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Lech STEMPNIEWICZ

Chair of Ecology and Vertebrate Zoology, University of Gdańsk,
Czołgistów 46, 81 – 378 Gdynia, Poland

FACTORS CAUSING CHANGES IN THE RHYTHM OF ATTENDANCE OF THE LITTLE AUKS, *PLAUTUS ALLE* (L.), AT A COLONY DURING THE BREEDING SEASON IN SVALBARD

ABSTRACT: As the breeding season progresses, the rhythmic periods of the little auks' presence and absence in a colony are subject to a gradual shortening (from several days to 24 h). The breeding season stage, behaviour of little auks and gulls, meteorological conditions and variation in zooplankton availability may exert an influence on the maximum number of little auks present in a colony during successive periods, as well as on the time of the day at which the peak numbers occur. There does not exist one superior factor responsible for the attendance rhythm of the little auks. This rhythm is governed by the resultant of many intra-population, biocoenotic and environmental factors whose intensity of action varies with the breeding season stages.

KEY WORDS: Svalbard, little auk, pattern of attendance at a colony.

1. INTRODUCTION

The main environmental factor determining the circadian rhythm in animals is the alternate light and darkness rhythm (A s c h o f f 1965, C y m b o r o w s k i 1984 and others). In connection with the above, of particular interest are studies carried out at high latitudes under the conditions of a 24 h polar day. Most papers on the activity rhythm in birds during the polar summer deal with passerine birds (R e m m e r t 1980). Sometimes in papers on the biology and ecology of some species more or less information can also be found about the circadian rhythm. In quite a number of papers concerned with the difficulty to assess the size of alcid populations the problem is also raised of circadian and seasonal variation in the number of birds in a breeding colony. The largest number of such papers was devoted to guillemots *Uria* sp. (L l o y d 1975, B i r k h e a d 1978, S l a t e r 1980, G a s t o n and N e t t l e s h i p 1982) and to some other species (L l o y d 1975, A s b i r k 1979, B y r d et al. 1983). Only part of the studies were carried out in the polar zone.

In the case of the little auk the references, dispersed in the literature, on the circadian rhythm either suggest that it exists (D e m m e 1934, F o s t e r et al. 1951, F e r d i n a n d 1969) or reject it (M a r s h a l l 1938, F e r e n s 1962, L ø v e n s k i o l d 1964). It was only E v a n s (1981) who has given more attention to it.

In the present paper a pattern has been presented of the attendance of little auks at a breeding colony and its variation with the breeding season stages, from the arrival of the birds at the breeding grounds to their deperture from them. A trial has also been attempted to analyse the effect of various environmental, biocoenotic and intrapopulation factors on the activity rhythm in the little auks.

2. MATERIAL AND METHODS

Field work was conducted in the Hornsund region, SW Spitsbergen during two breeding seasons, 1980 and 1983. In the 1980 breeding season, observations were continued from May 13 to August 20, and in the season of 1983 – from July 30 to August 27.

On the slope of the Arie mountain (Ariekammen), in 3 uneven-sized breeding subcolonies 3 sample areas were marked out with a steelon line. They were of the size 10 by 10 m (in the case of the "small" subcolony – A – of about 150 m^2 in area), and 10 by 20 m (in the case of the "medium-sized" subcolony – B – about 600 m^2 in surface area, and the "large" subcolony – C – about 3500 m^2). Every 3 hours a census was made of all little auks present in the marked-out sample areas, and of glaucous gulls, *Larus hyperboreus* Gunn., over the whole slope and at the foot of the Arie mountain. Depending on the place from which the census was made, a telescope 20 – 40 × 50, field-glasses 15 × 50, or 10 × 50 were used, or the counting was done with the naked eye. The census data presented in the paper have been calculated per 100 m^2 sample area. In the sample areas studies of the rhythm of attendance of the little auks at the colony were carried out in the periods: 1 June – 20 August 1980, and 30 July – 27 August 1983.

At the beginning of the breeding season (May) the meteorological situation (a thick snow cover on the slopes and frequent snowfall) and the behaviour of the birds (landing in different places over the slope because of the lack of visible landmarks) made it impossible to mark out sample areas and make census. For this reason, the data for this period in the 1980 breeding season are only estimates, but can be used in the analysis of the pattern of attendance of little auks at the breeding colony.

Checking of 51 marked nests made it possible to establish starting and completion dates for the more important stages of the breeding season. In the presentation of the results of the study local time, 2 h ahead of GMT, was used.

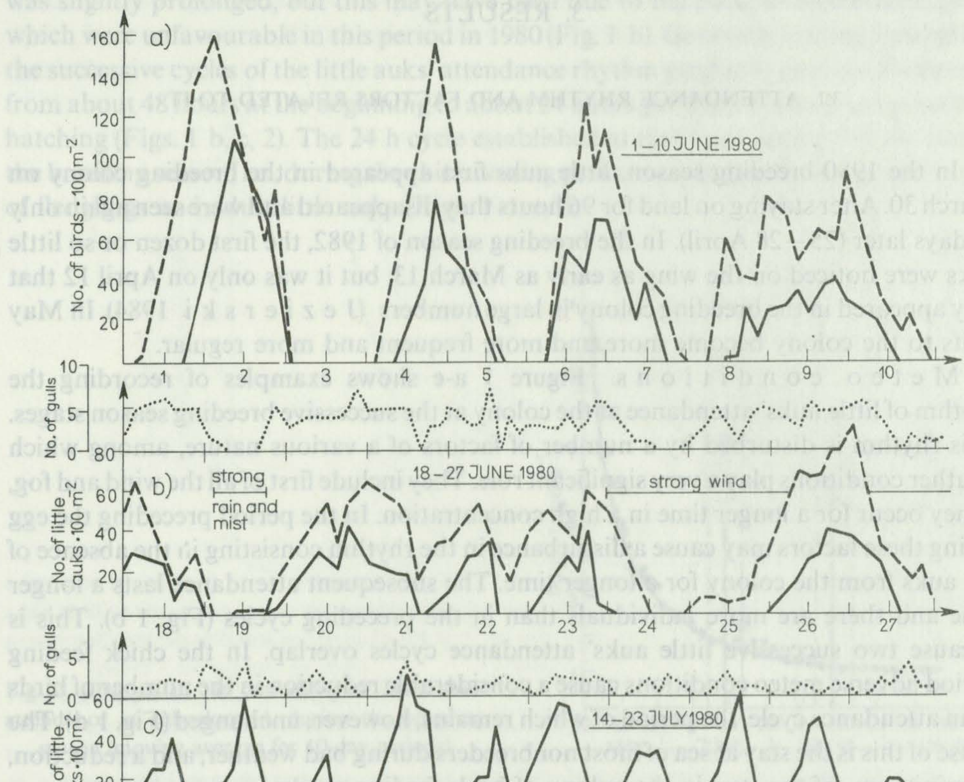

Fig. 1. Examples of the rhythm of little auks' attendance at a colony and of glaucous gulls near a colony in different periods of the breeding season (solid line – subcolony A, dashed line – subcolony C, dotted line – number of glaucous gulls near little auks' colony)

a – prelaying period, b – laying and early incubation periods, c – periods of late incubation, hatching and brooding of newly hatched chicks, d – chicks' nest period, e – period of fledglings' departure from colony

3. RESULTS

3.1. ATTENDANCE RHYTHM AND FACTORS RELATED TO IT

In the 1980 breeding season, little auks first appeared in the breeding colony on March 30. After staying on land for 96 hours they disappeared and were seen again only 22 days later (25 – 28 April). In the breeding season of 1982, the first dozen or so little auks were noticed on the wing as early as March 13, but it was only on April 12 that they appeared in the breeding colony in large numbers (J e z i e r s k i 1984). In May visits to the colony become more and more frequent and more regular.

M e t e o c o n d i t i o n s. Figure 1 a-e shows examples of recording the rhythm of little auks' attendance at the colony at the successive breeding season stages. This rhythm is disturbed by a number of factors of a various nature, among which weather conditions play a very significant role. They include first of all the wind and fog, if they occur for a longer time in a high concentration. In the period preceding the egg laying these factors may cause a disturbance in the rhythm consisting in the absence of the auks from the colony for a longer time. The subsequent attendance lasts a longer time and there are more individuals than in the preceding cycles (Fig. 1 b). This is because two successive little auks' attendance cycles overlap. In the chick feeding period adverse meteo conditions cause a considerable reduction in the number of birds in an attendance cycle, the period of which remains, however, unchanged (Fig. 1 d). The cause of this is the stay at sea of most nonbreeders during bad weather, and a reduction, to minimum, of the stay in the colony of birds feeding chicks.

P r e s e n c e o f g u l l s. The number of glaucous gulls present in the region of a little auks' colony fairly well reflects the rhythm of little auks' attendance on land (Fig. 1 b-e). This relationship is more conspicuous in the egg laying and incubation periods and in the period of little auk fledglings' departure to sea (Fig. 1 b, c, e). It is less marked in the period of little auk chicks' stay in the colony (Fig. 1 d). The number of glaucous gulls present in the region of a little auks' colony is also clearly affected by strong winds. Their number is then larger in spite of the lower numbers of little auks (Fig. 1 b, d).

3.2. CHANGES IN THE ATTENDANCE PATTERN WITH THE PROGRESS OF THE BREEDING SEASON

In the changes of the rhythm of little auks' attendance at a colony with the course of the breeding season a very clear tendency can be seen. It consists in the shortening of the periods of the successive cycles, and thereby the duration of successive stays and absences of birds in the colony.

C y c l e l e n g t h. The number of days per 1 cycle falls rapidly, from about 10 to about 2, in the period preceding egg laying (Figs. 1 a, 2). After egg laying the cycle was slightly prolonged, but this may have been due to the effect of meteo conditions which were unfavourable in this period in 1980 (Fig. 1 b). Generally, during incubation the successive cycles of the little auks' attendance rhythm gradually become shortened, from about 48 hours at the beginning to about 24 hours per cycle in late incubation and hatching (Figs. 1 b, c, 2). The 24 h cycle established at that time persists till the end of the breeding season, i.e., during the chick nesting period and during the departure to sea of fledglings and adult little auks (Figs. 1 d, e, 2).

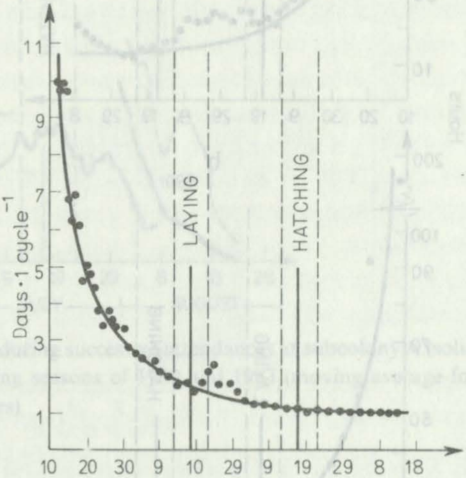

Fig. 2. Changes in the periodicity of little auks' attendance at subcolony A during the breeding season (moving average for 10-day periods)

P r e s e n c e a n d a b s e n c e o f b i r d s i n / f r o m a c o l o n y. With the course of the breeding season, the time of auks' stay at a colony, and the time of their absence during a single cycle show a tendency similar to that described above (Fig. 3 a, b). The average time of the birds' presence in a colony becomes shortened from over 80 h at the beginning of the 2nd 10-day period of May to about 24 h in the laying period. This situation persists almost throughout the incubation period. With the hatching of the first chicks the time of the birds' stay at the colony is clearly shortened down to about 12 h (Fig. 3 a). Towards the end of the breeding season a tendency is observed towards a prolonged stay of the birds on land. But this is probably an error resulting from very low number of birds visiting the colony at that time (Fig. 1 d, e), and from the adopted attendance criterion (see the legend to Fig. 3).

The average time of little auks' absence from a colony in the successive cycles becomes shortened drastically, primarily in the period preceding egg laying. At the beginning of the 2nd 10-day period of May it comes up to over 190 h, and with the appearance of the first eggs in a colony already as little as 20 h. During the incubation period certain disturbances can be observed which can be related to the bad weather period mentioned above. In general, the average time of the absence of birds from a colony is shorter in this breeding season phase, amounting to about 12 h at the time of hatching. A situation like this persists till the end of the breeding season (Fig. 3 b). In

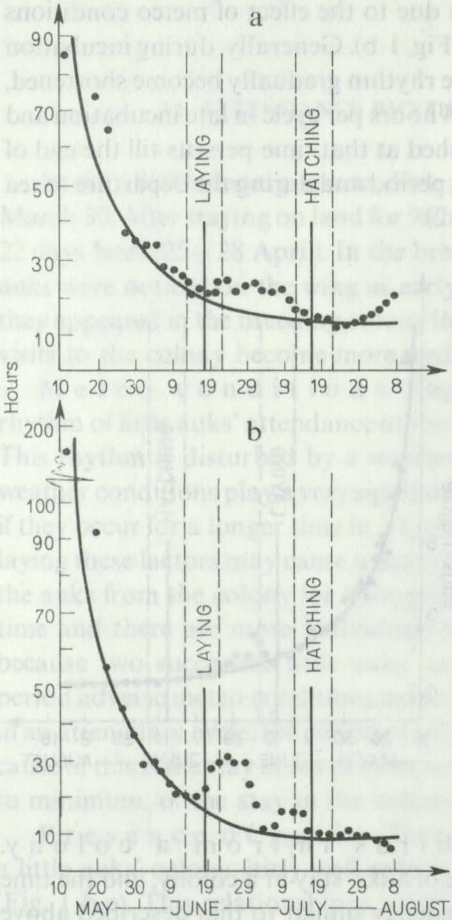

Fig. 3. Variation in the duration of successive attendances (a) and absences (b) of little auks at/from subcolony A during the breeding season (moving average for 5 cycles)

With the progress of the breeding season there occurred a tendency that some of birds stay in the colony even when most of them are absent from the colony and feed at the sea (see Fig. 1). For this reason, 30% of the maximum number of birds in a particular cycle was arbitrarily adopted as a criterion of the presence or absence of birds in/from the colony

fact towards the very end the average absence time seems to be still reduced, but this is an error the same as that described in the discussion of Figure 3 a.

N u m b e r o f b i r d s a t p e a k a t t e n d a n c e. With the progress of the breeding season subject to characteristic changes is the maximum number of birds observed during successive cycles of their attendance at a colony (Fig. 4). During the period preceding egg laying it decreases 2 – 3-fold due to several causes. Firstly, the length of the cycles is shortened and thereby the frequency is increased. Secondly, there is less synchronism in flights out to sea and returns to land. Associated with these phenomena is the fact that both at sea and at colony an ever-growing number of birds remain at periodicity stages in which they have not been found there at all. In the period immediately preceding egg laying the females stay in nesting crevices while other individuals of the colony are absent. Later on, during incubation the same applies to one bird of each pair. Some time prior to egg laying the females nearly always stay in nesting crevices, also in the presence of the remaining members of the colony, trying to avoid sexual aggressiveness of the males. The above has been confirmed by the results from bird censuses in the sample areas during peak attendance at the colony in this period.

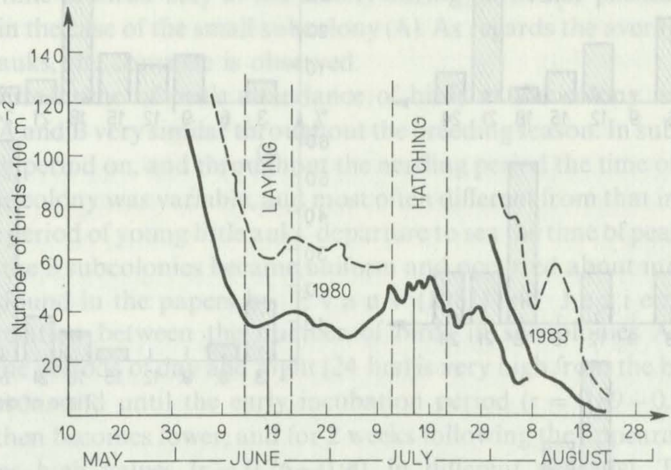

Fig. 4. Variation in the maximum number of little auks during successive attendances at subcolony A (solid line) and subcolony C (dashed line) during the breeding seasons of 1980 and 1983 (moving average for 5 cycles)

At incubation period the average number of birds present during the successive attendance peaks remains at about the same level. The variations that were observed were caused by the influence of the adverse meteo conditions that prevailed in the 2nd half of June in 1980. Towards the end of the incubation period, and as soon as chicks appear in a colony, the maximum number of adult little auks, gradually terminating incubation, grows with the successive cycles of attendance. From then on, however, and until the end of the breeding season it decreases steadily (Fig. 4). This is due to the shorter and shorter time spent in the colony by adult birds feeding the nestlings, and later on also to the gradual departure from the colony of nonbreeders, and finally also of breeders which accompany the young during their departure to sea. A strong predatory pressure of gulls on little auk chicks exercising their wings in the colony area (S t e m p n i e w i c z 1983) contributes to the number of adult birds without clutches, which "prematurely" leave a colony.

P e a k a t t e n d a n c e p e r i o d. Another clearly visible, becoming conspicuous with the progressing breeding season is the change of the time of day at which peak numbers of birds occur in a colony (Figs. 1 a-e, 5). In the period preceding egg laying there is no clear preference of a particular time of day or night, and peak attendances of birds at the colony were most often observed about 21,00 hrs (30%), 6,00 (21%), 12,00 and 3,00 (17.5% each time) (Fig. 5 a). This state should be related to the length of the cycle which changes quickly at that time (Fig. 2).

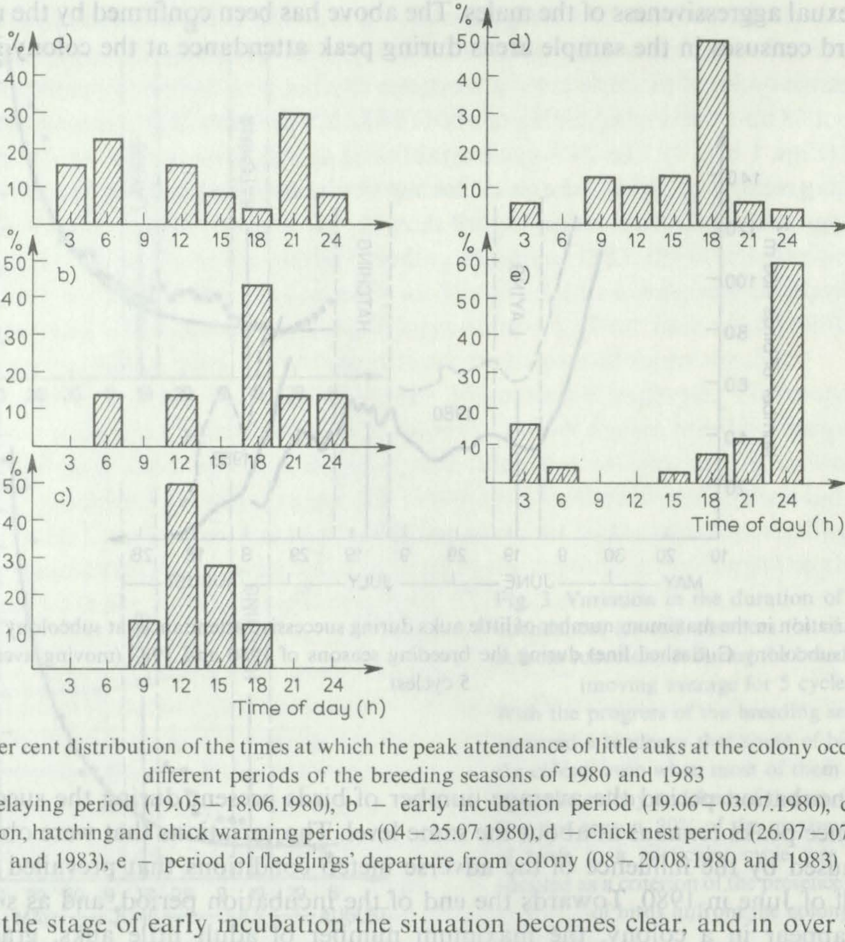

Fig. 5. Per cent distribution of the times at which the peak attendance of little auks at the colony occurred, in different periods of the breeding seasons of 1980 and 1983
a — prelaying period (19.05 – 18.06.1980), b — early incubation period (19.06 – 03.07.1980), c — late incubation, hatching and chick warming periods (04 – 25.07.1980), d — chick nest period (26.07 – 07.08.1980 and 1983), e — period of fledglings' departure from colony (08 – 20.08.1980 and 1983)

At the stage of early incubation the situation becomes clear, and in over 40% of cases the peak numbers of little auks present in the colony fell on 18,00 hrs (Fig. 5 b). But here also one must remember the unfavourable meteo conditions which could have an effect on the per cent distribution of the preferred time of the presence of maximum number of little auks.

The next periods are late incubation, hatching of chicks and their continuous warming by one parent during the first several days of their life. Peak attendance of little auks at a colony was at this stage most frequently observed at noon (Fig. 5 c). In the last two breeding season periods distinguished the peak attendance time is delayed. In the chick nesting period this time is shifted to 18,00 hrs (Fig. 5 d), whereas in the period during which fledglings leave the colony — to 24,00 hrs (Fig. 5 e).

3.3. COMPARISON OF DIFFERENT SUBCOLONIES

In spite of the general similarities of the attendance of little auks at all the three subcolonies studied, certain differences can also be noticed. They are to a large extent connected with the number of little auks being larger in larger subcolonies (Figs. 1 a, b, e, 4). As a result of this, a large subcolony becomes deserted at a later date, and in each cycle birds appear in it at an earlier-time. Hence in the case of the large subcolony (C) the average time of birds' stay at the colony during particular phases is significantly longer than in the case of the small subcolony (A). As regards the average absence time of the little auks, the converse is observed.

The preferred time of peak attendance of birds at the colony is in the case of subcolonies A and B very similar throughout the breeding season. In subcolony C, from the egg laying period on, and throughout the nestling period the time of peak numbers of birds in the colony was variable, and most often different from that in subcolonies A and B. In the period of young little auks' departure to sea the time of peak attendance of adults at all the 3 subcolonies became uniform and occurred about midnight. Similar data can be found in the papers by E v a n s (1981) and J e z i e r s k i (1984).

The correlation between the number of birds in subcolonies A and B in the particular time periods of day and night (24 hrs) is very high from the beginning of the breeding season, and until the early incubation period ($r = 0.89 - 0.97$, in different pentads). It then becomes lower, and for 2 weeks following the appearance of chicks it again reaches high values ($r = 0.76 - 0.90$, in different pentads). The correlation between the birds' attandance at subcolonies A and C, and B and C generally attains lower values. However, towards the end of the breeding season, when the attendance rhythm in all the 3 subcolonies becomes uniform, the relationship between the numbers of little auks, varying during the 24 hrs period, in subcolonies B and C, becomes higher than between A and B, and A and C, because of a very low attendance, at this stage, of birds at subcolony A (Fig. 1 e).

3.4. COMPARISON OF BREEDING SEASONS

Though they only covered part of the breeding season, the studies carried out in 1983 confirm the general results obtained in 1980. However, there have been several differences. In the 1980 breeding season, all the breeding season stages began and ended about a week earlier than in 1983. This time correction should be taken into account in the interpretation of, e.g., Figure 4. Another difference observed was a higher, in August 1983, number of little auks in all the subcolonies observed (Fig. 4). This may, however, be attributed to a much better weather in August 1983 than in August 1980, and therefore a more abundant presence of birds in the area of the colony.

4. DISCUSSION

4.1. INTRODUCTION

In considerations on birds' activity rhythms during the Arctic summer one must take into account three different groups of factors connected with them. Group I includes factors that are the possible "time givers" (Zeitgebers), enabling the birds to orientate themselves in the cycle of the Earth's rotation. Group II consists of factors which disturb or modify the activity rhythm, and may sometimes be mistaken for Zeitgebers, or for factors of the next group. Group III comprises factors that are at least partly responsible for a particular activity rhythm.

4.2. ZEITGEBERS

The author is convinced that the birds staying in the polar zone in summer have no problems with orientating themselves in the time of the day-night (24 hrs) period. Horizontal changes in the position of the sun during the 24-hour period are very clear and noticeable even to man. Moreover, birds can perceive changes in the composition of the solar light spectrum (K r ü l l 1976a, 1976b).

In a breeding colony the circadian time rhythm is marked yet more clearly owing to the regular "sunrises" and "sunsets" behind the mountain on whose slope the colony is situated (it is usually a slope more or less facing south). With the course of the breeding season the sun, the position of which over the horizon lowers gradually, "rises" later and later and "sets" earlier and earlier. About mid-August, when young little auks leave a colony, during "night" hours (that is when the departure takes place) it is dark both in the colony and on the way from the colony to the sea. This periodicity of the times over the 24-th period is yet more marked in breeding colonies located on rock cliffs.

4.3. FACTORS DISTURBING THE PERIODICITY

Included among these are some environmental factors if they act sufficiently long and are sufficiently intensive, as well as the predatory activity of gulls, to some extent related to the meteorological conditions.

E n v i r o n m e n t a l c o n d i t i o n s. Disturbances in the periodicity of little auks' attendance at colony due to high, long-lasting winds, and thick fog have already been described (Fig. 1b, d).

Unfavourable weather conditions obviously occur at sea as well, and the preference by little auks of staying at sea at this time to staying on land is primarily related to the growing danger from gulls acting in the breeding colony area (S t e m p n i e w i c z 1983). There is no convincing proof that sea state makes it difficult for the little auks to obtain food, as suggested in the case of the guillemots by B i r k h e a d (1976). The chick feeding rate in the little auk does not fall significantly during bad weather (L. Stempniewicz and J. Jezierski – in prep.)[1], which is confirmed by N o r d e r h a u g's (1980) data, but it is limited primarily by an increased threat of gulls at high winds. This effect is mainly due to different abilities of taking advantage of the wind during the flight by alcids and gulls.

[1] Incubation shifts and chick feeding rate in the little auk (*Plautus alle*) in Svalbard.

Thus the decrease in number of birds in a breeding colony during a windy weather, noticed by many authors in different alcid species (B i r k h e a d 1976, 1978, S l a t e r 1980, G a s t o n and N e t t l e s h i p 1982), may be related, at least to some extent, to difficulties with air locomotion, especially with the taking off and landing. Under such weather conditions some little auks on rising from the ground knocked against stones; also, far more often, Brünnich's guillemots *Uria lomvia* (L.) could be seen bumping against the wall of a colony during landing and falling down to the foot of the cliff where they fell victims to Arctic foxes *Alopex lagopus* (L.).

Another environmental factor that can affect the activity rhythm of the little auks is the ice cover on the waters. However, this effect is limited, for little auks feed in very large numbers even in a dense ice pack. Only when the waters of a whole fiord and the foreground are covered with solid ice (most often at early stages of the breeding season) are little auks forced to feed in more distant areas, which may cause a longer absence of birds from a colony. Considerable body-weight differences, coming up to 10% of adult little auks, weighed on consecutive days (L. Stempniewicz – unpublished data), indicate that they may fly even to very distant feeding grounds (B r o w n 1976).

A c t i v i t y o f t h e g u l l s. The effect of gulls' activity on the behaviour of the auks has been known and has been described by many authors from different auk and gull species (N e t t l e s h i p 1972, C o d y 1973, S l a t e r 1980, S t e m p n i e w i c z 1981, 1983, P i e r o t t i 1983 and others). The interactions between the auks and glaucous gulls vary with the breeding season stages and are connected with weather conditions. The relationship between the number of auks staying at a breeding colony and the number of glaucous gulls is the strongest at early breeding season stages (in the period preceding egg laying and during incubation) and towards the end of the breeding season, when juvenile birds leave the colony.

At the beginning of the breeding season only adult little auks are available as prey to gulls which hunt for them. Little auks arrive at the breeding grounds after having spent 7–8 months at sea far from the land. Hence in the first period of their visits to a breeding colony little auks do not land at all, but hover over a slope, are excited and shy, and their behaviour is hesitant. They no longer have the possibility, in case of need, to immediately dive in the sea to get rid of a predator, and do not yet have the possibility to dive to the ground to hide in the rock rubble. Snow still lies thick everywhere, and black-and-white little auks are clearly visible against it. All these factors, which are disadvantageous to little auks, are advantageous to glaucous gulls. Most of the prey, particularly at this stage, are less experienced sexually immature individuals. Out of 112 gulls' pellets examined 87 (77.7%) contained brown wings of sexually immature little auks (L. Stempniewicz – unpublished data).

In the egg laying and incubation periods, the main predatory pressure is exerted on adult birds, although some of the eggs laid in places accessible to gulls fall prey to the latter (S t e m p n i e w i c z 1981). In the nesting period, when nestlings begin to walk out to the colony surface and exercise wings, it is for them that gulls hunt (S t e m p n i e w i c z 1983). This disturbs the relationship between the rhythm of adult little auks' attendance at a colony and the number of glaucous gulls present there.

At the last land breeding season stage of the little auks, i.e., the departure of young birds to sea, the presence of gulls is again closely related to the number of adult little auks in a colony. The peak attendance of adult little auks now occurs at a time of the day-night period at which the departure of the young to sea takes place (Fig. 5). The young little auks are now the only object of hunting, whereas the relationship between the number of gulls and the number of adult little auks present in a colony, and taking part in the departure of the young to sea, is of an indirect nature.

The activity of gulls and adverse weather conditions often act jointly as factors disturbing the rhythm of little auks' attendance at a colony. During high winds gulls considerably dominate over little auks in respect of air-locomotion possibilities, which causes an increase in their hunting efficiency (S t e m p n i e w i c z 1983). On such days the number of gulls present in a colony is large (Fig. 1 d), although the number of adult little auks is small, and their incessant harassing and flushing limits the time of their stay at a colony, not affecting the periodicity of attendance. Thus during bad weather the activity of gulls causes greater disturbances in the pattern of little auks' attendance, but the fact remains unchanged that the attendance rhythm of the little auks imposes the activity rhythm on the gulls and not vice versa.

4.4. FOOD AVAILABILITY AND INTRA-POPULATION CONDITIONS

One of the factors that really can determine the attendance rhythm of little auks may be a periodicity in food availability changes, of course if there is one at all. Unfortunately, there have not been any studies so far that would unequivocally solve this problem. At lower latitudes circadian zooplankton migrations are a common phenomenon (H a r d y 1957, A s h m o l e 1971), but there are discrepancies of opinions as regards Arctic waters. B o g o r o v (1946) found a limited vertical movement of zooplankton over the 24-hour period in the Barents sea in summer, more pronounced in autumn. D i g b y (1961) also noticed a limited effect of circadian variation, low in summer, in light intensity on zooplankton abundance in the waters of western Spitsbergen. According to his opinion, this relationship is clearer in water regions that are not disturbed by currents, and disappears where there are various translocations of water masses. However, the data included in his paper, if ordered according to sampling hours, give the picture of a very clear rhythm of circadian variation in numbers of *Calanus finmarchicus* (Gunn.) (the main food item of the little auk) in the surface (down to 1 m) water layer in July and August (Fig. 6).

I n c u b a t i o n a n d c h i c k f e e d i n g p e r i o d s. If superimposed on the food availability rhythm, the numbers-variation cycle of birds in subcolonies A and B in the incubation and chick feeding periods appears to be its fairly exact converse (Fig. 6), which means that the little auks really may feed when food is most available (similar results were obtained by E v a n s 1981, particularly for the incubation period).

The preferred time of peak numbers of birds in the colony, different in the case of

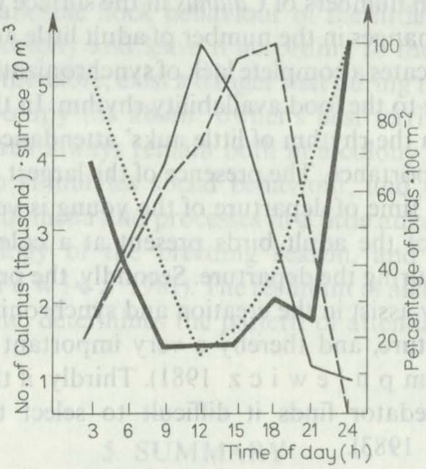

Fig. 6. Little auks' attendance at the breeding colony at different times of the 24 h period (averaged for 10-day periods and expressed in percentages) in the period of late incubation (14 – 23 July – thin solid line), in the chick feeding period (26 July – 4 August – dashed line) and in the departure period (11 – 20 August – dotted line) against circadian variation in *Calanus finmarchicus* density in the surface layer of the waters of western Spitsbergen (19 July – 24 August – thick solid line; from Digby 1961)

subcolony C, suggests that there may also be involved a different location (and thereby also distance and richness) of feeding grounds used by birds from different subcolonies. This supposition may be supported by the data reported by Evans (1981) and Jezierski (1984). Both authors give an earlier (by 3 up to 6 h) time of the peak attendance of little auks at a colony, at this stage of the breeding season, than has been found in the present investigations. However, in both cases the feeding grounds of the little auks were most likely located much nearer. Evans (1981) gives a distance between the colony and feeding grounds of the range of 2.5 km. But in the case of Hornsund, where little auks mainly feed in the fiord foreground, the birds of the colony studied by Jezierski (1984) are about 20 km closer to the fiord foreground than are the birds of the colony studied in the present study.

As regards the quality of the feeding grounds, the question remains open as to whether feeding in calm water regions, with an undisturbed water bulk stratification and more marked circadian zooplankton movement, and thereby predictable food availability, is more advantageous to the little auks. Or whether it is better for them to feed in zones, numerous in that area, where various water masses clash periodically, abounding in easily-available food (Hartley and Fisher 1936, Stempniewicz and Węsławski – in press), but not always predictable. It is likely that, depending on the conditions (hydrometeorological conditions, seasonal variation in zooplankton numbers, breeding season stage of the little auks, location of a breeding colony in relationship to feeding grounds, etc.), both water regions are used as feeding grounds by the little auks.

Period of leaving the breeding colony. An entirely different picture is seen at the stage of young little auks' departure from a colony when the circadian variation in numbers of *Calanus* in the surface waters is reflected almost exactly by the cycle of changes in the number of adult little auks staying at a breeding colony (Fig. 6). This indicates a complete lack of synchronization of the feeding rhythm of the little auks relative to the food availability rhythm. In this case, however, we are dealing with a change in the rhythm of little auks' attendance at a colony, which is of great anti-predatory importance. The presence of the largest possible number of adult birds in a colony at the time of departure of the young is very important for several reasons. Firstly, some of the adult birds present at a colony are the parents that accompany the young during the departure. Secondly, the presence of a large number of birds in a colony may assist in the creation and synchronization of a state of social readiness for the departure, and thereby a very important temporal concentration of the departure (S t e m p n i e w i c z 1981). Thirdly, if there is a large number of birds in a flock, a predator finds it difficult to select the victim of its attack (S t e m p n i e w i c z 1983).

P r e l a y i n g p e r i o d. From the period preceding the laying of eggs there are no data on any possible circadian changes in zooplankton numbers, and besides, the activity cycle of the little auks is at this stage longer than 24 h (Figs. 1 a, 2). By contrast to what S l a t e r (1977, 1980) assumes for the common guillemots, the activity rhythm of the little auks is not related to the tidal rhythm either. The tidal rhythm is about a half shorter than the shortest little auks' attendance cycle, and the latter occurs at later breeding season stages. Moreover, the time of high (or low) tide is shifted by about 8 h during a 10-day period, which has not been recorded for the time of little auks' peak attendance at a colony.

The factors on which the little auks' attendance pattern in that period depends to a large extent include environmental (wind, fog, snow cover, ice cover on waters) and biocoenotic (activity of gulls) factors. This is because at this stage their action is extremely intense, whereas the breeding season advancement stage does not make it necessary for the little auks to be present in the colony regularly, every day (there are no eggs to incubate, or nestlings to feed).

There are, however, other causes which make little auks visit the breeding colony more and more often and regularly. It is here that important phenomena and processes, such as courtship, mating and copulations take place, as well as taking over, keeping and defending nest territories (S t e m p n i e w i c z 1981). Birds staying in pairs in their nest territories really contribute to the acceleration of the melting of snow in those places. By digging hollows in the snow with their feet they speed up the uncovering of dark-coloured parts of stones which absorb the solar radiation heat, as a result of which the snow around the stones melts fast. This makes possible earlier egg laying, which is of great importance under the conditions of extreme time limitation of the Arctic summer. All these kinds of intensive activity of the little auks in a colony are very energy-consuming, hence an increased demand for food which is then available in really small amounts (D i g b y 1954) and has to be looked for probably very far. Besides, the females must accumulate additional amounts of energy needed for the production of eggs which are comparatively very large (S t e m p n i e w i c z 1980).

At this stage the remarkable flock behaviour of the little auks is most marked. Individuals arrive in the colony and leave it according to the principle: all or none (Fig. 1 a). There does not, therefore, exist a danger that during the absence of an owner another individual will occupy the absent owner's nest territory (at later breeding season stages a part of birds always remain both in a colony and at sea; Fig. 1 b-e). The flock behaviour also stimulates social behaviour, and thereby causes a high synchronization of all phenomena and processes in a little auks' colony, which is very important to the phenology of the breeding season, and as an anti-predatory mechanism (S t e m p n i e w i c z 1981). The resultant of all these factors, the effects of which are often opposite, determines the pattern of attendance of little auks at a breeding colony.

5. SUMMARY

There does not exist any one superior factor that would control the rhythm of little auks' attendance at a colony during the breeding season. It seems that the little auks adjust their activity rhythm to the resultant effect of many environmental, biocoenotic and intra-population factors. This is expressed by changes in the cycle length (Fig. 2), duration of attendance and absence (Fig. 3) and the time of peak attendance of birds at a colony (Figs. 4, 5), observed with the progressing breeding season.

In the period preceding egg laying this complex of factors determines a pattern for the little auks of their stay on land, this pattern being characterized by a long – multicircadian and irregular cycle, a clear predominance of the absence time over the duration of attendance, and a very high synchronization of departures to sea and returns to a colony (Fig. 1). The birds stay on land in this period for reasons of intra-population nature (occupation and defence of nest territories, courtship, mating, copulations and the like). Factors that incline birds to stay at sea for as long as possible include the following: a relatively high demand for energy at low zooplankton numbers, a particularly intensive action of environmental factors, and a very strong predatory pressure.

As the breeding season advances, the intra-population factors (connected with egg incubation and chick feeding) make birds change their attendance rhythm. The change consists in a gradual shortening of the time spent at sea and reduction of the cycle to 24 h. This is favoured by an increase in zooplankton density, possibility of feeding at a shorter distance from a colony, and probably a 24 h cycle of food availability (Fig. 6). At this stage weather conditions and the activity of gulls only play the role of disturbing factors. In the period of young little auks' departure from a colony the rhythm of adult birds' attendance at a colony becomes reversed relative to the former period, and overruled by the rhythm of the departure of the young to sea (Figs. 1, 5). Here also intra-population reasons predominate over all external factors.

6. POLISH SUMMARY

Nie ma jednego, nadrzędnego czynnika, który rządziłby rytmem obecności traczyków lodowych w kolonii w ciągu sezonu lęgowego. Wydaje się, że traczyki dostosowują swój rytm aktywności do wypadkowej wielu czynników środowiskowych, biocenotycznych i wewnątrzpopulacyjnych. Wyrazem tego są zmiany w długości cyklu (rys. 2), czasu trwania obecności i nieobecności (rys. 3) oraz pory szczytu obecności ptaków w kolonii (rys. 4, 5), zaobserwowane z biegiem sezonu.

W okresie poprzedzającym składanie jaj ten kompleks czynników wyznacza traczykom wzorzec przebywania na lądzie, charakteryzujący się długim, wielodobowym i nieregularnym cyklem, wyraźną przewagą czasu nieobecności nad czasem obecności i bardzo wysoką synchronizacją lotów na morze i

powrotów do kolonii (rys. 1). Za przebywaniem ptaków na lądzie w tym okresie przemawiają względy natury wewnątrzpopulacyjnej (obejmowanie i obrona terytoriów gniazdowych, ceremoniał godowy itp.). Natomiast do jak najdłuższego przebywania na morzu skłaniają ptaki względnie wysokie potrzeby energetyczne przy niskiej liczebności zooplanktonu, szczególnie ostro działające czynniki środowiskowe oraz wyjątkowo silna presja drapieżnicza.

Wraz z zaawansowaniem sezonu lęgowego czynniki wewnątrzpopulacyjne (związane z wysiadywaniem jaj i karmieniem piskląt) zmuszają ptaki do zmiany rytmu obecności. Polega ona na stopniowym ograniczaniu czasu spędzanego na morzu i skracaniu cyklu do 24 h. Sprzyja temu wzrost zagęszczenia zooplanktonu, możliwość żerowania w mniejszej odległości od kolonii oraz prawdopodobnie 24-godzinny cykl dostępności pokarmu (rys. 6). Warunki pogodowe i działanie mew mają na tym etapie jedynie charakter czynników zakłócających. W okresie opuszczania kolonii przez młode traczyki rytm obecności ptaków dorosłych w kolonii ulega odwróceniu w stosunku do okresu poprzedniego i staje się podporządkowany rytmowi wylotu młodych na morze (rys. 1, 5). Tu również względy wewnątrzpopulacyjne biorą górę nad wszystkimi czynnikami zewnętrznymi.

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