At this NATO Advanced Study Institute we are concerned with the changes that occur in the visual system throughout life from the embryo through the juvenile phase, adulthood and senescence. The research that will be discussed at this meeting has been performed on a variety of species: various non-human mammalian species, birds, humans, fishes, etc. Since many of these animals differ in their life span and in their life expectancy, we must consider how to compare changes observed in one species with a short life span with comparable changes that occur in a species with relatively long longevity. This problem is of particular concern to those who would compare animal data with human data.

In this paper, I shall (1) discuss some of the reasons for studying aging in non-human animals; (2) make some recommendations as to which groups of animals are the most appropriate for various purposes; and (3) suggest a method for comparing animal species that differ in their life span.

Before I begin, let me define some of the terms that will be used in this paper. "Life span" is the maximum reported age for a given species or other group. "Mortality rate" is the cumulative percentage of a population that have died at a particular age. "Life expectancy" is the age at which the mortality rate is 50%. "Longitudinal studies" are those in which the same group of individuals is studied at several (or many) different ages or stages of development. "Cross-sectional studies" are those in which different groups of individuals are studied, each at a different age or stage of development.

WHY ANIMAL MODELS?

1. Most animals have shorter lives than humans, which means that life-span longitudinal studies can be carried out within a reasonable proportion of the experimenter's life.

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2. Many animals show age-related changes in one or more biological systems that are very similar to age-related changes in comparable systems in humans.

3. Some experiments cannot be done on humans for bioethical reasons.

4. Rapid feedback from the effects of experimental treatments on longevity is possible.

5. The relatively shorter animal life offers the possibility to separate "age-related" or "developmental" effects from mere "calendar" effects.

Developmental or age-related effects are those that are determined, at least in part, by intrinsic, genetically determined mechanisms that come into operation at a certain phase in the life span. Various theories have been proposed to account for changes that occur at the senescent end of the life span (Sacher, 1978; Merry, 1987). These include, the notions of specific genes that induce aging, failure of the organism to tolerate DNA damage, or an accumulation of errors of transcription and translation from DNA during protein synthesis. Kirkwood (1981, 1990) has proposed a natural-selection theory of aging, the disposable-soma theory, which states that organisms that inhabit high-risk environments improve the survival of their species if they invest their bodily resources heavily in reproduction and related activities, such as parental care, rather than in the maintenance of their own somatic cells. Such creatures will tend to have large numbers of offspring and relatively short life spans due to an accumulation of unrepaired somatic defects. Species in low-risk environments, however, can afford the luxury of investment in the repair of their somatic tissues and thereby will have greater longevity. These classes of theories are not necessarily mutually exclusive.

Changes that occur at a particular phase of the life span also may occur because the individual has been progressively exposed to certain environmental factors. Such causes may be termed "exposure" effects or "calendar" effects. For example, we can easily show that the seasonal darkening of Caucasian skin during the summer months is a calendar effect due to number of hours of exposure to ultraviolet light and not a genetically programmed annual event. An example closer to the subject of this conference has to do with the age-related yellowing of the human crystalline lens. The human lens becomes progressively more pigmented with increasing age to the extent that by the sixth decade, the effective light reaching the retina has been reduced to 40% of the intensity that reaches the retina in a 20-year old (Weale, 1982). A widely accepted theory is that a major contributory factor in the yellowing is caused by exposure to short-wavelength light (Weale, 1982, 1989). In contrast, the lenses of old pigeons and old quail are colorless. Is this difference due to the fact that pigeons and other birds are capable of detecting ultraviolet light (Remy and Emmerton, 1989) and therefore have evolved a mechanism to protect their lenses from yellowing with exposure? Or are we merely observing a calendar effect? In other words, if years of exposure are the culprit in lens yellowing, why would we expect a deeply yellow lens in a 17-year old (elderly) pigeon any more than we would in a 17-year old (young) human? An answer to this would be to compare pigeons with parrots, which have a life span that is more comparable to that of humans. Indeed, Christopher Murphy, a veterinary ophthalmologist at the University of Wisconsin, who specializes in birds, has informed me that there is no reported