The Ecology and Evolution of Reproductive Synchrony

Rolf Anker Ims

The temporal pattern of breeding in populations is often characterized by a pronounced temporal clustering of births, flowering or seed set. It has long been suspected that this phenomenon is not caused by climatic seasonality alone but that reproductive synchrony represents a strategy that individuals adopt to maximize reproductive success. The classical hypotheses predicting an adaptive advantage of reproductive synchrony incorporate both sociobiological and ecological explanations. However, new theoretical and empirical analyses have shown that the predicted advantage of reproductive synchrony depends on the ecological setting in which populations reproduce, and processes earlier thought to be responsible only for synchrony may under some ecological conditions lead to asynchronous reproduction being the best strategy.

Reproductive synchrony has been defined as the tendency of individuals to carry out some part of the reproductive cycle at the same time as other members of the population[1,2]. This phenomenon is best known from its rather extreme manifestations, for instance in bamboos[3], cicadas[4] and sea turtles[5]. However, besides these famous examples, a pronounced temporal clustering of reproduction is rather widespread in both the animal and the plant kingdoms.

In seasonal environments there is commonly some degree of temporal clustering of reproduction, usually because reproduction at certain times of the year will be best for offspring survival. Hence, what is often termed 'reproductive synchrony' may simply be the consequence of individuals selecting the same favourable time for reproduction in relation to climate. However, reproduction is often far more synchronous than would be expected from environmental seasonality alone. For example, a pronounced temporal clustering of reproduction is quite common in relatively aseasonal, tropical regions[6]. This fact has led biologists to search for explanations other than environmental seasonality (climate) to explain the temporal pattern of reproduction in animal and plant populations, and it is now acknowledged that the temporal pattern of reproduction may be shaped by several ecological and sociobiological processes (Fig. 1).

In this review I will refer to *reproductive synchrony*, or *synchronization of reproduction*, as a phenomenon caused by biological interactions operating to produce a tighter clustering of reproductive events than would have been imposed by environmental seasonality alone.

Fraser Darling[7] suggested in 1938 that the degree of reproductive synchrony in colonial birds may affect nest predation rates. Subsequently, a number of other processes interacting with the temporal pattern of reproduction has been suggested. When such interactions (e.g. predation) affect the reproductive success of individuals, natural selection can modify the temporal pattern of breeding which initially may be determined by environmental seasonality (Fig. 1). Reproductive synchrony will then evolve as a result of a reproductive advantage (e.g. reduced predation on offspring) accrued to individuals capable of synchronizing their reproduction with their neighbours.

Several of the classical hypotheses about the ecological/sociobiological implications and the resulting evolution of reproductive synchrony have long escaped closer theoretical examination and relevant empirical testing. Although recent theoretical and experimental studies lend some support to the older ideas, these new studies also show that the ecology of reproductive synchrony is far more complicated than was earlier believed.
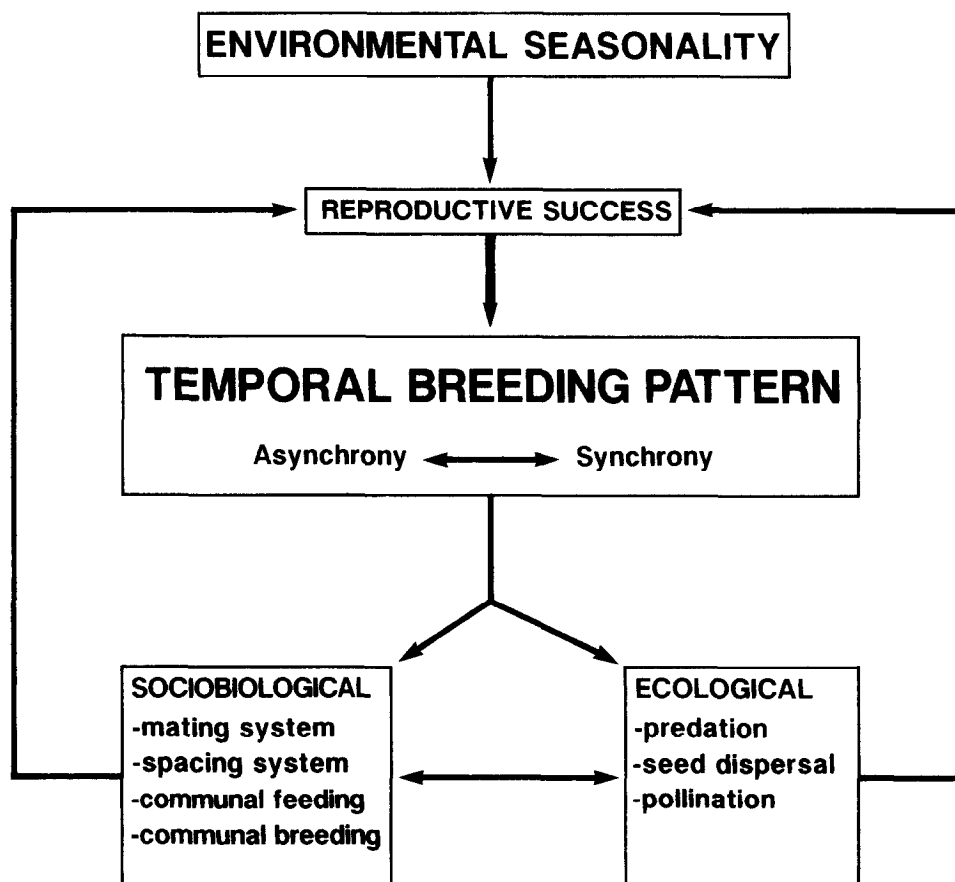

Fig. 1. Environmental (climatic) and biotic (ecological and sociobiological) factors that potentially interact with the temporal pattern of reproduction. The temporal pattern of reproduction may have immediate consequences for ecological processes (e.g. predation) or sociobiological processes (e.g. communal feeding). These processes may in turn affect the relative reproductive success of individuals and ultimately select the degree of reproductive synchrony.

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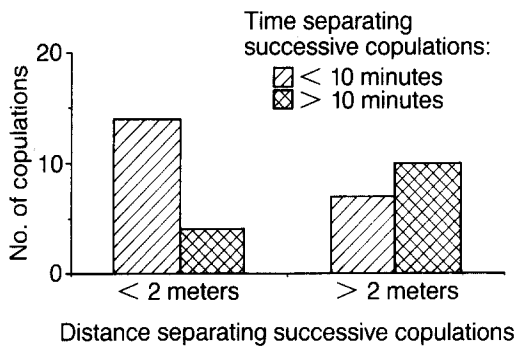
Time separating
successive copulations:

Fig. 2. Indirect evidence for social stimulation of reproductive synchrony within a breeding colony of the black-headed gull (*Larus ribundus*). The bars show the sum of observed copulations that followed another copulation in < 10 min or > 10 min either in the direct vicinity (radius < 2 m) or at some distance away (radius > 2 m). *Data from Ref. 8.*

Temporal clustering of reproduction in a seasonal environment: climate or biological interactions?

Various environmental factors can function as external cues for organisms to time their reproduction according to climatic seasonality. How can the impact of climatic seasonality be separated from biological determinants of the temporal pattern of reproduction? One clue to this question, which ultimately relates to whether the observed pattern is an adaptation or not, can be provided by the specific cue used by the organism to initiate reproduction.

Three main classes of such cues can be distinguished. The first class represents *environmental* cues that are directly connected to climatic seasonality, such as photoperiod, temperature, humidity and food availability. *Internal* cues from endogenous rhythms in the organisms themselves (e.g. biological clocks) constitute the second class.
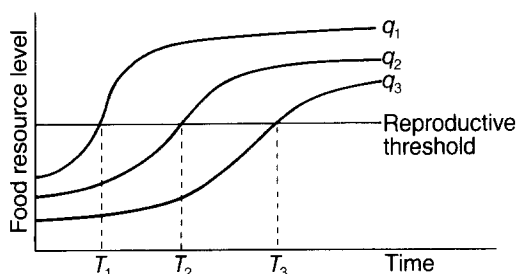

Fig. 3. Environmentally induced reproductive asynchrony among territorial females for which the onset of reproduction is triggered by the amount of food in their territories. The three curves depict the changes in three hypothetical territories of different quality $(q_1 > q_2 > q_3)$ from the start of the plant growing season. The horizontal line represents the minimum food-resource level needed for initiation of reproduction by a single female (reproductive threshold). The intersections between the curves and the reproductive threshold (T_1-T_3) give the times of onset of reproduction in the three territories. *Reproduced with permission from Ref. 12.*

Finally, the third class of cues – signals exchanged between the individuals within a population – can be labeled *social* cues. The last two classes are of particular interest because they can operate to uncouple the temporal pattern of reproduction from environmental seasonality, and can thus indicate that individuals actively synchronize their reproduction and that the temporal clustering of reproduction is not simply a direct consequence of changing climate.

What is the evidence for the occurrence of the different classes of cues? Reproduction-initiating cues have been explored for relatively few organisms. Hence, although some generalizations can be drawn, for example that environmental cues are more predominant among plants than among animals and that social cues are probably more common among vertebrates than among invertebrates, the examples selected below may not reflect the relative occurrence of the different classes of cues in different taxa.

In several species of birds[2] and mammals (including humans)[8], social stimuli exchanged between neighboring females have been shown to be the proximate cause of reproductive synchrony. For mammals, laboratory experiments have shown that oestrus synchrony can be achieved among group-living females through exchange of pheromonal stimulation or as a result of exposure to a novel male[5]. Male-induced reproductive synchrony has also been seen under natural conditions for lions (*Panthera leo*) when the takeover of a pride by a new coalition of males causes birth synchrony within the pride[9].

Although other mechanisms for socially mediated reproductive synchrony are more difficult to discover in the field, evidence other than the mechanism itself may be available to indicate that reproductive synchrony is socially induced. For example, the spatial pattern of reproductive events within a population can be indicative. In particular, the finding that reproduction is significantly more synchronized among neighboring individuals than among more widely separated ones in gulls[10] (Fig. 2) and in ruminants[11], may indicate that synchrony is socially induced within groups of individuals. However, spatial het-

erogeneity of environmental factors functioning as reproduction-triggering cues may produce similar spatio-temporal patterns of reproduction[12]. In animals with several consecutive litters and young that become sexually mature within the same breeding season, maintenance of reproductive synchrony throughout the season is another indication of socially induced reproductive synchrony[12,13]. Laboratory studies[14] have shown that young maturing golden hamsters (*Mesocricetus auratus*) are able to entrain their oestrus cycles to older, dominant ones by means of olfactorial cues.

The evidence for the existence of internal cues is even more sparse. However, endogenous rhythms may be responsible for some cases of synchronized reproduction at supra-year intervals. In particular, cicadas[4] and bamboos[3] are well known for the long intervals between successive breeding seasons (13 or 17 years in cicadas and up to 120 years in bamboos). Such species have probably evolved a genetically determined internal clock[3] as a response to external selective pressures such as predation (see below). However, these hypothesized clocks can themselves be altered by environmental conditions. Furthermore, within-season reproductive synchrony may be determined by environmental factors; for example, the day of emergence seems to be determined by the ground temperature in periodical cicadas[15].

For species having clustered reproduction on a seasonal basis, and for which the timing of reproduction is determined at least to some degree by environmental factors, it may be more difficult to tell whether individuals actively synchronize their reproduction. In such instances, multivariate statistics may be useful to determine the relative importance of climatic variables and biotic interactions.

Rutberg[16] used multiple regression analysis to examine the importance of climate for birth synchrony in 27 populations of ruminants. He found that climatic seasonality accounted for a significant amount of variation in synchrony in only one of two ecologically distinct groups of species ('hiders') and concluded that birth synchrony of the other

group ('followers') had evolved as an antipredation strategy (see below). Sinsch[17] used the same approach to conclude that breeding synchrony in the natterjack toad (Bufo calamita) was uncoupled from environmental seasonality, and that this was probably due to an endogenous mechanism.

In some cases, the temporal pattern of breeding may result from the combined action of environmental and social variables. For example, animals living in an environment with unpredictable food availability often use the amount of food, or some of its properties, as a cue to initiate reproduction[18]. In such species, the temporal pattern of breeding may be determined by the social organization of breeding females together with the spatial distribution of the food resource.

In a spatially homogenous environment – a situation that facilitates space sharing between reproductive females[19] – individual females should be exposed to the same reproduction-triggering cue at the same time, and reproductive synchrony will result[12]. Note that for space-sharing females there will also be rich possibilities for exchange of, for example, pheromonal stimuli facilitating socially mediated reproductive synchrony[8]. In a spatially heterogeneous environment, on the other hand, females will tend to maintain individual territories[19] of different quality, resulting in different onsets of the triggering cue and consequently asynchronous reproduction[12] (Fig. 3). The opportunity for exchange of social stimuli and hence for socially mediated synchrony will probably be less among territorial females than in group-living females[8,12]. The predicted relationship between female social system and temporal pattern of breeding has recently been examined in microtine rodents[12,13], and it seems to hold true for species for which there is information about both spacing system and temporal breeding pattern.

Finding that reproductive events are tightly clustered according to some environmental factor(s) does not necessarily imply that the clustering in itself has no adaptive value. For example, some marine polychaetes use lunar cycles to time their swarming[20], whereas some tropical plants flower immediately

after heavy rain showers[6]. Although it has been suggested that the environmental factors in such cases most likely act merely as cues to attain reproductive synchrony, the potential causes are hard to separate. Here, as for all possible cases of reproductive synchrony – irrespective of the type of reproduction-initiating cue – the ultimate test for an adaptive advantage is to compare the reproductive success of asynchronously versus synchronously breeding individuals in a population. However, few critical tests of this kind have been done.

Adaptive hypotheses of reproductive synchrony
Sociobiological causes

Emlen and Demong[21] compared the feeding efficiency and reproductive success of pairs of synchronously breeding, colonial swallows (Riparia riparia) that reproduced at the reproductive peak of the colony with pairs that reproduced off-peak. Off-peak breeding pairs fed less efficiently and had lower reproductive success than on-peak pairs. Swallows and many other colonial birds feed communally on unpredictable food patches, and information about such food patches is spread most efficiently among colony members[22] when their reproductive cycles are synchronized.

In addition to enhancing the reproductive success of the individuals, as in the case of communal feeding systems, reproductive synchrony is a necessary condition for communal breeding systems. In such systems, groups of breeding females share the parentage of the young and it is necessary for the group members to synchronize their breeding so that the young can be communally nursed (mammals[23,24]) or eggs can be jointly incubated (birds[25]).

For solitary breeding females, it has been argued that reproductive synchrony may have evolved as a means of enforcing monogamy on males[26] when paternal investment in the young increases their probability of survival. Reproductive synchrony is generally expected to decrease the potential for polygamy in animals[27,28] (Fig. 4). Hence, reproductive synchrony may have evolved as a result of sexual selection. However, for females the suc-
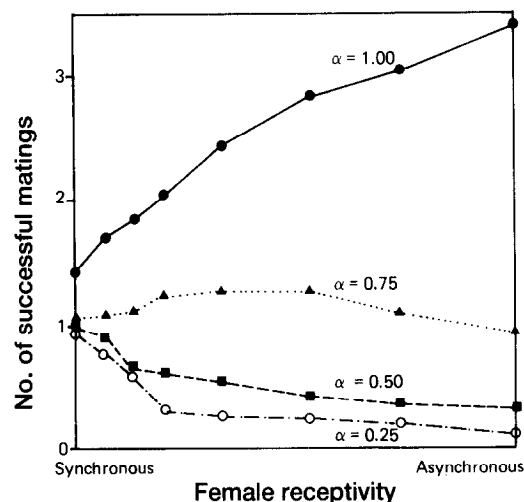

Fig. 4. Predicted number of successful matings for four males of different quality (i.e. ability to find and compete successfully for females) in relation to the degree of synchrony of female sexual receptivity. The prediction is derived from a simulation model assuming a promiscuous mating system characterized by male–male competition and active searching for receptive females. The α values are positively correlated with the males' competitive abilities. The potential for polygyny increases with the degree of asynchrony in the population. Reproduced with permission from Ref. 28.

cess of this strategy is not only dependent on the temporal pattern of reproduction and paternal investment, but also on other factors such as the operational sex ratio, the spatial distribution of receptive females, and the mode of mate acquisition in males[28]. For example, if males have the capacity to monopolize spatially aggregated females – either by means of territories or by guarding grouped, mobile females (harem formations) – female reproductive synchrony can result in polygyny rather than monogamy[12,28]. Accordingly, recent genetic evidence for birds indicates that a high degree of reproductive synchrony does not hinder extra-pair copulations in males[29].

It should also be noted that sexual selection may be responsible for reproductive asynchrony rather than synchrony in species where paternal investment in young is unimportant. Reproductive asynchrony can increase the opportunity for optimal mate choice, since each receptive female can attract more males when no other receptive females are around[13].

The temporal pattern of reproduction can also be an important mating system variable in plants. Although some degree of flowering synchrony is necessary for outcrossing, inbreeding avoidance or sexual selection are probably not the reasons for the widespread occurrence of pronounced flowering synchrony[6]. On the contrary, a slight

asynchrony will promote outcrossing in animal-pollinated plants, since it forces pollinators to move longer distances between individual plants[30].

Recently, McShea[31] has proposed a new hypothesis to explain the widespread occurrence of pronounced reproductive asynchrony in many territorial female microtine rodents[12]. He suggests that reproductive asynchrony may be an adaptation to a territorial spacing system rather than a passive consequence of it[12]. In microtines, female territory size shows a regular oscillation during the course of the reproductive cycle, being smallest around the time of birth and early lactation[31] (Fig. 5). When space is limiting, it can be advantageous for females with oscillating territories to reproduce out of synchrony with their neighboring territory holders, because this will result in the most efficient temporal space partitioning among females (Fig. 5). However, no data are presently available to suggest that females are actively staggering their reproduction.

Ecological causes

Apart from the possibility that reproductive synchrony has evolved as a result of social interactions between individuals within populations, the temporal pattern of reproduction may be the ultimate consequence of interactions with *other* species. In fact, causes of reproductive synchrony are most often sought in interspecific interactions.

Predation is the oldest and prob-

ably still the most widely known explanation for reproductive synchrony[7]. In many species, early life stages are particularly vulnerable to predation. Reproductive synchrony can reduce predation on offspring in three ways[16]. First, many individuals breeding at the same time and place have a higher probability of detecting and repelling predators than solitary asynchronously reproducing adults. Collective defence of offspring is common in colonial birds, and so is reproductive synchrony[9,32]. Second, the presence of many offspring can interfere with a predator's ability to pick out a specific target (predator confusion). Third, since there will always be a limit to the number of prey that a predator can catch and handle per time unit, a sudden mass appearance of prey in the vulnerable stage may *swamp* or satiate the predator population, and thereby reduce the fraction of the prey population taken by the predators[7,33].

These three mechanisms can act singly or in symphony to form an antipredation strategy. However, predator swamping is potentially the most general mechanism, since it can explain reproductive synchrony in both animals and plants, as well as the synchrony of other risky life history transitions such as molting in crustaceans[34], metamorphosis in anurans[35] and leaf production in tropical plants[36].

Very long-lived organisms synchronizing their reproduction at supra-year intervals (e.g. cicadas and bamboos) can escape a *numerical* predator response by reproducing at intervals longer than the life

span of their offspring's predators[3]. Most organisms, however, reproduce seasonally and if offspring predation is important, their reproductive strategy should be shaped more by the *functional* response of predators than by their numerical response[37].

Several types of frequency-dependent predation (predator functional response) have been identified[38,39]. Although their importance for the ecological stability of predator–prey interactions has been analysed in detail[39], the interaction between different functional responses by predators and the temporal pattern of breeding of the prey population has not until very recently[37] received a formal theoretical analysis. It can be shown that, under different degrees of reproductive synchrony, offspring predation rates are very dependent on the type of predator functional response (Fig. 6), the total reproductive output of the prey in relation to the density at which predators become satiated[37], and the spatial structure of the prey population[37].

In contrast to conventional wisdom, highly asynchronous reproduction may be the best reproductive strategy when predators have a typical generalist-type functional response[38] (Type III; Fig. 6). This is particularly so when prey switching occurs at high offspring densities (Fig. 6) and/or the satiation density of the predator is high relative to the total reproductive output of the prey population[37]. Furthermore, spatially clumped prey populations are expected to experience a dramatically increased predation rate if reproduction is synchronized *within* but not *between* clumps[37]. Hence, mechanisms that promote within-group reproductive synchrony are unlikely to have evolved as a predator swamping strategy in patchily distributed populations.

Although the predator swamping hypothesis was developed originally with animal prey (birds[7]) in mind, few empirical studies have actually tested this hypothesis for animals. Karban[33], studying periodical cicadas, found that reproductive synchrony increased as adult density increased, that avian predator density was independent of cicada density (indicating the lack of numerical response), and that as
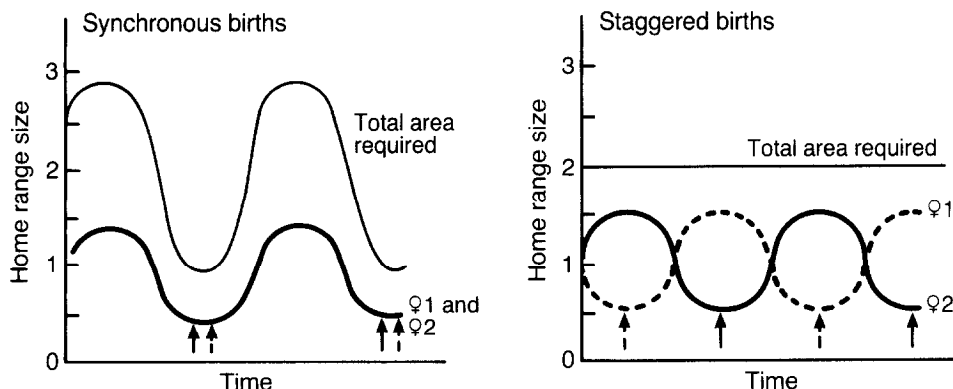

Fig. 5. A graphical model illustrating how birth synchrony may affect the space requirement for two territorial females with home range oscillations coupled to the reproductive cycle. The arrows represent the parturition dates (broken arrows, female 1; solid arrows, female 2). The degree of staggering of births (reproductive asynchrony) will be positively correlated with the amplitude of the home range oscillations and the total area required. *Based on Ref. 31 and W. McShea, pers. commun.*
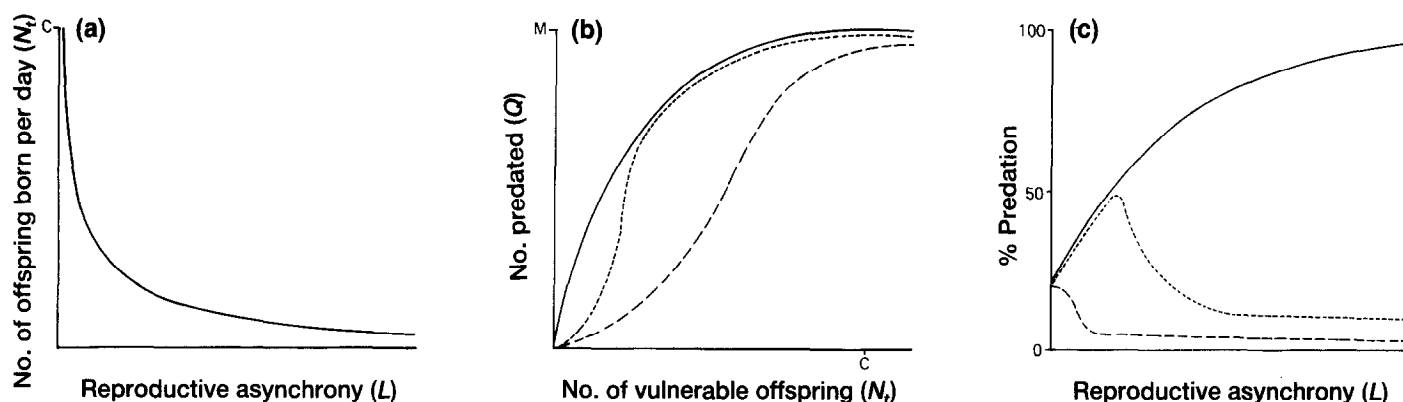
Fig. 6. Expected offspring predation rates imposed by predators with different functional responses to varying degrees of reproductive synchrony of the prey population. For simplicity it is assumed that the offspring are vulnerable to predation only during the day of their birth, that the distribution of births within the breeding season is rectangular (uniform), and that the total reproductive output (C) is constant such that the degree of synchrony and hence the number of young born per day (N_t) is a monotonically decreasing function of the length of the breeding season (L) (part a). Three predator functional response curves are considered (part b): solid curve, Type II response[36] (specialist predator); dashed curves, Type III responses[38] (generalist predators) with different prey-switching points (inflection points). All predators have the same satiation density (M) such that $Q(M)=C/5$ where $Q(M)$ is the daily predation rate of the predator population when $N_t \geq M$. The total loss of offspring due to predation resulting from the different functional responses can be calculated as $P = C^{-1} \sum_{t=1}^{L} Q(N_t)$ where $Q(N_t)$ is the daily predation rate for a given degree of reproductive synchrony. In this model a specialist predator will cause highest predation rates when reproduction is completely asynchronous (part c), whereas the predation peak will be realized at a high degree of reproductive synchrony when the predators show prey switching. Note the effect of different prey-switching points (the two dashed curves in part c) on the location of the predation peak on the reproductive asynchrony axis. *Reproduced with permission from Ref. 37.*

cicada density increased the number of cicadas taken per predator did not increase (suggesting that predators were satiated). Studies on ungulates support the predictions that predator functional responses and the spatial structure of the population are crucial factors[11,16].

For plants, a number of recent studies have examined the relationship between reproductive synchrony and predation. Furthermore, in plants there are two types of functional relationship with animals in addition to predation – seed dispersal and pollination – to which the conventional 'swamping logic' has been applied. For animal-dispersed and/or pollinated plants it is essential *not* to swamp dispersal agents or pollinators, and reproductive *asynchrony* rather than synchrony has been predicted to be the best strategy for maximizing visitation rates of pollinators and seed dispersers.

Recent studies[40-44] on pollination, seed predation and seed dispersal have challenged the conventional 'swamping logic' by showing that synchronous fruiting or flowering often does not swamp seed predators/dispersal agents or pollinators. Consistent with the expected effects of different functional responses[37], specialist dispersal agents/predators are more likely to be swamped by a synchronized seed set than are generalists[42,45]. Note that for plants interacting with different animals with different functional responses, conflicting selective pressures on

the temporal pattern of reproduction may occur. For example, this will be the case if the pollinator behaves as a generalist while the major seed disperser behaves as a specialist. In such cases the strategy (the degree of reproductive synchrony) that provides the best compromise between the opposite selection pressures, in terms of reproductive success, is expected to evolve.

There are empirical results also indicating that the spatial pattern of plant reproduction may determine the success of reproductive synchrony as a strategy for avoiding predators or attracting dispersal agents or pollinators. Reproductive synchrony within trees or patches of plant individuals that are *asynchronous* with the rest of the population often causes local aggregations of mobile non-territorial seed predators/dispersers, resulting in especially high removal rates[43,46].

Conclusion

There now exists a rich array of hypotheses explaining the adaptive significance of reproductive synchrony, and it is clear that it is at least theoretically possible that synchrony can have various causes including processes both intrinsic and extrinsic to the population. However, the many factors that potentially may be involved in the timing of reproduction complicate the analysis, and it is important to be aware that any observed pattern of reproduction may reflect the com-

bined selective pressures from multiple factors. The recent theoretical studies reviewed above, showing that the same process (e.g. predation) may select for or against reproductive synchrony depending on the ecological setting, demonstrate that even single-factor hypotheses may not always lead to straightforward predictions. Obviously, more theoretical work is needed to evaluate the different
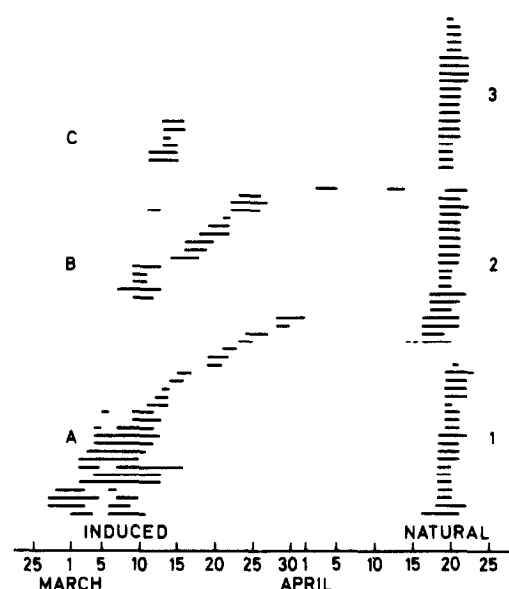

Fig. 7. Example of an experimental manipulation of the temporal pattern of flowering in a naturally synchronous-flowering shrub[45]. Flowering times of individual flowers (horizontal lines) are shown for three naturally synchronous populations (1,2,3), one experimentally induced synchronous population (C) and two experimentally induced asynchronous populations (A,B). Flowering in this species is induced naturally by heavy rain showers in the dry season. However, flowering can be induced at an earlier time by artificial watering. *Reproduced with permission from Ref. 45.*

hypotheses on reproductive synchrony. In particular, it is important to understand how reproductive synchrony at different spatial scales may affect ecological and socio-biological interactions.

However, there is an even stronger need for empirical tests. Although observational studies followed by multivariate statistical analyses may be valuable in assessing the relative importance of different variables for the temporal pattern of reproduction[16,17], an experimental approach is likely to be more rewarding. Recent experimental studies on plants[42,45] have shown that it is possible to manipulate the temporal pattern of reproduction within populations (Fig. 7) and subsequently compare the reproductive success of individuals in populations with more or less temporally clustered reproduction. In particular, experiments performed in different ecological settings, for instance on populations with different spatial structuring and predators, will be essential to advance further our understanding of the ecology and evolution of reproductive synchrony.

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Microbial Mats and the Early Evolution of Life

David J. Des Marais

Microbial mats have descended from perhaps the oldest and most widespread biological communities known. Mats harbor microbes that are crucial for studies of bacterial phylogeny and physiology. They illustrate how several oxygen-sensitive biochemical processes have adapted to oxygen, and they show how life adapted to dry land long before the rise of plants. The search for the earliest grazing protists and metazoa in stromatolites is aided by observations of mats: in them, organic compounds characteristic of ancient photosynthetic protists can be identified. Recent mat studies suggest that the $^{13}C/^{12}C$ increase observed over geological time in stromatolitic organic matter was driven at least in part by a long-term decline in atmospheric carbon dioxide levels.

Microorganisms play a major role in the production and recycling of organic matter, nutrients and bio-

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minerals. Furthermore, the earliest two-thirds of the 3.5 billion year fossil record consists exclusively of single-celled organisms. Most of the fossils recognized from this period are stromatolites, which are laminated structures produced by the successive deposition of layers of microbial mat[1]. Microbial mats are therefore probably the oldest biological communities known. Their modern counterparts offer an opportunity both to study living homologs of ancient ecosystems and to interpret the stromatolite record.

What are microbial mats?

The term 'mat' refers to the coherent organic-rich layer formed by microbes at the surface of a soil, rock or aquatic sediment (see Fig. 1a). This coherence arises from binding by intertwined microbial filaments, extracellular slimes, or precipitated minerals. Mats built by photosynthetic organisms, particularly cyanobacteria, created the most obvious and best-studied stromatolites in the fossil record.

Microbial mats are remarkably cosmopolitan in their occurrence,