the regression coefficient (see Sokal & Rohlf 1981).

4. Results

4.1. Sex differences

In none of the 12 samples with a sufficient number of females did the frequency of *rufous* differ significantly between males and females.

4.2. Seasonal and annual variation

As most samples were collected during a comparatively short period, only 11 samples yielded data suitable for analysis of seasonal variation. Only one of these, Ole Irgensvei (loc. 11), showed a near-significant difference ($P<0.05$) in the distribution of *rufous* throughout the season (Table 2). The seasonal variation is therefore considered negligible.

Samples from more than one year are available from five localities (Table 3). No significant annual differences were found.

4.3. Geographic variation

Samples within each of the five regions in western Norway and within southeastern Norway were tested for independence in the frequency of *rufous*. In western Norway significant or near-significant differences were found in two instances only: between Eidesvåg (loc. 3) and Ongeltveit (loc. 4) on Sotra ($P<0.01$), and between Kalandseid (loc. 12) and Lundatræ (loc. 13) in the Bergen area ($P<0.05$). When 75 tests are involved, 3 to 4 tests can be expected to give a P value of <0.05 even

between homogeneous samples, due to chance alone. However, as the test on material from Sotra yielded a highly significant difference, it must be assumed that differences do really exist in the frequency of *rufous* on this island. In spite of this, we have lumped the samples from Sotra and likewise all the samples within the other four western Norwegian regions.

In southeastern Norway the frequency of *rufous* in the sample from Mostranda (loc. 37) was found to be significantly to highly significantly different from all other samples taken in the region. Hence, this sample has been excluded from further tests. None of the other samples differ significantly from each other, and they have been lumped.

Differences in the frequencies of *rufous* were tested between the five regions in western Norway, and between these regions and southeastern Norway. The frequency of *rufous* in southeastern Norway was significantly to highly significantly higher than in all five regions in western Norway. The frequency of *rufous* in Outer Hardanger was significantly higher than in Bergen and on Sotra, on the northern side of the Hardangerfjord. Likewise, the frequency of *rufous* in Inner Hardanger was found to differ significantly from that on the island of Sotra. These two regions are separated by more than 80 km. Differences in morph frequencies were not demonstrated between Bergen and the two regions in the central parts of western Norway, Inner Hardanger and Central Hordaland, or between the latter two regions.

To test clinal variation, the frequencies were arranged according to the position of the locality along a west-east gradient, separately for samples from western Norway and southeastern Norway. In western Norway the frequency of *rufous* ranged from 37 to 62%. A slight decline in the frequency of *rufous* towards the east, i.e. inland, was observed; 12% of this colour variation can be ex-

Table 2. Seasonal variation in the frequency of the *rufous* morph in males of *Noctua pronuba* in 11 localities in southern Norway.

	–30 July		1–15 Aug.		16–31 Aug.		1–30 Sept	
	Sample	% *ruf*	Sample	% *ruf*	Sample	% *ruf*	Sample	% *ruf*
Ongeltveit	47	55	343	45	250	40	169	48
Saudalskleivane	6	–	40	68	142	45	14	–
Straume (1975)	91	47	168	49	276	49	25	40
Straume (1976)	64	45	118	45	58	52	35	49
Ervik	66	50	196	45	165	47	26	50
Ole Irgensvei	51	53	65	52	226	45	19	–
Kalandseid	6	–	27	37	176	46	20	–
Lii	32	41	84	56	52	48	31	36
Rosendal (1977)	7	–	329	41	100	50	2	–
Hasselåsen (1980)	136	54	173	47	123	59	–	–
Gravastranda	63	62	573	56	259	54	–	–

Table 3. Annual variation in the frequency of the *rufous* morph in males of *Noctua pronuba* in five localities in southern Norway.

	1975		1976		1977		1978		1980		1981	
	Sample	% *ruf*	Sample	% *ruf*	Sample	% *ruf*	Sample	% *ruf*	Sample	% *ruf*	Sample	% *ruf*
Eidesvåg	82	52	91	62	–	–	–	–	–	–	–	–
Austervågen	–	–	–	–	452	50	80	48	–	–	–	–
Straume	560	49	275	47	35	40	–	–	–	–	–	–
Rosendal	153	41	529	44	438	43	–	–	–	–	–	–
Hasselåsen	–	–	–	–	–	–	–	–	432	53	134	51

plained by the gradient ($r^2 = 0.12$) although the coefficient is near-significantly different from zero ($t_{33} = -2.131$; $P < 0.05$).

In southeastern Norway the frequency of *rufous* ranged from 50 to 73% and showed an increase towards the east, 44% of the variation being explained by the gradient ($r^2=0.44$, $t_8=2.513$; $P < 0.05$). If we leave out Mostranda (loc. 37), whose frequency of 73% differs significantly from the others, the analysis yields an r^2 value of 0.72 ($t_7=4.225$; $P < 0.01$).

5. Discussion

As the seasonal and annual variation in the morph frequencies was negligible, the frequencies could be compared between samples obtained in different years and at different times of the season.

The frequency of *rufous* was found to vary significantly between different regions in South Norway. This is not in accordance with results obtained from the British Isles. On the British Isles, 80 samples (9147 individuals) of *N. pronuba*, collected from Scotland to Wales, were scored, and the frequencies of the three morphs were found to be fairly constant throughout the country (Cook & Sarsam 1981). In France, however, where more than 57 000 individuals from four geographical provinces in the southwestern and southeastern parts of the country were scored, the distribution of the three morphs varied significantly between the geographical provinces (Poitout & Bues 1976). The frequencies of *rufous* were somewhat higher in southern Norway than those reported from the British Isles and France, while the frequencies of *silver* were similar. In Finland, however, the frequency of *rufous* was relatively high (67%), but this result is based on one sample only, consisting of 238 specimens (Mikkola & Jalas1977) (Table 4).

The results from Norway suggest a relatively high degree of mobility in *N. pronuba*. In southeastern Norway, where the sampling sites were not separated by major geographical barriers, the samples are most probably taken from a continuous population. The observed cline, with an increase in the frequency of *rufous* toward the east, is probably smoothed by gene flow caused by the mobility of the adults. Migration is known to cause rapid spreading of genes in populations and, hence, to reduce regional variation (e.g. Hartl 1980). The importance of gene flow in the maintenance of this cline is emphasized by the high frequency of *rufous* obtained in the more isolated locality on the island of Tjøme.

Significant differences were obtained between three regions in western Norway, all separated by mountains and wide fjords. Likewise, significant differences were found between southeastern Norway and all the regions in western Norway. These results are in accordance with observations from France (Poitout & Bues 1976), indicating reduced mobility, most probably caused by distance and geographical barriers. According to Poitout & Bues (1976), *N. pronuba* is intermediate in behaviour between migrating and non-migrating species.

In general, polymorphism is maintained by differences in the selection pressures on the morphs, in many instances differences in predation pressures. The selective forces acting on *N. pronuba* are still obscure. However, Cook & Sarsam (1981) suggested that the polymorphism in *N. pronuba* is the result of opposing selection pressures in the two sexes, as they obtained different fitness values for *rufous* males and females. In the present study no difference was found between the sexes. The reason for this may partly be sought in the restricted number of samples available for comparison.

Breeding experiments on the British Isles and in France have yielded contradictory results concerning the inheritance of the phenotypes in *N. pronuba*. After performing breeding experiments with 62 couples, Poitout & Bues (1976) reported

Table 4. The range in frequencies (%) of the *rufous* and *silver* morphs of *Noctua pronuba* in western Norway, southeastern Norway, England, France and Finland.

Region	*rufous*	*silver*
West Norway	37 – 62	0 – 17
Southeast Norway	50 – 73	8 – 13
England [a]	21 – 41	0 – 8
France [b]	39 – 49	9 – 14
Finland [c]	67	13

[a]Cook & Sarsam 1981; [b]Poitout & Bues 1976; [c]Mikkola & Jalas 1977.

that *rufous* is dominant over *silver*, which again is dominant over *ochre*. On the other hand, Cook & Sarsam (1981) suggested that *rufous* is dominant over *ochre*, and that *silver* is recessive to non-*silver*, situated at another locus. These conclusions are based upon the progeny of a series of 14 crosses, of which the parentage was unknown in eight instances. Further breeding experiments are necessary to clarify the inheritance of the different morphs in *N. pronuba*.

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References

Andersen, T. 1982: Some studies on Macrolepidoptera in coastal heathland habitats in western Norway. — Fauna Norv. Ser. B. 29:85–104.

Cook, L. M. & Sarsam, V. 1981: Polymorphism in the moth Noctua pronuba (L.). — Heredity 46:443–447.

Hartl, D. L. 1980: Principles of population genetics. — Sinauer Assoc. Sunderland. 488 pp.

Heath, J. & Emmet, A. M. 1979: The moths and butterflies of Great Britain and Ireland. 9. — Curven Books, Oxford. 288 pp.

Mikkola, K. & Jalas, I. 1977: Suomen perhoset. Yökköset 1. — Otava, Keuruu. 256 pp.

Nordstöm, F., Kaaber, S., Opheim, M. & Sotavalta, O. 1969: De fennoskandiska och danska nattflynas utbredning (Noctuidae). — CWK. Gleerup, Lund. 160 pp + 403 maps.

Poitout, S & Bues, R. 1976: L'incidence des migrations d'adultes sur le degré et sur la variabilité structurale de l'hétérogénéité genetique dans les populations naturelles de lépidoptères Noctuidae. — Ann. Zool.-Ecol. Anim. 8:69–81.

Robinson, R. 1973: Lepidoptera genetics. — Pergamon Press, Oxford. 687 pp.

Sokal, R. R. & Rohlf, F. J. 1981: Biometrics. — W. H. Freeman, New York. 860 pp.

Søli, G. E. E. 1987: Light trap catches of Bombycoidea, Sphingoidea, Notodontoidea and Noctuoidea (Lepidoptera) in two forest communities in Southern Norway. — Cand. scient. thesis, University of Bergen. 39 pp.

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