exceeds the proportional loss through the other sex function.

The author approaches the problems by developing the theoretical trade-off between male and female function in a fitness set, inserting this relationship in the appropriate form of the Shaw-Mohler equation, and solving for the equilibrium. The biological conditions that give rise to different trade-off relations are discussed, and the predictions are tested by taxonomic and geographic comparisons or experiments; if such information is not available, suitable test organisms are suggested.

How do the theoretical predictions stand up to reality? Qualitatively, quite well in most cases, and even the quantitative details are sometimes remarkably accurate. Some of the strongest evidence for sex ratio adaptation comes from ingenious experiments on parasitic wasps, in which females can control the gender of each offspring by laying fertilized (female) or unfertilized (male) eggs. As predicted, if females gain most from being large (for example because large size enhances egg production), the proportion of female eggs increases with host size; the size of the adult parasite increases with that of the host on which it was born. However, although it seems likely that females in these wasps benefit more than males from being large, this remains to be shown. Other important aspects of the theory are also untested. Moreover, as G. C. Williams has pointed out, the equilibrium sex ratio could be achieved in several different ways. For example, some females might have all sons, others all daughters; yet females usually produce mixed broods. Charnov describes two possible reasons, but the problem is not yet resolved.

Marked deviations from unit sex ratio are sometimes predicted where siblings compete for mates in a local breeding group, or over other resources: a female should produce most offspring of the sex with least sib competition. The quantitative predictions are fulfilled to an impressive degree in experiments on superparasitism by several wasps (*Nasonia vitripennis*) laying eggs on the same host.

With few exceptions, there is little evidence for marked short-term adaptations of the sex ratio in higher vertebrates; several observed deviations seem maladaptive. A remaining key problem is what favors the stability of the chromosomal sex determination, which apparently makes early sex ratio adaptation difficult in birds and mammals. But that question concerns the evolution of proximate mechanisms, which the book does not attempt to cover.

Under what conditions is sex reversal adaptive? The "size advantage hypothesis" predicts that it may evolve if reproductive success increases with body size more rapidly in, say, females, whereas small males can have higher success than small females. Starting as male and later changing to female sex may then be favored over dioecy. Any cost of changing sex promotes dioecy; Charnov suggests several such costs that may explain why sex reversal is limited to a minority of organisms.

Simultaneous hermaphroditism according to the "resource allocation model" may evolve if offspring production through male or female function follows a law of diminishing returns; sharing the reproductive effort between the two sex functions can then be better than concentrating it on one. Diminishing returns may occur for many reasons, such as limited capacity for parental care in females, or limitation of the number of mates that a male can fertilize in a small breeding group, as Charnov suggests for certain barnacles. Selfing and inbreeding depression are important for the optimal allocation of male versus female function and for the stability of hermaphroditism. If inbreeding depression is < 0.5, selfing may be adaptive; it will then enhance the stability of hermaphroditism. Evidence from many plants supports theory in that hermaphrodites spend less resources on male function as the selfing rate (and hence "local mate competition" among an individual's own pollen) increases.

Like most previous volumes in this series, the present one provides a stimulating theoretical perspective and review of its subject. The book has the additional merit of testing the theory with numerous critical experiments and observations, also considering alternative explanations. Many assumptions and predictions are still to be studied empirically, however, and the main task for some time may remain the gathering of data for further tests of the exciting ideas that Charnov develops and reviews. His monograph is an excellent guide and incentive to such efforts.

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Chronobiology and Neuroscience

Vertebrate Circadian Systems. Structure and Physiology. Papers from a symposium, Schloss Ringberg, Germany, Oct. 1980. J. ASCHOFF, S. DAAN, and G. A. GROOS, Eds. Springer-Verlag, New York, 1982. xiv, 364 pp., illus. $56. Proceedings in Life Sciences.

Biological rhythmicity has been appreciated and exploited by humans since the dawn of recorded history. Earlier workers conceived of geophysical fluctuations as the proximate factors behind daily, lunar, and annual cycles in animal behavior. However, many cellular and behavioral rhythms of eukaryotic organisms are endogenous and under constant environmental conditions persist with periods that differ from those of the external cycles to which they are normally entrained. These rhythms have properties similar to those of self-sustained oscillators and provide evidence for the existence of biological clocks.

The book under review celebrates the recent marriage of chronobiology and neuroscience. It is yet another case of academics imitating life: the couple had been living together for some time before legitimizing their union; they are the parents of a four-year-old (*Biological Rhythms and Their Central Mechanisms*, M. Suda, O. Hayaishi, and H. Nakagawa, Eds., Elsevier/North-Holland, 1979) and from the look of things may require a lecture on contraception sometime in the near future.

The editors of this well-produced book, which is marred only by an excessive number of typographical errors, identify Maynard Johnson's 1939 report as the first in which the endogenous nature of animal rhythms was clearly demonstrated. Johnson's earlier work (1926) and several investigations summarized by J. H. Welsh in 1938 pointed to the same conclusion. Why then did we have to wait almost a half century for so much as a clue about the neural organization of vertebrate circadian rhythms? Many, if not all, cells in any complex metazoan organism are potential circadian clocks that can measure intervals of approximately 24 hours in the absence of periodic cues from the external environment. Nevertheless, not all cells are created equal, and the notion of one or more driving pacemakers that would impose temporal order on multiple target issues was not far from the consciousness of chronobiologists. With millions of neurons as clock candidates, let alone myriad cells in more modest organs such as the adrenals and pituitary, it is small wonder that few rushed in to attempt localization of vertebrate timekeeping mechanisms. Instead, chronobiologists were mainly content to perform "empty-organism" studies that enumerated the important formal properties of biological rhythms and to neglect the underlying physiological substrates. Into this void stepped Curt Richter, the innovative psychobiologist to whom this book is dedicated and whose many contributions to chronobiology span more than 60 years. After conclusively eliminating the endocrine organs as the site of the rodent "master" circadian clock, Richter succeeded in prying the lid off the circadian black box when he showed that unspecified lesions of the hypothalamus eliminated circadian activity and feeding rhythms. More precise localization became possible with the subsequent discovery of a direct visual projection from the retina to the hypothalamic suprachiasmatic nuclei (SCN) of mammals. This retinohypothalamic tract, although it constitutes a very small percentage of the visual afference to the mammalian brain, appears to be the main pathway by which light entrains circadian rhythms. In 1972, two separate investigations implicated the SCN as the long sought after "master" oscillator. Ablation of these structures reliably eliminated or disrupted several circadian rhythms of rats. In the flush of early enthusiasm, claims were made for the role of the SCN as *the* biological clock. Stephan and Rusak indicate in papers in the book that circadian oscillators also are located outside the SCN, although their work and that of Kawamura, Inouye, and co-workers, who also have a paper in the book, argues for the preeminence of SCN involvement in rodent circadian rhythms. Rusak speculates that the SCN couple self-sustained oscillators located elsewhere; localization of these pacemakers remains to be accomplished. Recent evidence suggests that some of the non-SCN pacemakers can be entrained via visual projections distinct from the retinohypothalamic tracts.

The visual structures subserving entrainment appear to be separate from those that mediate more classical functions of visual perception. This theme emerges in papers by Menaker and Groos. There is multiple photoreceptor input to the circadian system of non-mammalian vertebrates, with major contributions by extraocular photoreceptors. A special class of retinal ganglion cells may project to the SCN and subserve photic entrainment; furthermore, the responsiveness of rat SCN cells to light is unlike that of most other "visual" neurons with respect to the sustained nature of changes in discharge rate.

Recent anatomical detail on the SCN is well summarized in the paper by Sofroniew and Weindl. The SCN comprise a heterogeneous population of neurons that manufacture several polypeptides. Neurons containing vasopressin and vasoactive intestinal peptide are localized in separate parts of the SCN. Although the exact projections of the SCN neurons to neural target tissues are the subject of controversy (*Brain Res.* **243**, 235 [1982]), the potential clearly exists for direct SCN innervation of effector systems that express circadian rhythms. It is now clear that exclusive localization of so complex a function as circadian organization to a discretely localized nuclear group such as the SCN, comprised of a mere 20,000 cells in the rat, is but a pipe dream. The history of earlier localization campaigns should warn us of experimental and conceptual errors associated with this kind of subcortical phrenology. A dynamic approach that emphasizes neural networks and transmitter systems is more likely to succeed in unraveling the generator apparatus for circadian rhythms.

The pineal gland of non-mammalian vertebrates plays a major role in rhythm generation or expression and is implicated as part of the circadian apparatus of passerine birds. A paper by Takahashi indicates that in the house sparrow the SCN also are an important part of the circadian network; ablation of these nuclei severely disrupts rhythms recorded in constant darkness. The persistence of synchronized daily activity cycles in sparrows with substantial SCN damage suggests a major difference between birds and mammals.

The effects of hormones on the circadian system are reviewed by Turek and Gwinner. Changes in the endocrine milieu modulate the frequency of several circadian parameters. This does not invalidate the generalization that the circadian system is buffered from changes in the internal milieu. The magnitude of the effects produced by chemical perturbations is relatively small, and the functional significance of such effects is yet to be established.

The neurotransmitters that underlie vertebrate circadian organization are unspecified. A paper by Wirz-Justice and collaborators presents evidence that some of the common effects of the antidepressants lithium, clorgyline, and imipramine on circadian rhythms may be mediated via a serotonergic system. However, pharmacological investigations so far do not point in compelling fashion to a single transmitter as responsible for the observed effects on circadian rhythms. In this as in several other domains of neurocircadian research, investigators working with invertebrate model systems are much further along than those working with vertebrate systems.

Daan and Aschoff provide a fascinating overview of the potential survival value of circadian rhythms. The daily temporal organization of food intake in kestrels, presumably handled by a circadian mechanism, contributes a small energetic savings that may be translated into a large increase in reproductive fitness. I suspect that traditional neuroscientists will be allergic to the speculative scenario painted by Daan and Aschoff and sorely tempted to dissolve their marriage with the chronobiologists. I hope they eschew the divorce courts; the perspective offered is rich, if not necessarily correct concerning details, and promises a true neuroethology of circadian rhythms in the not too distant future.

Kenagy and Vleck illustrate the ecophysiological approach and demonstrate that resting metabolic rate is 28 percent higher during the active than the resting phase for strictly nocturnal or diurnal small mammals; however, several species whose ecological life-styles preclude or prevent segregation of behavioral activity into two distinct phases (for example, nearly continuously fossorial rodents) do not manifest diurnal fluctuations in metabolic rate.

Other papers describe the role of circadian rhythms in photoperiodism, sleep, temperature regulation, and copulation. A few of the papers are not directly concerned with structure or physiology but deal with formal properties of vertebrate circadian rhythms. If the marriage between chrono- and neurobiology is to remain viable, "wet" physiologists will have to remain informed of such developments. The recent progress and ferment in elaborating neuroendocrine bases for circadian rhythms, as documented in this book, will continue to benefit from the conceptual insights and formal analyses of the model builders.

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