distribution will be of the Poisson form. In this case, $Ke^{-bN_t/K}$ spots will be left vacant and $K(1 - e^{-bN_t/K})$ spots will be seeded, so the population in the following year will be

$$N_{t+1} = K(1 - e^{-bN_t/K})$$

Skellam shows that this type of difference equation yields a discrete analog of logistic growth.

Now let us assume that we have two species with numbers N_1 and N_2 "struggling" for the K spots and, to be certain that we do not introduce anything that can be called a niche difference, we will assume that individuals of the two species produce the same number of seeds. Both species would be expected to miss seeding $Ke^{-b(N_1+N_2)/K}$ of the spots, species 1 should occur alone on

$$Ke^{-bN_2/K}(1 - e^{-bN_1/K})$$

spots, species 2 should occur alone on

$$Ke^{-bN_1/K}(1 - e^{-bN_2/K})$$

spots, and both species should fall on

$$K(1 - e^{-bN_1/K})(1 - e^{-bN_2/K})$$

spots.

If we assume that the species are equally good competitors, so that each "wins" on one-half of the spots seeded by both, it is easy to see that both species can be expected to persist. For example, the proportion of species 1 in the $(t+1)$st year is given by the formula

$$\tfrac{1}{2} + \frac{e^{-bN_2/K} - e^{-bN_1/K}}{2(1 - e^{-b(N_1+N_2)/K})}$$

so that, if at some point, $N_1 = N_2$, the species will continue indefinitely to be equally abundant.

If one objects to the assumption of random distribution of the seeds, he should note that the nonrandom spatial distributions which are typical in natural situations are usually of the type in which the number of occupied spots is smaller than predicted from the Poisson theory, thus increasing the opportunity for even an inefficient competitor to persist by seeding vacant spots. Skellam considers ecologically more interesting cases in which one of the competing species always loses on the spots seeded by both, and he shows that even in these cases the species can coexist, provided that the poorer competitor produces more seeds than the other species. He also shows that in a "good" habitat (where K/A is large) the inefficient competitor will be driven out, but that in a poor habitat greater fertility may outweigh competitive ability. I submit that it would be very unfortunate if ecologists should be persuaded by a doctrine that such matters are not worthy of consideration.

It has been suggested (*7*) that Skellam's model "is primarily applicable to annual plants with a definite breeding season, . . ." but it could doubtless be applied almost without change to, for example, woodducks or other hole-nesting birds, where the availability of "spots" suitable for reproduction limits population size. I am confident that such an approach can be applied to perennial species with modifications that leave it still at least as biologically realistic as the logistic model of competition.

Why, then, do empirical data seem to support the competitive exclusion principle? First, because, by definition, no two species are identical, so that if one looks closely enough he is bound to find something that can be considered a difference in the ecological niches. Second, because survival and reproduction are processes that always contain chance elements and have finite probabilities of failure. Hardin seems to believe that if Park could control environmental conditions accurately enough the competition between the two species of *Tribolium* would give "an invariable result." It is more probable, in fact I regard it as certain, that Park is correct in believing that he has discovered environmental conditions under which the two species are so nearly evenly matched that the stochastic elements take over and mediate the outcome. No amount of tinkering with temperature and relative humidity is going to cause the little ball always to hop into the same slot of a roulette wheel. Third, if a population is being held below the carrying capacity of its habitat by the necessity of sharing some limited environmental resource with another species, it should be self-evident that there will be a selective advantage for any new gene that reduces or eliminates this sharing. I consider that Darwin's finches have differentiated not because *"Ecological differentiation is the necessary condition for coexistence"* but simply because natural selection will promote the spread of genes that permit a population to enlarge by exploiting an unfilled ecological niche.

If we really must have a competitive exclusion principle for pedagogic purposes, I am willing to subscribe to something like: "Species cannot coexist indefinitely because of the inevitability of random extinction, but, for species that conform to certain rather restrictive rules, competition may speed the process of species elimination." Each ecologist can decide for himself whether or not such a principle should become one of the foundations for a branch of science.

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Pupil Size as Related to Interest Value of Visual Stimuli

Abstract. Increases in the size of the pupil of the eye have been found to accompany the viewing of emotionally toned or interesting visual stimuli. A technique for recording such changes has been developed, and preliminary results with cats and human beings are reported with attention being given to differences between the sexes in response to particular types of material.

Qualities which have nothing to do with vision as such have long been attributed to the eyes. Perhaps the most poetical expression of this is found in the lines of Guillaume de Salluste: "These lovely lamps, these windows of the soul." Even if the eyes are not the "windows of the soul," there is an increasing amount of evidence that the eyes, more specifically the pupils, register directly certain activities of the nervous system, including, but not restricted to, the effects of visual stimulation.

Kuntz (*1*) discusses the control of the constriction and dilation of the pupil by the sympathetic and parasympathetic divisions of the autonomic nervous system. The light reflex, which is a change in pupil size due to changes in environmental light conditions, is controlled by the parasympathetic division through the action of the ciliary ganglion. The role of the sympathetic division in determining the size of the pupil is more complex, but Kuntz points out that "strong emotional states are accompanied by general sympathetic stimulation" and that "deep emotions of pleasure as well as fear are commonly accompanied by pupillary dilation."

Evidence that control of pupillary dilation by the sympathetic division of the autonomic nervous system is governed by hypothalamic centers is discussed by Gellhorn (*2*), who concludes that "pupillary dilation is one of the most constant symptoms observed on stimulation of the hypothalamus." Furthermore, Gibbs and Gibbs (*3*) report that hypothalamic stimulation will elicit purring in cats, which is generally con-

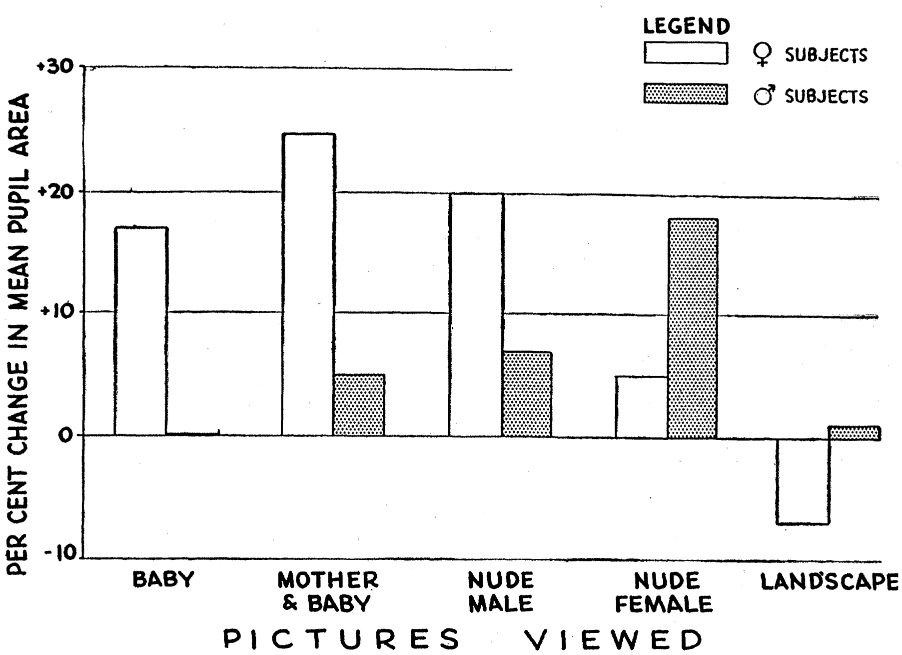

Fig. 1. Changes in mean pupil size, in terms of percentage of decrease or increase in area, from size during viewing of control patterns, in response to various pictures.

sidered to be an emotional expression of pleasure.

These findings are, of course, consistent with the vast amount of research done by Cannon and his collaborators, and also with their hypothesis that emotion is based on discharge over the sympatheticoadrenal system.

Some preliminary studies have been conducted at the University of Chicago with cats reared as pets and with intact laboratory animals, which indicated that under constant light conditions there were marked pupillary dilations in response to such stimuli as a relatively strange cat introduced into the home territory, a familiar object of play, and food. When food was not recognized, either because it was wrapped in paper or because it was an item foreign to the animal's normal diet, maximal dilation of the pupil did not occur until the scent of the food reached the animal.

To test the hypothesis that pupillary changes mediated by the sympathetic division, such as the changes we found in animals, could be used in human beings as both a quantitative and a qualitative measure of greater or less interest value and pleasure value of visual stimuli, we developed a technique for recording pupil size while the subject was shown visual material of different kinds.

Briefly, this technique involved obtaining exposures of the subject's eye on 16-mm film while he viewed a series consisting of test pictures alternated with a control pattern. Brightness was kept relatively constant in order to rule out any effect of changes in level of illumination on the size of the pupil. It was found that the most expedient way to analyze the film record was to project the 16-mm frames with a Percepto-Scope (*4*) and measure the pupil size in the projected image. In the pilot study reported here, the six subjects consisted of one single female, one married female, three single males, and one married male. Neither of the married subjects had children.

The figures shown in Fig. 1 represent the mean area of the pupil in 20 exposures taken over a 10-second period during which a test picture was viewed in relation to the area in 20 exposures taken during the preceding 10-second presentation of the test pattern. This relationship is given for the six subjects for a picture of a baby, of a mother holding a young child, of a partially nude man, of a partially nude woman, and of a landscape.

These data show that there is a clear sexual dichotomy in regard to the interest value of the pictures, with no overlap between sexes for the first four pictures.

We purposely report the data for the small sample used in our first study to indicate the type of results obtainable with this technique with a minimum number of subjects. Further studies, in which we utilized similar materials and more subjects, gave essentially the same results. Test-retest series, given after an interval of 1 day, show an extremely reliable result for the subjects tested. The probability of getting results of this degree of similarity by chance for any one subject falls below the .01 level.

The responses made to the picture of the baby and the picture of the mother and child substantiate an experiment conducted by Cann (*5*), who asked subjects to choose which picture they liked best in each of a series of pairs. Each pair consisted of an infant animal and an adult of the same species. Cann found that significantly more of the "baby" pictures were preferred by single women and by childless women than by single men and childless married men.

The responses to the pictures of the partially nude man and woman are what logically would be expected. Men are more interested in partially nude women, while women are more interested in partially nude men.

A comparison of the responses to the first four pictures with responses to the last emphasizes the possibilities for rating a wide range of material on the basis of interest value. It is also clear that differences in interest value of the various stimuli may be discerned within as well as between sexes.

Work now in progress deals with the range of visual materials for which reliable differences of pupil size can be found, as well as an exploration of how fine a discrimination will be possible with this technique. Further work deals with investigations of possible auditory effects on pupil size—for example, whether pleasant music causes pupillary dilation as compared to unpleasant sounds. Other avenues include the investigation of possible differences in pupil size when material dealing with experimental esthetics is presented.

The implications of this line of research seems to be far-reaching and could lead to a clearer understanding of behavior and its development at the human and infrahuman levels, through the study of a response with a basic mechanism which transcends gross species differences (*6*).

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