

THE COLONY LIFE CYCLE

Mating.—The seasonal occurrence of the sexuals, the climatic conditions accompanying mating activity, and the behavior of the sexuals at the onset of the flights have received recent attention in detailed accounts by Geijskes (56), Kanno (80, 81, 83, 84), Marikovskiy (114), and Talbot (163, 164), while fragmentary accounts on these subjects abound in the literature [e.g., review by Donisthorpe (45)]. Prior to the flights the workers dig supernumerary exit holes and the sexuals mill over the nest surface (3). Mating typically occurs in the air and is seldom seen. Some ponerines, the army ants, and the advanced social parasites are exceptional in mating on or near the nest (105, 141, 190, 202). In *Myrmecia regularis* Crawley, queens shed their wings in the nests and are fertilized on the ground outside by low-flying males, but other *Myrmecia* have more "normal" flights (72). Male swarms and copulation have been described in several non-parasitic myrmecine species by Brian & Brian (22), Kanno & Kanno (80, 84), and Wilson (195). Chapman (31) has gathered records of sexual swarms on the summits of mountains in the western United States and believes that these insects actively gather there to mate, a view supported by similar observations made by Collingwood (36) in England. The production and release of sexual forms in many species are timed in such a way as to enhance exogamy (114, 164), and it is tempting to accept the view of Scherba (135) that this represents organization shaped by natural selection at the interpopulation level.

The flights are species-specific in form and occur at predictable times of the day. The conventional view has been that one or more environmental factors, especially temperature and moisture, combine to trigger the behavior. Recently, however, McCluskey (111, 112) has demonstrated the existence of endogenous circadian activity in males of *Veromessor* and *Iridomyrmex* synchronous with the times of the nuptial flights. This points up the possibility that the environment is limiting instead of causative and suggests one important direction that future research on social behavior will take. Hodgson (74), for instance, has already cited indirect evidence that a persistent circadian rhythm initiates daily foraging in *Atta*. But not all castes conform: in *Iridomyrmex humilis* Mayr, at least, queens and workers lack persistent rhythms (112). The foraging of *Crematogaster scutellaris* (Oliver) workers is exogenously determined by temperature (149). Furthermore, the experiments of Grabensberger (65), purporting to prove a circadian time sense in ant workers, have been repeated by Reichle (129) and Dobrzański (43) with negative results. Jander's careful experiments (78) prove that *Formica* workers have a time sense which allows them to correct for the sun's movement in sun-compass orientation, but this does not add evidence for circadian rhythms, as Renner (130) points out.

The sperm stored in the spermatheca during the nuptial flight must last the lifetime of the queen and supply the ova for the entire worker