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The behavior of animals around twilight with emphasis on coral reef communities

W. McFARLAND[1], C. WAHL[2], T. SUCHANEK[3] and F. McALARY[1]
[1]Friday Harbor Marine Laboratory, University of Washington, 620 University Drive, Friday Harbor, WA 98250.
[2]Department of Anatomy, Veterinary College, Cornell University, Ithaca, NY 14853.
[3]Division of Environmental Studies, University of California, Davis, CA 95616.

19.1 Introduction

Light, which represents a limited range of the electromagnetic spectrum, is characterized by three primary qualities – spectral frequency, intensity and polarization. Natural ambient light that organisms respond to emanates primarily from astronomical light sources and to a lesser extent from bioluminescence. For both sources, be it due to the earth's daily rotation and the moon's monthly procession about earth, or the flashing of fireflies on land or fishes in the deep sea, light is presented to animals with a distinct temporal component. From midday through night-time light intensities on earth's surface can vary 8 to 9 orders of magnitude, with the most rapid changes of 5 to 6 decades of intensity occurring during twilight (Figure 1). Animals exhibiting visual behaviors over this dynamic range are few, and those that do usually possess duplex visual mechanisms, one sensitive to the 'bright' light of day (photopic), and the other sensitive to the 'dim' light of night (scotopic).

Temporal separation of daily activities such as feeding is widespread in animal communities, and recognized in the designation of animal species as diurnal, as nocturnal, and more rarely as crepuscular. There are also arrhythmic species that show no demonstrable change in activity patterns from day to night (Yamanouchi 1956, Southward and Crisp 1965, Curio 1976). Most animals show structural adaptations suited to the light characteristics of their activity cycle. These include, for example, cryptic body coloration in diurnal species (Cott 1940), or optically specific visual structures (invertebrates-Land 1981, vertebrates-Walls 1942, Crescitelli 1972, Lythgoe 1979). Often such visual adaptations also reflect phylogenetic lineages, as primarily diurnal birds and nocturnal mammals (Charles-Dominique 1975) or Lepidopterans, divided into primarily diurnal butterflies and nocturnal moths (Kennedy 1928, Cloudley-Thompson 1960).

Shifts in the daily activities of a variety of animals are often dramatic, usually coincide with the twilight periods, and usually involve movement from active feeding to a quiescent mode of activity. Extensive literature describes the

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temporal patterns for different animals from varied ecosystems (e.g., Calhoun 1944 and 1945, Harker 1958 and 1964, DeCoursey 1960, Aschoff and Wever 1962, Beck 1968, Aschoff 1969, Aschoff *et al.,* 1970, Blaxter 1970, Segal 1970, Charles-Dominique 1975, Thorpe 1978, Naylor and Hartnall 1979, Mills 1983). Most investigators have considered only a single or related species, and provide little information about other community members or specific light levels. As a consequence, relationships of precisely when and how the constituent species of animal communities slip into and out of their daily behavior modes is poorly documented. Ebeling *et al.,* (1966) investigated the behaviors of several benthic temperate marine invertebrates and concluded that their stereotyped movements around twilight functioned to separate prey from predators, a conclusion also applied forcefully to the twilight transitions of coral reef fishes (see Hobson 1979, and following citations). Several studies document the timing of diel transitions in specific taxonomic categories and, importantly, many provide measures of changing light levels with which the behavior changes can be correlated (vertical plankton movements – Clarke and Backus 1964, Boden and Kampa 1967, Kampa 1976; tropical marine fishes – Hobson 1965, 1968 and 1972, Collette and Talbot 1972, Domm and Domm 1973, Sbikin 1976; temperate marine fishes – Ebeling and Bray 1976, Hobson *et al.,* 1981; temperate freshwater fishes – Emery 1973, Helfman 1979, 1981 and 1993; non-primate mammals – Kavanau 1971, Voute *et al.,* 1974, Zawhlen 1975, Kenagy 1976; primates – Charles-Dominique 1975, Pariente 1974, 1979 and 1980, Pages and Petter-Rousseaux 1980). The temporal precision in these daily behavior transitions introduces ordered chronology into the changes in communal structure that occur at dusk and dawn, and presumably benefits each individual – e.g. increasing foraging time vs. reducing predation.

Because these tightly orchestrated shifts in behavior usually occur at twilight, it is generally inferred that the changes in light, in some manner, act as a signal to elicit the transitions (McFarland *et al.,* 1979). As a result it is the transitional behavior of animals at twilight and their relationship to changes in ambient light that we consider in this chapter. We focus on the transition behaviors in coral reefs because of our familiarity with these ecosystems and, especially, because of their high faunal diversity, the leading role that predation plays in molding community interactions (Grigg *et al.,* 1984, Huston 1985, Sorokin 1993), and the relative constancy of photoperiod and the duration of twilight in the tropics. What then is the temporal precision in the daily behavior transitions of the highly diverse invertebrates and fishes that inhabit coral reef communities?

19.2 Diel changes in coral reefs

19.2.1 Light

Twilight represents the period during dawn and dusk when the sun continues to illuminate the sky even though it is below the horizon. The optical causes of