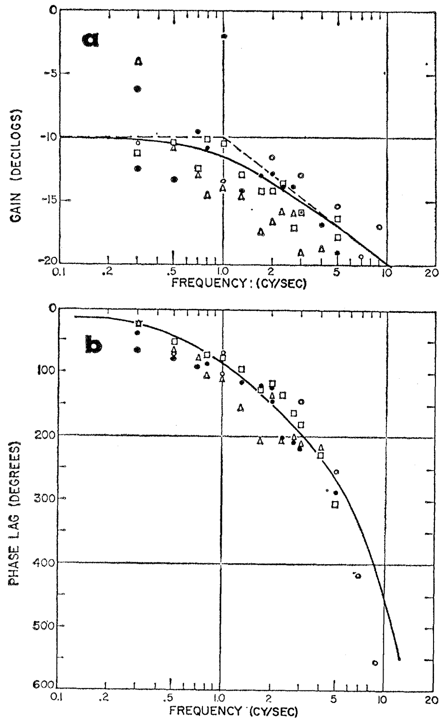

Fig. 3. Open-loop gain and phase lag of sinusoidally excited pupillary reflex. Symbols: □, run No. 1; △, run No. 2; ●, run No. 3; ○, run No. 4.

gain of the system may be defined as follows. Consider the case where $\bar{I}$ photons per second are impinging upon the retina and the pupillary system has been allowed to stabilize its response about an area $\bar{A}$. Then, let ΔI = change in the total number of photons per second striking the retina, and ΔA = change in the area. Under the equivalence assumption, the gain may be written:

$$G = \frac{\Delta A\,(\bar{I}/\bar{A})}{\Delta I} = \frac{\Delta A/\bar{A}}{\Delta I/\bar{I}}$$

The owl's pupil area has a range of 6 to 115 mm^2. Under our experimental conditions, the pupil area varied over the range 95 to 115 mm^2. The range of the human pupil area is 2 to 40 mm^2; under similar experimental conditions, the human pupil area varies over the range 16 to 30 mm^2.

Transient responses of the owl's pupil are shown in Fig. 1. Among the points to be noted is the short latent period: 0.05 to 0.10 second for constriction, 0.15 to 0.20 second for dilatation. There is also a high velocity of constriction as compared to the human. The velocity of constriction is greater than the velocity of dilatation and this asymmetry is also seen in the human. Changes in input amplitudes so as to obtain different response amplitudes demonstrate that the velocities of constriction and dilatation were directly dependent upon stimulus amplitude. Occasionally, marked overshooting and "ringing" were seen.

Adaptive processes which probably represent retinal light adaptation were seen after constriction. The time constants of these adaptive processes were dependent upon amplitude.

Noise was much less apparent in these recordings of the owl than in analogous human pupillary records. The noise also seemed to occur with larger amplitude in the constricted phase than in the dilated phase.

By performing experiments wherein the amplitude of the light step as well as the mean level of light were changed in order of magnitude by means of neutral density filters, it was clearly apparent that the effective stimulus was a percentage change of amplitude rather than the change in absolute value.

When driven with a sinusoidally varying intensity, most of the power of the output signal was in the fundamental frequency component of the input signal (Fig. 2). The lack of harmonic distortion argues in favor of the linear gain approximation derived above.

Low-frequency gain and mid-frequency gain were quite low (Fig. 3*a*). This means that the open- and closed-loop gains are not very different, a fact observed experimentally. There was a break frequency at 1 cy/sec and thereafter an attenuation with a slope approaching −1, or 10 decilogs per decade (6 decilogs per octave). The phase characteristics indicate that, in addition to the minimum phase lag element, there is also a nonminimum phase lag element due to the latent period. The minimum phase lag element is most likely due to the physiological mechanism involved in moving the thin sheet of iris muscle in the anterior chamber of the eye between the lens and the cornea.

From these graphical frequency response displays, we can construct a transfer function representing a linear lumped parameter approximation to the pupillary system in the frequency range studied:

$$G(s) = \frac{0.1\,e^{-0.15s}}{1 + 0.15\,s}$$

This consists of a low-frequency gain, a transport delay, and a simple lag element.

On a vector plot of gain and phase lag, the stability characteristics of the system can be seen. As is the human case, the system is stable, since a characteristic high phase lag is offset by a relatively low gain.

Figure 2 illustrates a time-dependent change in gain with change in stimulus amplitude. In other experiments, no "ringing" was observed after abrupt termination of a sinusoidal input.

It was stated above that under our experimental conditions the owl's pupil area is close to maximum. This leads to the prediction that a stimulus gain change would lead to a change in the mean size of the pupil, that is, that an increase in stimulus intensity would elicit a decrease in mean pupil area. Figure 2 shows an experiment where this was observed.

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2. We thank Dr. B. C. Abbott, University of Illinois, Urbana, for suggesting this study, and the Massachusetts Audubon Society for supplying the animals. Supported by Sperry-Rand Corporation Research Fellowship (to L.G.B.) and grants AF-49(638)-1313, MH-6175-02, and Nonr-1841(70) (to L.S.). The technical assistance of Julie Redhead is acknowledged.

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Territorial Behavior among Puku in Zambia

Abstract. *Territorial behavior of a species of antelope, the puku,* Adenota vardoni *(Livingstone) consists of the defense by males during the mating season of relatively widely spaced territories on a "territorial ground." Females wander about on this area for the purpose of mating.*

Since it appeared plausible that the territorial behavior reported by Buechner (*1*) for a species of antelope, the Uganda kob, [*Adenota kob thomasi* (Neumann)], would also occur among the closely related puku, *Adenota vardoni* (Livingstone), I studied these antelopes in an area of 100 ha in the

Luangwa Game Reserve, Zambia, during the period 25 September to 10 October, 1964. Daily records were obtained on males considered resident in a circumscribed area (*2*).

Four male pukus, drugged with succinylcholine chloride, were individually marked and then released. One of these was observed 46 times in an area of 7.5 ha and another, 23 times in an area of 21.0 ha. Data obtained on three other males that could be recognized by natural characteristics indicated that they occupied areas varying in size from 5.0 to 12.5 ha. In addition, at least four other males occupied rather circumscribed areas during parts of several days. In all, nine areas could be recognized (Fig. 1). The sizes of ranges occupied by individual males were determined on the basis of daily records, as well as data obtained from driving these males around intentionally or unintentionally. When a disturbed male deserted his territory he would usually return within 10 to 20 minutes.

I consider the ranges described to be territories, since they were (i) occupied intermittently or continuously by the same males and (ii) defended against intruding males who also occupied territories. This concept does not imply that territories were occupied for a much longer time than the study period. Several territories overlapped because males invaded neighbors' territories which were temporarily vacated. That part of the study area which was regularly occupied by territorial males was considered "territorial ground" (*1*). This ground was the most open part of the study area.

Most interactions among males, and matings with females, took place in the center of the territorial ground. Boundaries were defended more by ritualized display than by fighting. No serious fights were observed. Displays included the animals' facing each other and rapidly wagging their tails, but erection of the phallus and laying back of ears as described by Buechner for the kob (*3*) were not observed. On several occasions an intruder was evicted in a chase by a residential male. On one occasion an intruder was pursued by a territorial male to the opposite boundary of his territory. Most interactions by territorial males were stimulated by outside disturbances, such as human beings or lions walking through the study area. A "bachelor" band of young adult males occupied a range west of the "territorial ground." Occasionally some of these males were seen on territories, and sometimes they were chased off by occupants of the territories (Fig. 1).

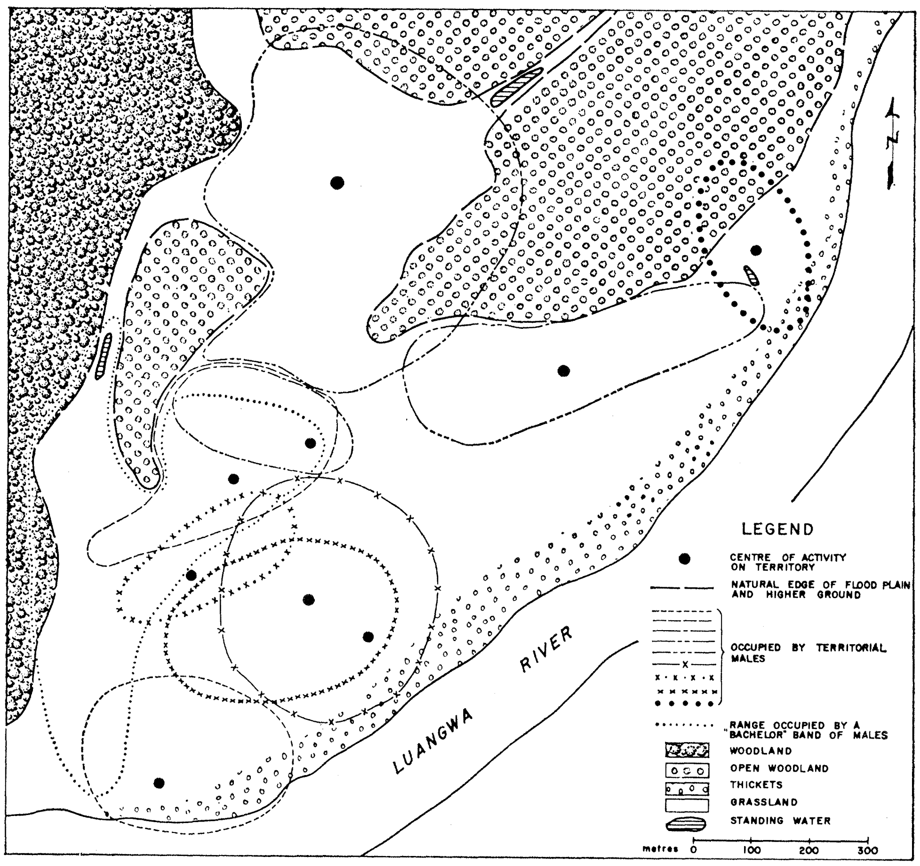

Fig. 1. Territories of puku in the Luangwa Game Reserve, Zambia.

Contrary to Buechner's statements (*1*), the centers of territories were not closely cropped or heavily trampled; the territories defended by male pukus were much larger than those he described for the Uganda kob. This may be because the population density was lower or because of different environmental factors.

Individual females did not associate with a particular male. Rather, groups of females wandered continuously and associated for relatively brief periods with territorial males.

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Mus musculus: Experimental Induction of Territory Formation

Abstract. *In groups of house mice* (Mus musculus) *an experimentally imposed sequence of experience led to the establishment of male territories in suitably designed observation pens. This sequence consisted of familiarization with the area followed by combat with and social dominance over another male who was then removed, and a final step in which defeat on the home ground of a similarly experienced male was coupled with victory over the latter on familiar ground.*

Territoriality, as used here, is any behavioral phenomenon which effects the exclusion of some category of conspecific organisms from space inhabited by the territorial individual or group. For *Mus musculus*, the general consensus has been that territorial behavior is absent, or at most weakly