Chapter 4

Synchronization of Circannual Rhythms

4.1 Zeitgebers

Under seasonally constant conditions circannual rhythms usually free-run with periods somewhat different from 12 months as discussed in the previous chapters. Under natural conditions, on the other hand, their period normally matches that of the natural year. This implicates the existence of zeitgebers, i.e., seasonally varying environmental factors that are capable of synchronizing (entraining) circannual rhythms with the yearly cycle of the seasons.

The action of such circannual zeitgebers is illustrated by the results of a displacement experiment carried out on the woodchuck (*Marmota monax*), a species with an annual cycle in body weight that depends on a circannual rhythmicity (Table 2.1). In the experiment summarized in Fig. 4.1, woodchucks were first kept in the United States at about 40° north, but were then displaced to Sydney, Australia, about 34° south. This displacement corresponds to a phase shift of the seasonal environmental cycles by 180°. It can be seen that the rhythm in body weight gradually followed this phase shift, although it took more than

Fig. 4.1. Resynchronization of the circannual rhythms of body weight in seven woodchucks (*Marmota monax*) after displacement from the northern hemisphere (Pennsylvania, USA, about 40° N) to the southern hemisphere (Sydney, Australia, about 34° S). At both locations the animals were exposed to natural conditions of photoperiod and temperature. *Upper diagram* photoperiodic variations to which the animals were exposed before (solid curve) and after (dashed curve) displacement. *Lower diagram*: symbols connected by lines indicate the dates at which the animals attained maximal body weights before (year 0) and after (years 1–4) displacement. (After Davis and Finnie 1975)
one cycle until the expected phase relationship to local calendar time became re-established.

Although this type of experiment demonstrates the existence of circannual zeitgebers, it gives no insight into the concrete nature of the factors involved. To investigate this question, organisms must be held under conditions in which only one environmental factor is manipulated with all the others being held constant. Basically, four types of experiments can be carried out to test whether an environmental variable is a zeitgeber of a circannual rhythmicity (Aschoff 1960; Hoffmann 1969; see also Appendix).

1. *Exposure of a free-running rhythm with period* $\tau_n$ *to the environmental cycle, with period* $T$. If the latter is effective as a zeitgeber, the endogenous rhythm should assume its period so that $\tau = T$. After removal of the environmental cycle the endogenous rhythm should free-run again with its natural period $\tau_n$.

2. *Varying the period of the environmental cycle*. In this case the period $\tau$ of the biological rhythm should follow changes in the period of the environmental cycle within certain limits.

3. *Phase shifting the environmental cycle*. If it is a zeitgeber, the biological rhythm should follow that phase shift within some cycles.

4. *Exposure of animals kept under constant conditions to pulsatile or stepwise changes of an environmental variable*. If it is a zeitgeber, the pulse or step should induce a phase shift, the size and direction of which should depend on the circannual phase exposed to the stimulus. It must be emphasized, however, that the existence of such a phase response curve is only a necessary but not a sufficient condition for the function of this variable as a zeitgeber, because entrainment will only be possible if the phase-response curve has certain properties (Pittendrigh 1981a).

In searching for circannual zeitgebers, mainly procedure (2) has been employed so far, although a few phase-shift experiments [procedure (3)] have been carried out as well; furthermore some evidence comes from data suggesting the existence of phase-response curves [procedure (4)]. From the available results, it appears that the annual cycle of photoperiod is the most powerful zeitgeber for circannual cycles, at least in most vertebrate species, but seasonal temperature cycles also seem to play a role both among vertebrates and invertebrates. In addition, there is one report suggesting that social stimuli may have zeitgeber qualities.

### 4.1.1 Photoperiod

Figure 4.2 provides a first example demonstrating that the annual cycle of photoperiod is capable of synchronizing the circannual rhythms in gonadal size and molt in an avian species, the European starling (*Sturnus vulgaris*). Two groups of starlings were exposed to sinusoidal changes in photoperiod mimicking their general shape and amplitude those occurring at 40° latitude. They differed from each other only with regard to their period length. In one group the period of the photoperiodic cycle was $T = 12$ months, in the other $T = 6$ months. It can be seen in the upper diagram that the birds exposed to a 12-month cycle went through