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Spring Migration in the Skylark (Alauda arvensis) in Denmark. Influence of Environmental Factors on the Flocksize and Correlation between Flocksize and Migratory Direction

By Jørgen Rabøl and Henning Noer

1. Introduction

Most diurnal migrants are migrating in flocks, and the flocksizes and flockstructures could be considered as determined of species, season, environmental factors, and the internal states of the birds.

Several investigators, e. g. BERGMAN & DONNER (1964), DOLNIK & BLYUMENTHAL (1967), GRYUS-CASIMIR (1965), RUDEBECK (1950), and WEST et al. (1968) have dealt with the flocking behaviour of migrant birds. However, there seems to have been no thorough attempts towards a quantitative analysis of the flocksize groups, and the dependence of the flocksizes on environmental factors.

For the following purposes we have investigated the flocking behaviour in the Skylark (Alauda arvensis):

1) To demonstrate the influence of behavioral, topographical, and especially meteorological factors on the daily mean flock size and the frequency distribution of the flocksizes.

2) To show differences in the patterns of migratory directions within different flocksizes.

3) To demonstrate the general fitness of negative binomial distributions to the flocksize distributions.

2. The Spring Migration of the Skylark in Denmark

The migration of the Skylark in Denmark is well studied, e. g., SAKTORPH (1917), HANSEN (1954), RABØL (1964 a, 1967, 1971), RABØL & HINDSBO (1972).

The spring migration is passing from the end of December to the beginning of May. Most birds are migrating in the period medio March – primo April. The migratory directions are often extremely variable both within the same day and from day to day. The migration in the presumed standard direction (NE) is often weak, lacking or suppressed by leadingline and/or headwind migration – at least in the lower (visible) altitudes of the diurnal migration. The situation of Denmark being at the northern range of the wintering area of the species might be one of the reasons for this variable migratory pattern and the very prolonged migratory season.

Skylarks are seldom migrating in flocks containing other species. Breaking up and fusion of flocks are fairly frequently seen (Fig. 1). The former is the more common. Flocks migrating in different directions often shift directions and/or interchange individuals when encountering each other (Fig. 2).

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Fig. 1: Examples on breaking up and fusion of migrating Skylark flocks, Knudshoved.



Fig. 2: Migrating flocks which influence and make parallel displacement at each other, Knudshoved. Also shown is the leading line effect of the breakwater. Emigrating flocks are typically more easy to disturb, whereas the immigrating flocks as a rule are proceeding undisturbed and straightlined.

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Flocks consisting of more than 10 birds are seldom stable in the air over distances more than a few hundred meters. In general the flocks are loose and the distances between the individuals are often 5 to 15 meters.

3. Material

In two spring seasons the migration of Skylarks was studied at four sites (Fig. 3). At Knudshoved daily observations were carried out in the period 3 February – 26 April 1964. The observations lasted from 15 minutes before sunrise 3–5 hours onwards. At Hvalsø, Gilleleje, and Nivå simultaneous observations were carried out 50 days in the period 1 March – 7 May 1971. These observations all lasted 4 hours and started 15 minutes before sunrise.

For every migrating flock, time, number of birds in the flock, migratory direction, and altitude were noted. Many map sketches of the migratory movements were made. Several meteorological factors, such as wind, temperature, visibility, precipitation, and cloudiness were booked during the observations.

Two concepts, daily mean flocksize (g) and flocksize distribution are used throughout the text. The daily mean flocksize is the number of migrating birds divided by the number of migrating flocks. The daily mean flocksize is not calculated for days with fewer than 5 flocks, and such days are not included in the material. The flocksize distribution for a certain group (a single day, all days with cloudiness 0-5/8, etc.) informs about the number or percentage of flocks consisting of 1, 2, 3, ... n individuals.

The flocksize distributions given in the tables are frequency distributions. In many aspects the "shape" of the flocksize distributions resembles the poisson and negative binomial distributions used in the ecological demography in describing the distribution of animals in area or time.

Flocksize $\div 1$	Number of Flocks	Negative Binomial	Poisson
0	99	98.97	64.04
1	37	35.87	65.13
2	17	18.05	33.12
3	8	9.92	11.23
4	6	5.69	2.85
5	5	3.34	0.58
6	2	1.99	0.10
7	1)	0.01
8	1	3.16	0
9	1	J	0

Table 1: The flocksize distribution at Knudshoved 16 March 1964 (0 accumulation). The mean flocksize is 2.017. The agreement with the corresponding negative binomial distribution (m = 1.017, and k = 0.563) is very good (Chi-square test, 0.80). The agreement with the corresponding poisson distribution (<math>m = 1.017) is very low (p < 0.001).

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Fig. 3: The eastern part of Denmark with the four observation sites (the crosses). Knudshoved (ploughed field, meadows) is the tip of a peninsula pointing ESE-SE. Hvalsø (ploughed field) is a glade in a wood. Gilleleje (village, open fields) is at the bend of the northcoast of Zealand, and Nivå (meadow) is in the bottom of a shallow bay. Woods are indicated with bars.

Flocksize $\div 1$ Number of Flocks Negative Binomial 0 110 110.60 1 26 23.50 2 9.99 8 3 4 4.96 4 5 2.64 5 0 1.64 6 0 7 1 8 0 1.85 9 0 10 1

Table 2: The flocksize distribution at Hvalsø 15 March 1971. The agreement with the negative binomial (m = 0.5871, and k = 0.333) is good ($0.50 \le p \le 0.70$).

The poisson and negative binomial distributions (e. g., BLISS & FISHER 1953, and PIELOU 1970) both include a zero class, which of course does not exist in the flocksize distributions. The flocksize distributions could, however, be made available for the mathematical treatment when the number one is subtracted from all the different flocksizes.

Flocksize $\div 1$	Number of Flocks	Negative Binomial I	Negative Binomial II
0	13	18.05	14.29
1	16	8.16	12.57
2	6	5.39	8.21
3	3	3.94	4.74
4	5	3.02	2.56
5	1	2.38	
6	0	1.91	2.63
7	1		
8	3	9.47	
9	3		
29	1		

Table 3: The flocksize distribution at Knudshoved 12 March 1964 (degree of accumulation 3–4). The agreement with the negative binomial (m = 3.462, and k = 0.52) is very low (column I, 0.01 > p > 0.005). Flocks containing more than 8 birds are omitted (such flocks are considered instable and due to the accumulation). The negative binomial (m = 1.533, and k = 2.06) now fits the flocksize distribution much better (column II, 0.30).

Table 1 is a typical example of the poor fitness of the poisson distribution. Important assumptions of the poisson distribution - e.g., non-sociality - are neither fulfilled by the observation data.

Tables 1 and 2 show the general fitness of the negative binomial to the flocksize distributions, at least on days with no accumulation (concerning this concept, see later). On days with accumulation the large instable flocks certainly disturb the distribution, but when these flocks are omitted the fitness is much better (Table 3). The correspondence with the negative binomial is the best one for single-day flocksize distributions. Table 1 which yields averages for many days thus produces low probabilities of 0.025 - 0.05 and 0.20 - 0.25 for columns I and II, respectively. This

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can be ascribed to grouping of many daily flocksize distributions most of which are fitting negative binomials but with different numbers, mean flocksizes and dispersion coefficients (k).

A negative binomial might occur when there is an attraction (sociability) between the individuals. Also the flexibility of the negative binomial could explain its general fitness to the flocksize distributions. Negative binomials seem to fit most, more or less exponentially declining distributions.

5. Influence of Environmental factors

For the observer in the field the following environmental factors are of importance in the establishment of the flocks:

a) Cloudiness: The flocksize distributions during different degrees of cloudiness are presented in Tables 4-5. The flocksizes are significantly larger under condition of an overcast sky. If Skylarks (besides other cues) make use of sun orientation, this tendency to build up larger flocksizes when it is overcast could be considered as a compensatory mechanism to maintain the appropriate orientation.

Flocksize	I 0 0-5/8	II 0 8/8	$111 \\ 3-4 0-5/8$	IV 3-4 8/8
	PT,			
1	63.28	45.73	50.28	29.62
2	20.52	23.50	21.07	26.64
3	7.34	13.31	10.39	13.49
4	3.32	4.10	6.74	6.58
5	3.21	5.46	3.37	6.91
6	0.57	2.39	0.56	4.93
7	0.57	2.39	1.95	0.99
8	0.34	0.68	0.84	1.32
9		0.68	1.12	2.31
10	0.46	1.02	0.56	0.33
11	0.11	0.34		0.66
12			1.12	0.66
13	0.11	0.34		0.66
14			0.28	0.33
15	0.11		0.28	0.99
16			0.28	1.32
17			0.28	
20			0.28	0.66
25				0.66
27				0.33
30			0.28	0.33
35			0.28	
40				0.33
Number of Flocks	872	293	356	304

Table 4: Percentages of flocksize distributions during four different conditions, Knudshoved. The two numbers in the heading of each column show the degree of accumulation and the cloudiness. Days with degree of accumulation 1–2 and cloudiness 6–7/8 are omitted. The total number of flocks in each column is given at the bottom of the columns. The difference between I : II, I : III, II : IV and III : IV are all statistically significant (p < 0.01, KOLMO-GOROV-SMIRNOV two-sample test).

		Hvalsø			Nivå			Gilbjerg	
Flocksize	0 - 5/8	6 – 7/8	8/8	0 - 5/8	6 - 7/8	8/8	0 - 5/8	6 – 7/8	8/8
1	81.46	70.90	59.57	66.35	47.90	42.10	48.17	37.75	29.55
2	13.66	17.23	20.21	13.46	19.29	19.64	23.78	18.00	17.68
3	2.93	5.34	6.03	9.62	10.29	9.47	11.14	14.16	13.45
4	1.46	2.27	5.32	3.85	7.07	6.32	6.42	7.08	7.39
5	0.49	1.69	3.55	3.85	4.50	4.56	3.43	4.72	6.07
6		1.41	1.77		1.61	3.86	2.14	3.54	5.54
7		0.56	1.06	0.96	1.93	3.86	1.50	1.77	3.69
8		0.28	0.36	0.96	0.32	1.75	0.43	1.77	3.96
6					0.64	0.35	0.64	2.36	1.32
10			0.36		0.96	1.40	0.64	1.77	1.06
11–15		0.28	1.07		1.29	2.11	1.50	4.43	6.07
16-20			0.36		0.64	1.75	0.21	1.48	2.64
21–30			0.36		1.29	2.11		0.59	1.32
31-40				0.96	0.64			0.59	0.26
41-80			-		0.96		0.35		
More than 81					0.64	0.35			
Number of Flocks	205	354	282	104	311	285	467	339	379
	Table 5:	Percentages c	of flocksize dis	tributions dur	ing cloudines	s 0-5/8, 6-7	7/8 and 8/8 at		

definitely always 0. The positive correlation between flocksize and cloudiness is obvious for all three places. The flocksizes are furthermore much smaller at the inland post Hvalse than at the two coast posts – undoubtedly due to the higher number of migrants along Hvalsø, Gilleleje and Nivå. The degree of accumulation is not noted but at Hvalsø it is the coasts.

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Fig. 4. The degree of accumulation as a function of the visibility, Knudshoved. The inserted line connects the four arithmetic means of degree of accumulation in the four visibility groups 0–3 km, 4–6 km, 7–11 km, and more than 11 km. The correlation is statistically significant (SPEARMANN rank correlation coefficient = -0.31, 0.01 > p > 0.005).

b) V i s i b i l i t y: The flocksizes are larger during low degrees of visibility. If the daily visibilities and the mean flocksizes at Knudshoved are compared, the negative correlation is significant (SPEARMANN rank correlation coefficient = -0.34, n = 61, 0.001). Probably, part of the influence of low visibilities on the flocking is indirect and due to the correlation between the visibility and the degree of accumulation (Fig. 4). At Hvalsø no significant accumulation occurred. Nevertheless the SPEARMANN rank correlation coefficient between the daily visibilities and mean flocksizes was <math>-0.32. The correlation was, however, not statistically significant (0.10 > p > 0.05) – maybe due to the small sample size (n = 22).

c) Snowcover: During December and January snowcover often elicits SW-Wdirected Skylark-movements, which mostly consist of very large and dense flocks.

14 January 1964 could be mentioned as an example of these large flocksize winter movements. The temperature was below 0°C. The landscape was partly covered with snow, and the wind was light northeasterly. The visibility was at least 20 km, and the cloudiness 0/8. During the morning hours 6 Skylark flocks were observed at Knudshoved in a WSW-immigration from Zealand. The flocksizes were 1, 4, 16, 18, 30, and 100. The flocks were dense and silent.

However, from February and onwards, snowcover mostly stops the Skylark migration, and large flocks are built in the fields where the birds move around locally (RABØL 1964 b). Snowcover thus clearly produces large flocksizes in the spring migration season, but due to the strong correlation between snowcover and no or very few migrating flocks the influence of snowcover on the flocksizes of migrating Skylarks is obscure or masked — at least in the present material.

d) Number of resting Skylarks (accumulation): At Hvalsø, Nivå and Gilleleje the number of resting birds at or nearby the observation post was not estimated. At Hvalsø the number should certainly always be very close to zero.

At Knudshoved resting Skylarks were often present on the fields near the tip of the peninsula. The turnover of these birds during the observation period was often very pronounced. On many mornings most of the migrating Skylarks apparently 58

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Fig. 5: Accumulations of Skylarks, Knudshoved. The hatched and black arrows show immigration and emigration, respectively, for the accumulating birds. The patterns are somewhat wind dependent. The emigrating flocks often consist of 20–40 birds, but such large assemblies are highly instable. After a flight distance of 50–200 meters the large flocks differentiate in many small flocks which may diverge from each other in directions up to $90^{\circ} - 120^{\circ}$

were passing through what we designate as a state of accumulation. The migration was broken off when passing the fields, and for a certain time the number of resting birds was increasing. The birds often displayed restlessness, flying low over the fields in dense flocks, while their call-note could be heard. Finally, either caused by an external stimulus or when the number of accumulating birds grew sufficiently large, they would fly off in a dense flock, which would eventually break up into small fractions, normally after a flight of a few hundred meters. This pattern was especially observed before an emigration over the sea. Fig. 7 shows the accumulation and emigration patterns during different wind conditions.

The average number of resting birds at any time during the observation period was expressed by the degree of accumulation on a scale ranging from 0 to 4 corresponding roughly to 0, 5, 10, 20, and 50 or more birds, respectively.

Fig. 6: The daily mean flocksize as a function of the daily number of migrating birds, Knudshoved. A, B and C show days with degree of accumulation 0, 1–2, and 3–4, respectively. In B and C a positive correlation is found between the mean flock size and the number of migrating birds. The SPEARMANN rank correlation coefficient (SIEGEI 1956) is -0.13, +0.36, and +0.69 for A, B, and C, respectively. The correlations of B and C are statistically significant below the 0.05 level. Furthermore, the flocksizes increase with the degree of accumulation. This increase is independent of the just mentioned influence of the number of birds - as shown by the following test. When the number of birds is less than 190 no significant correlation is found between the mean flocksize and the number of birds in neither A, B, nor C. The two distributions in A and (B + C) may now be tested against each other, and the difference is found to be statistically significant (p = 0.018, MANN-WHITNEY U-test, SIEGEL 1956).





The positive correlation between the degree of accumulation and the flocksize seems obvious (Tables 4–5, Fig. 6).

The degree of accumulation at Knudshoved is, of course, a highly local factor. But in certain aspects it may contain general properties. During days when many Skylarks are displaying restlessness on the fields, the migrating flocks are presumably on average lesser time in the air. This makes possible the number of relatively many large, unstable flocks.



Fig. 7: Patterns of migratory directions for the four flocksize groups 1, 2, 3-5, and 6 or more birds, Knudshoved. Only days with eastern winds (NNE to SSE) are included. The mean wind direction is exactly E. The ratios of flocks migrating "W" (SSW – NNW) to the number of flocks migrating "E" (NNE – SSE) are 0.19, 0.08, 0.04 and 0.04 for the flocksize groups 1, 2, 3-5, and 6 or more birds, respectively. The difference between the flocksize groups 1 and 2 is statistically significant (Chi-square test, p < 0.001).



Fig. 8: Patterns of migratory directions for the four flocksize groups 1, 2, 3–5, and 6 or more birds, Knudshoved. Only days with western (SSW – NNW) winds are included. The mean wind direction is exactly W. The ratio of western to eastern directions for the flocksize groups 1, 2, 3–5, and 6 or more birds are 0.89, 0.60, 0.48 and 0.28, respectively. Again the difference between the flocksize groups 1 and 2 is significant (0.01 , Chi-square test). The directions in the eastern sector (N to SSW incl.) seems to be a little more "southern" in the higher flocksize groups. The mean direction for this sector in the four flocksize groups is 80°, 92°, 93° and 103°. The difference between 1 and 6 or more is statistically significant (<math>p < 0.01, KOLMOGOROV-SMIRNOV two sample test).

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e) Number of migrating birds: Normally there is a positive correlation between the daily mean flocksize (g) and number of migrating birds (N) (Table 5, Fig. 6). In the Skylark the relation seems to be on the form: g = k N (or g = k (k is a constant), Fig. 6A). Concerning other species such as Eider (Somateria mollissima), Oystercatcher (Haematopus ostralegus), and Starling (Sturnus vulgaris) a root transformation ($g = k \cdot N^x$, where x is a real number less than 1) seems to be the general rule (NOER & RABØL unpubl.). The cause(s) of these correlations is not yet fully understood.



Fig. 9: Patterns in migratory directions in the flocksize groups 1 and 2, Knudshoved. All days with cloudiness 0-5/8, eastern winds (meanwind direction = ESE), and 0 accumulation are included. "2" is an attempt to describe the pattern of 2 as evolved in a simple way from the pattern of 1. To facilitate the comparison the number of flocks in 2 and "2" are the same [95]. See the text for more details.

The positive correlation between g and N at Knudshoved during accumulation and the much smaller flocksizes at Hvalsø compared with Gilleleje (Table 5) is presumably due to the presence of many "over-saturated" flocks in those areas of concentration (coastlines etc.). Part of this "over-saturation" may probably originate from flocks fusing in the air, but accumulation at the fields should be by far the most common cause.



Fig. 10: Flocksize groups 1, and 2 or more birds, Hvalsø, 15 March 1971, wind SE 2–3 Beaufort, 7–8/8. The dispersion – and/or the degree of reverse migration – is much higher in the flocks consisting of just one bird.

6. Migratory Directions in Different Flocksize Groups

Figs. 7–10 show the patterns of migratory directions of the four flocksize groups 1, 2, 3-5, and 6 or more birds.

The degreee of reverse (western) migration is much more pronounced in western than in eastern winds (Fig. 8 compared with Fig. 7). The primary cause should be the presence of a "headwind migration tendency" (RABØL 1964a, 1967, 1969, and RABØL & HINDSBO 1972).

Otherwise, the degree of reverse migration - and or the dispersion of the migratory directions - becomes less as the flocksize increases.

This phenomenon can be "explained" in several ways. One of the most simple and still reasonable models should be presented (Fig. 9). The directional pattern of the single migrating birds (flocksize group 1) could be considered as the intrinsic directional frequency distribution in the Skylark population. Sometimes two (or more) birds happen to get close enough to each other to allow the formation of a common flock — supposing the directional preferences of the birds are not too different, e. g., are within 90° of each other. The migratory direction of such a common flock is supposed to be the mean direction of the two (or more) original directions (cf. HA-MILTON 1966). The evaluation of the migratory pattern of such a "2"-flock follows: The intrinsic probability for a bird to migrate in a certain direction is proportional to the number of single birds (1-flocks) migrating in that direction (d_i). We then have:

$$p_i = \frac{d_i}{16}$$
$$\sum_{i=1}^{16} d_i$$

The directional frequencies (r_i) of the "2"-flocks are calculated as:

$$r_{i} = \frac{q_{i} + \frac{1}{2} q_{i} - \frac{1}{2} + \frac{1}{2} q_{i} \frac{z}{t} + \frac{1}{2}}{16} \frac{16}{\sum_{i=1}^{2} s_{i}}$$

where $s_i = q_i + \frac{1}{2} q_i - \frac{1}{2} + \frac{1}{2} q_i + \frac{1}{2}$ and $q_i = p_i^2 + 2 p_{i-1} p_{i+1} + 2 p_{i-2} p_{i+2}$ and $q_i - \frac{1}{2} = 2 p_i p_{i-1} + 2 p_{i+1} p_{i-2}$ and $q_i + \frac{1}{2} = 2 p_{i+1} p_i + 2 p_{i+2} p_{i-1}$

 $q_i \pm \frac{1}{2}$ is introduced because of the transformation of the 16 original directions in 32 ones. In order to end up with the 16 original directions we have split the 16 new directions equally up between the two nearest original ones.

The concentration of the mean vectors in 2 and $2^{\prime\prime}$ is fairly close to each other (0.73 and 0.78). The difference could be purely due to chance, but otherwise the higher concentration of $2^{\prime\prime}$ could be reduced if the original direction of one of the birds is completely determining the mean direction of the common 2-flock.

7. Conclusion and Summary

The daily mean flocksizes and flocksize distributions are obviously influenced by a number of environmental factors.

Some weather factors such as the visibility and especially the cloudiness apparently have a pronounced and direct influence on the flocking behavior. An overcast sky and low visibility increase the flocksizes. Other parameters which are increasing the flocksizes such as the number of resting and/or migrating birds are in themselves dependent functions of other environmental (weather) factors.

It could be demonstrated that the flocksize distributions in general are well fitted by negative binomial (and not by poisson) distributions.

The migratory patterns in the four flocksize groups: 1, 2, 3–5, and 6 or more birds are somewhat different. The degree of reverse (western) migration is thus clearly decreasing with increasing flocksizes. Fig. 9 offers an "explanation" of this phenomenon.

Zusammenfassung

Frühjahrszug der Feldlerche in Dänemark. Einfluß von äußeren Faktoren auf die Schwarmgröße und Beziehungen zwischen Schwarmgröße und Zugrichtung.

Die täglichen Durchschnitts-Schwarmgrößen und Schwarmgrößen-Verteilungen werden offensichtlich von einer Reihe von Umweltfaktoren beeinflußt. Einige Witterungsfaktoren, wie Sicht und Bewölkung, haben einen deutlichen und direkten Einfluß auf das Schwarmverhalten. Bewölkter Himmel und schlechte Sicht verursachen Vergrößerung der Schwärme. Andere Faktoren, die zu Schwarmvergrößerungen führen, wie Anzahl von rastenden und/ oder ziehenden Vögeln, sind selbst von Witterungsfaktoren abhängig.

Die Verteilungen der Schwarmgrößen stimmen generell mit negativen Binomial-Verteilungen überein, nicht mit Poisson-Verteilungen.

Die Zugmuster in den vier Schwarmgrößen-Gruppen 1, 2, 3-5 und 6 oder mehr Vögel sind etwas verschieden. Westwärts gerichteter Umkehrzug ist am häufigsten bei den kleinsten Schwärmen.

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Authors address: Jørgen Rabøl & Henning Noer, Zoologisk Laboratorium, Universitetsparken 15, DK 2100 København Ø, Danmark.

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Aus dem Max-Planck-Institut für Verhaltensphysiologie, Vogelwarte Radolfzell

Zum Herbstzug des Zwergschnäppers (Ficedula parva) im Bereich der Deutschen Bucht

Von Rolf Schlenker

In zusammenfassenden Darstellungen haben sich kürzlich VAUK & HARTWIG (1969), DIESSELHORST (1971) und GATTER (1972) mit dem Zug des Zwergschnäppers auseinandergesetzt. Um das Bild des Auftretens dieser Art im Herbst westlich seines Brutareals zu vervollständigen, soll hier weiteres Datenmaterial aus der Deutschen Bucht, Helgoland ausgenommen, dargestellt werden.

Daten aus der Deutschen Bucht

Die Beobachtungen des Zwergschnäppers in der Deutschen Bucht sind in Abb. 1 dargestellt und im folgenden aufgeschlüsselt.

Sylt: 2.9. 1910 1 & [HAGENDEFELDT 1912]; 18.9. 1954 Hörnum 1 & [KRÜGER 1957]; 26.9. 1959 Ellenbogen 1 Ex. (SCHMIDT 1960); 29. 8. 1963 Nordsylt 1 Ex. (WITT briefl.) und 1 Ex. am 20. und 21. 10. 1972 Vogelkoje Kampen (BUCHWEITZ & GLOE briefl.).

Amrum: 21. und 29. 9. 1962 je 1 & Norddorf (SCHMIDT 1964); 19. 9. 1965 Norddorf und Nebel je 1 Ex. (Rонде briefl.) und Mitte August 1963 Nordspitze 1 Ex. (SCHLENKER 1966).

ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

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