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Variation in laying synchrony in a small Herring Gull colony

Mikael Kilpi

Kilpi, M., Department of Ecology and Systematics, Zoological Laboratory, P.O. Box 17, FIN-00014, Helsinki University, Helsinki, Finland

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I measured the laying span and laying synchrony in a small Herring Gull (*Larus argentatus*) colony over a 12-year period. Herring Gulls in the study colony adjust their onset of breeding in relation to prevailing ice-conditions, likely to escape predation, so that late springs lead to late breeding. Measured with the standard deviation of laying (Gochfeld 1980) synchrony varied in accordance with timing of laying, so that late initiation of nesting produced a higher degree of synchrony. Synchrony did not correlate with the number of pairs in the colony, and variation in synchrony is thus mostly a product of variation in environmental conditions. The level of synchrony did not affect production of young in the colony. The studied group of pairs was very synchronous compared with other studied Herring Gull groups, possibly because of the pronounced seasonality of the breeding environment they experience.

1. Introduction

The timing of reproduction must ultimately be tuned to variations in the environment, such as weather or availability of food, (Lack 1968) on a year-by-year basis. Another component of timing, which might be equally important, is timing in relation to other pairs in the same population. Reproductive synchrony, the tendency of individuals to carry out some part of the reproductive cycle at the same time as other members of the population has often been considered adaptive, particularly in colonial birds (Burger 1979, Gochfeld 1980, Findlay & Cook 1982a, Coulson 1985, Ims 1990).

Darling (1938, 1952) suggested that birds in larger colonies experience greater social stimulation than those in small colonies, which increases breeding synchrony, providing an efficient means to swamp predators (Nisbet 1975). This idea lies at the very core of what is thought to make coloniality adaptive (Burger 1981a, Wittenberger & Hunt 1985). Various authors have since tested this hypothesis, with mixed results (Burger 1979, Burger & Shisler 1980, Gochfeld 1980, Burger & Gochfeld 1990). For instance, in Herring Gulls (*Larus argentatus*), Burger (1979) found that synchrony increases in colonies up to 100–200 pairs, after which it decreases. In the Black Skimmer (*Rynchops niger*), on the other hand, synchrony seems to decrease with an increasing number of nesters (Burger & Gochfeld 1990).

Coulson & Dixon (1979), and Coulson (1985) argue that synchrony in Kittiwakes (*Rissa tridactyla*) operates within small units within colonies, groups too small to provide any benefit from predator swamping.

Burger (1979) suggests that units of up to 200 pairs of Herring Gulls behave as synchronous entities, while synchrony in larger groups no longer is evident. She suggests that the mechanism is social facilitation. However, there is little evidence that would actually support the notion of coloniality leading to increased synchrony, demonstrating the mechanism involved (see Gochfeld 1980, Wissel & Brandl 1988, Burger & Gochfeld 1990). In fact, Coulson (1985) in a novel approach, suggested that synchrony might be a by-product of other adaptive factors (see also Gochfeld 1980, Siegel-Causey & Kharitonov 1990). The adjustment of the breeding season to other factors is according to Coulson´s (1985) hypothesis, more important than the synchrony between members of a colony, and one of the main advantages of colonial breeding.

Some synchrony is to be expected in all environments that are in any way seasonal (Drent & Daan 1980). For many species, the time-window for breeding is always of a certain length. According to Coulsons (1985) model, colonial breeders should be more efficient at adjusting their breeding to prevailing environmental conditions than solitary breeders. There are few long-term studies on colonial seabirds showing that adjustment is taking place as a response to any measurable environmental variable (see Finney & Cook 1982 a,b, Morris & Chardine 1985, Murphy et al. 1991, Kilpi 1992, Laurila & Hario 1988). Also, it is not entirely clear to what extent the degree of synchrony achieved in a colonial situation is greater than that achieved within a population of solitary breeders, or if the degree of synchrony in a colony should be expected to remain unchanged from one year to another in relation to timing of breeding, and how this variation is controlled. In this paper I will examine the degree of synchrony in a small colony of Herring Gulls over 12 years. I will ask if (i) synchrony varies between years, and (ii) what influences this variation.

2. Study site and Methods

This study was carried out in a small Herring Gull colony (Tryskärsgrund) off the Hanko Peninsula, SW-Finland (60°N, 23°E) in 1978, 1983–1993. The colony was established in 1976, grew to about 50 pairs, and then levelled off at 35–40 pairs, remaining stable since 1986 (see Kilpi 1990). As a result, it is a group of presumably mostly experienced breeding pairs, with a low annual number of first-time breeders (Kilpi 1989). The analyses were done primarily on the total set of data, but a restricted set was also used. This restricted set comprised 1983 and 1986–1993, when the colony varied only between 32 and 38 pairs, essentially reducing the effect of population size variation on synchrony measures.

Each year, laying was followed, from the start for each pair, ice conditions permitting. If otherwise, the timing was checked at hatching (Kilpi 1990). The timing of the ice break-up was established each year (Kilpi 1992). Break-up refers to the date that the breeding islet lost permanent contact with the nearby large islands and the mainland. The variation in the date the ice disappeared varied by up to three months (Kilpi 1992).

Breeding success at fledging was monitored each year. In analyzing the breeding synchrony, late 2-egg nests were excluded because they were likely nests of first-time breeders, and known relayings. These have little to contribute to the understanding of the timing within the synchronous group. These pairs comprised only 1–3 annually, so they do not affect the results to any appreciable extent, though admittedly they would be part of the tail constituting the asymmetry in the typical breeding-date distribution in seabird studies in larger colonies (Gochfeld 1980).

The measure of synchrony used is the standard deviation of the mean laying date (in days) for the entire group (Gochfeld 1980, Gochfeld & Burger 1990).

3. Results

3.1. Timing of breeding

The onset of breeding as measured by the first egg in the first nest varied considerably over the years, spanning 23 days, from 6 April to 29 April (see also Kilpi 1992). The median dates spanned 16 days, ranging from 18 April to 4 May. The onset of breeding is significantly correlated with the day of the ice break-up, an early break-up leading to an early onset of laying ($r = 0.92$, $df = 10$, $P = 0.0001$). The onset of laying in turn is significantly correlated with the median laying

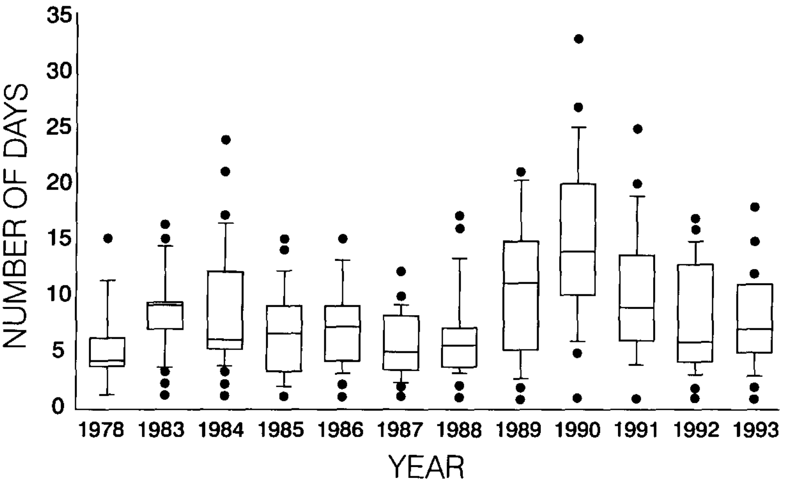

Fig. 1. Box-plot showing the 10, 25, 50, 75 and 90th percentile (lines) of the laying distribution each study year. Individual observations above and below the 90th and 10th percentile also plotted.

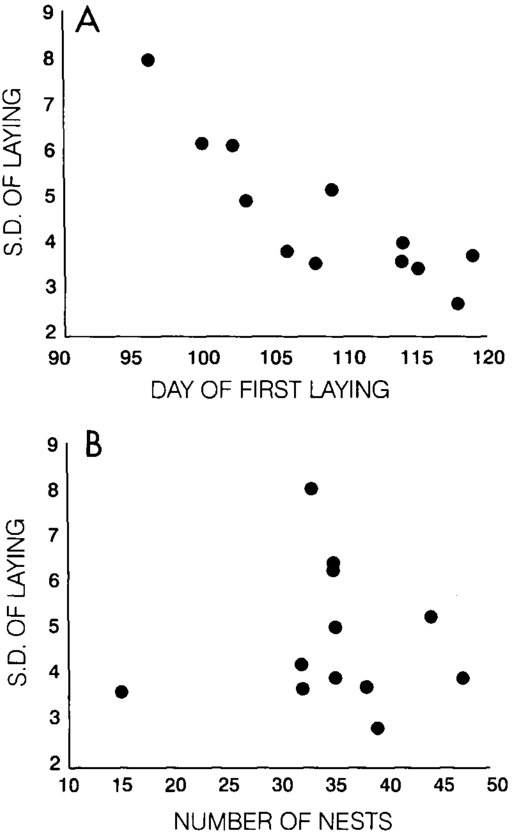

Fig. 2. The relationship between synchrony (S.D.) and the day of first laying (a:upper) and the population size (b:lower).

date (r = 0.98, df = 10, P = 0.0001, see also Kilpi 1992). There was, thus, considerable variation in timing of breeding in relation to environmental variation. Timing of breeding was not influenced by number of pairs in the colony (r = 0.10, df = 10, P = 0.75).

3.2. Synchrony

The box-plot in Fig. (1) shows that there was also considerable variation in synchrony in laying over the years. This variation in synchrony decreased with laying date (Fig. 2a), with early years being less synchronous than late years (r = –0.86, df = 10, P = 0.0003). The number of nests in the colony did not influence the synchrony in breeding (r = 0.04, df = 10, P = 0.90). The negative relationship between synchrony and annual onset of breeding holds also when the years 1983 and 1986–1993 were analysed separately (colony size varied only by a few pairs, annual totals 32–38, r = –0.89, df = 7, P = 0.001). The earliness of breeding in these years had a clear effect on the total time span used for laying, the span ranging from 12 to 32 days, and becoming progressively longer as breeding became earlier (r = –0.82, df = 7, P = 0.007). Span and standard deviation of laying dates were tightly correlated (r = 0.83, df = 10, P = 0.0008).

3.3. Production of young

The mean number of young raised per pair was 1.98 ± 0.2 over the entire period, varying from 1.32 in 1984 to 2.31 in 1988. For all years combined there was no relationship between synchrony and production of young ($r = 0.25$, df $= 10$, $P = 0.43$), and no correlation in the restricted set either ($r = 0.23$, df $= 7$, $P = 0.54$). The date of laying had no effect on reproductive success ($r = 0.003$, df $= 10$, $P = 0.99$). Synchrony thus is not related to average fledging success.

4. Discussion

Synchrony in breeding activities stem from factors operating at both the ultimate and the proximate level. If birds′ breeding seasons are somehow adjusted to any kind of seasonality (Perrins 1970, Drent & Daan 1980), this will ultimately lead to some degree of synchrony. Laying late in the season means a lower reproductive value of the nest compared with early layers in a number of species (Daan et al. 1990). The Herring Gull has a comparatively long breeding season in terms of laying and incubation (30 days) and chick rearing (at least 70 days, often more, see Burger 1981b), so in any seasonal environment the boundaries for breeding time are constrained (Findlay & Cooke 1982a, Kilpi 1990). Thus temporal clustering can result from selective pressures acting on timing rather than on synchronization.

There might also be selection for synchronization between pairs, as originally suggested by Darling (1938). The selective advantage may be predator avoidance by satiation, giving synchronous pairs a high fitness (Findlay & Cooke 1982b). In Herring Gulls, Parsons (1975) found a higher breeding success in peak breeders. Synchrony thus would be adaptive and would have evolved as an anti-predator strategy, as well as against predation by conspecifics in the case of the Herring Gull (Burger 1984).

On a proximate level, timing varies in response to environmental variation such as weather, food or social stimulation (Perrins 1970). Three classes of cues for timing have been defined by Ims (1990); environmental cues, internal cues (biological clocks) and social cues.

In Herring Gulls, Morris & Chardine (1985) found that ice on the colony site delayed breeding, and Kilpi (1992) found that ice around the colony site affected timing. Similar effects have been recorded for other waterbird species in seasonal environments (Coulson 1985, Harris & Birkhead 1985, Findlay & Cooke 1982a, Laurila & Hario 1988). Burger (1979) lists a number of other environmental factors influencing synchrony.

Presumably the ability to use environmental cues is of prime importance in the process of timing breeding to between-year variation in the environment (see Coulson 1985, Pietiäinen & Kolunen 1993). Herring Gulls seem capable of adjusting their timing of breeding in a seasonal environment (Kilpi 1992). The study colony was stable and had high offspring production (this study, Kilpi 1989,1990), and many of the pairs were involved from year to year, yet there was variation in laying date. Ice connecting the mainland with the islands may be the cue to the gulls. Ice permits predators, such as Red Foxes (*Vulpes vulpes*) to reach the colonies (see Hildén & Hario 1993). Thus, melting ice is the likely explanation for the variation in starting dates of breeding for the studied Herring Gull population (see also Kilpi 1992, Hario & Selin 1987). The high degree of adjustment in timing of breeding fits the suggestion by Coulson (1985) that coloniality allows for efficient adjustment of breeding times, but it is unclear to what extent this would be more efficient than in solitary breeding pairs. On the other hand, one might ask why synchrony in early years should be of lesser importance than in late years, since the degree of synchrony is lower in those years. A simple explanation would be that there is a limit to the breeding season in late summer, which is of a more or less fixed character, and staying in the colony later than this date would bear a high cost on fitness (Parsons et al. 1976). This would automatically lead to more synchronous breeding, the later the birds are able to start. The nature of such a mechanism is, however, unknown.

If synchrony is advantageous and subject to intense selection, one would expect to find little variation in the relative date of breeding in any colony (Findlay & Cooke 1982a), i.e., synchrony should remain the same despite the yearly adjustment of breeding date. Parsons (1975) experimentally manipulated synchrony, and found an effect of synchrony *per se* irrespective of date effects in Herring Gulls, so that peak nesters in both controls and delayed breeders had the highest success. It is evident from his data that the period over which success was high was comparably short, in the range of 2–3 weeks for groups of several hundreds of nests. Parsons (1975) did not manipulate synchrony so that experimental groups with the same general timing would have had different within-group synchrony, so it remains an open question whether such variation would have had any effect on reproduction. I did not find any effect of synchrony on breeding success in the study colony, even though synchrony varied between years.

Compared with other studies on Herring Gulls, the gulls on Tryskärsgrund were very synchronous (see Burger 1979). The standard deviation at Tryskärsgrund varied between 3 and 8 days, whereas the deviations in colonies smaller than 100 pairs listed by Burger (1979) were between 10 and 12 days, with total laying spans of 30 to 60 days, compared with a range from 12 days to 32 days in this study. I suggest that most of this variation stems from the differences in seasonality between colony locations in more temperate areas and more arctic ones. This seems supported also by data provided in Gochfeld (1980), listing colonies of Herring Gulls from several locations. At Tryskärsgrund, Herring Gulls are able to adjust their breeding in accordance with proximate environmental cues. Under some circumstances this produces very synchronous breeding, overriding the possible effect of social stimulation. A comparision between solitary and colonial Herring Gulls would facilitate a test of whether colonial pairs can adjust their timing better than solitary pairs.

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