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AN EVALUATION OF LINE TRANSECT CENSUS METHODS
IN A WEST AFRICAN WOODED SAVANNA

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AN EVALUATION OF LINE TRANSECT CENSUS METHODS
IN A WEST AFRICAN WOODED SAVANNA

By

STANLEY HENRY KOSTER

A DISSERTATION

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ABSTRACT

Three census methods, foot, roadside counts and aerial surveys, were compared for their usefulness to estimate population densities of 11 species of large mammals in a West African savanna woodland. For foot and roadside count data, 18 line transect estimators were evaluated for their consistency and usefulness under a wide variety of sampling conditions.

Foot transect counts, though time consuming, were the most useful for estimating population densities. Aerial counts were reliable for buffaloes and elephants, but not for antelopes. Roadside counts were unreliable, despite a relatively good road distribution.

Among the 18 estimators evaluated, three radial and four perpendicular distance estimators were recommended. The most consistent radial estimators included the Geometric and Modified Hayne. For certain data sets where flushing distances were small, the King estimator performed better. Among estimators based on perpendicular distances, three nonparametric estimators, the Fourier Series, Polynomial and Kelker and one parametric, the Generalized Exponential, performed well. Nonparametric estimators were preferred because of their robust properties. With small data sets, however, only the Generalized Exponential was recommended. The Hahn estimator, based on disappearing distances, consistently yielded low estimates.

Among the many factors which can lead to biased estimates, animal movements prior to detection was the most serious. For 6 of the 11 species, at least 10% of the animal groups were moving rapidly when sighted, resulting in inaccurate distance measurements. Body size and group size did not significantly influence the detection of groups.

The transition from group density estimates to population estimates required reliable estimates of both mean group size and species distributions within the study area. Density estimates of kobs, waterbucks, bushbucks and reedbucks were most meaningful when based on actual areas occupied along streams.

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INTRODUCTION

One of the central problems in the study of animal populations is that of assessing population size. Though not always necessary, knowledge of population size and density can provide a basis for sound management decisions. Leopold (1933) felt that the game census was the first step in initiating management on an area. In spite of the interest in population studies for many years, Eberhardt (1978) noted that field biologists still do not have an array of reliable methods for population study available to them.

Among the methods for counting large mammals in Africa, aerial transects are perhaps the most widely used, especially in East and South Africa. In the wooded savannas of West Africa, however, aircraft may be somewhat less useful, even for the largest animals. Availability and high cost, too, may restrict their use. Mark-recapture studies are also costly and time consuming, especially where multiple species are involved. The rapid disintegration of feces limits the utility of pellet group counts, too, as a technique to estimate abundance.

Among the most feasible methods for West Africa are roadside and foot transect counts. They are relatively inexpensive, rapid, and, as shown by Hirst (1969) in southern Africa, can be reasonably accurate. While many investigators have applied line transect methods to large mammal counts (Barber, 1980; Harris, 1970; Child, 1974, Sihvonen, 1977;

Bosch, 1977), evaluations of these methods in Africa have been limited. Some theoretical considerations of line transect estimators have been rigorously examined (Burnham et al., 1980, Gates, 1979), but many practical ones have not.

The wildlife manager is confronted with a number of challenges in designing line transect counts. First, there is the choice between aerial, roadside and foot transect counts, each having advantages and disadvantages. If ground counts are chosen, the best estimator must be selected from among the array of more than twenty. The estimator selected ideally should be useful for a variety of species and under a wide range of environmental conditions.

The large mammals commonly censused in Africa range in size from the diminutive duikers to elephants, and each species is unique in behavior and habitat selection. Visibility in the wooded savannas is highly variable and animal distributions are often clustered near water. Furthermore, some animals occur singly while others are found in large groups. The challenge for the field biologists is to design a sampling procedure which will provide reliable estimates for all or most of the large mammal species present in the diverse habitats present on this management area.

The objectives of this study were first, to examine the usefulness of foot, roadside and aerial counts for large mammals in a West African wooded savanna, and second to evaluate the validity of the various line transect estimators.

Review of Line Transect Methods

Mathematical Background

Line transect history and concepts have been discussed in some detail (Eberhardt, 1978; Gates, 1979; Jolly and Watson, 1979; Burnham et al., 1980). The underlying theory is relatively straight-forward. The observer moves along a transect line (Figure 1) and, as animals are encountered either as a result of detection by the observer or as a response by the animal, one or more measurements are recorded. These measurements include radial distance r , from the observer to the animal at z ; the perpendicular or right angle distance x from the line of travel; or the disappearing distance d from the line of travel. The perpendicular distance can also be obtained by either measuring both the angle θ and r ($x = \sin \theta \cdot r$) or by measuring both θ and y , the distance from the observer to a point directly perpendicular to the animal ($x = \tan \theta \cdot y$). The most common and usually recommended measures (eg. Burnham et al., 1980) are r and θ . These measures, when used with an unbiased estimator, are expected to give an unbiased estimate of the average population density. If sampling procedures were representative of the entire management area, a reliable population estimate for that area can be obtained.

The general formula used to estimate animal density for all line transect estimators is $D = \frac{n}{2L\hat{c}}$, where n is the number of objects counted, L is the transect length and D is the estimated density. The parameter $\hat{c}$ or its alternate form c' , where $c' = \frac{1}{c}$ $D = \frac{NC}{2L}$, is the only unknown in the equation. The parameter c is determined

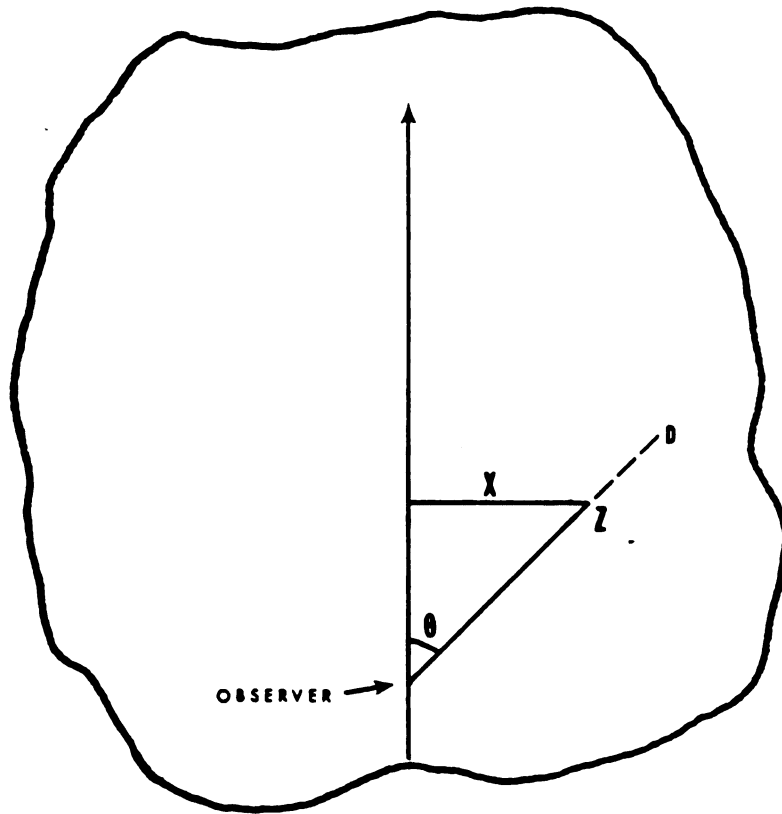


Figure 1. Diagram of the measures recorded in line transect surveys.

by measuring the distances x or r along the transect line, and is sometimes referred to as one-half of the effective strip width. (For estimators based on perpendicular distances, the measures of x and n represent the information required to estimate densities.)

Gates et al. (1968), Seber (1973) Gates (1979), Burnham and Anderson (1976) and Burnham et al. (1980) have discussed the general model that must be followed to estimate density from the above measures, and their discussions are summarized here. The model is based on the concept that the probability of detecting an animal decreases as the perpendicular distance from the line increases. This probability of detection has been represented by a function $g(x)$, termed the detection function (Burnham et al., 1980). It is the conditional probability of observing an object (animal) at some perpendicular distance x from the transect line. The model requires only that all objects directly on the transect line are detected (eg. $g(0) = 1$). The form of the detection function can assume a variety of shapes (Figure 2), depending on the objects being counted, the observer, and a wide variety of environmental factors which influence the detection of objects in the field. Thus, for any set of distances x , there is a probability density function, which forms the basis for a mathematical expression.

The form $f(x)$ has been adopted from Burnham et al. (1980) to represent the probability density function, since it is directly related to $g(x)$ where $f(x) = g(x)/c$. This function can then be used to represent the unknown parameter in the generalized formula $D = \frac{n f(0)}{2L}$, since $f(0) = 1/c$. The central problem in describing the probability density function, then, is finding an appropriate mathematical form for $f(0)$.

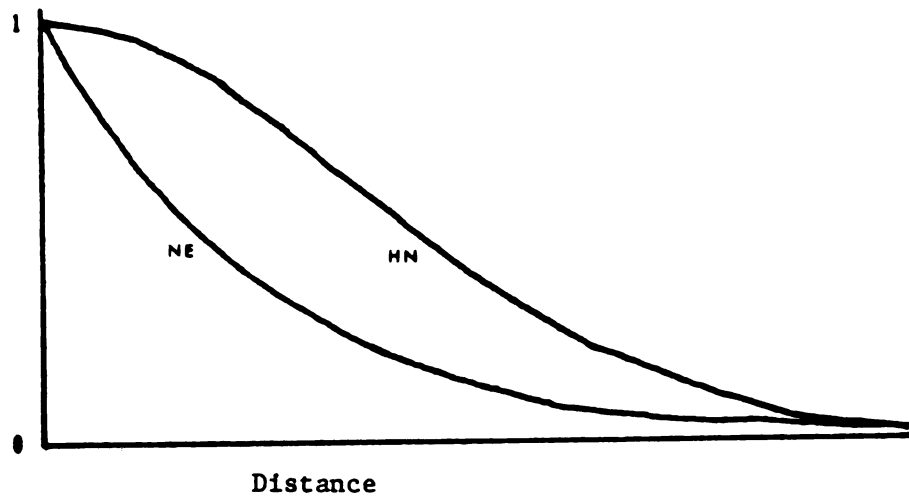


Figure 2, Examples of a negative exponential (NE) and a half-normal (HN) detection function curves $g(x)$.

Grouped data

Some estimators require that the data be grouped into discrete class intervals. This is normally done by constructing a frequency histogram of the data (Figure 3). The shape of the probability detection function often can be subjectively altered to follow a smooth curve by decreasing the class interval size.

Truncation

Often with line transect data, there are several observations which are very large in relation to most others. These extreme values can bias the estimation of $f(0)$, and it has been recommended (Burnham et al. 1980) that they be eliminated or truncated at some distance, w^* . In practice, Burnham et al. found that 1-3% of the data should be truncated to minimize bias.

Assumptions of estimators

The underlying assumptions of line transect estimators were first mentioned by Hayne (1949) and later elaborated by Gates et al. (1968), Seber (1973) and Burnham and Anderson (1976). They are:

- (i) Objects to be sampled are randomly distributed in the area, or the transect lines themselves are randomly located.
- (ii) The sighting of one animal is independent of the sighting of another.
- (iii) No animal is counted more than once.
- (iv) When animals are seen upon being flushed or spotted, each animal is seen at the exact position it occupied when startled or spotted.

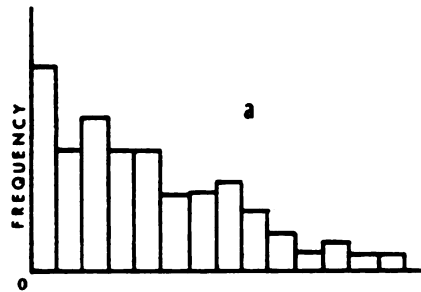


Figure 3. Examples of data grouped into 14 (a) and 7 (b) equal class intervals.

- (v) The probability of sighting an animal directly on the transect line is unity. (no animals on the transect line are missed).

The above assumptions apply to animal groups as well as to solitary individuals. Failures of the data to meet these assumptions have been discussed by Gates et al. (1968), Seber (1973), Eberhardt (1978) and Gates (1979).

Historical Review

Line transects were first used for counting animals early in this century. Only in the past few years, however, have efforts been made to establish a solid theoretical framework for line transect estimators. Forbes and Gross (1921) were evidently the first to report using a fixed strip transect while counting songbirds in Illinois. During the 1930's and 1940's, interest in monitoring wildlife populations arose out of the need for a more scientific approach to management. The first reported use of distance measures for estimating density was the procedure devised by R. T. King for ruffed grouse (Bonasa umbellus) in Minnesota, as reported by Leopold (1933). King's method was based on measurements of r , and Leopold introduced the term "effective strip width" to describe the average area sampled during the count. Breckenridge (1935), working with songbirds, felt that by constructing a frequency table of perpendicular distances, he could determine the strip width to a point after which frequencies sharply declined. His strip, therefore, was based on the distance within which he was reasonably sure that all or most birds were detected.

Gradually, line transect methods were adapted to counts of various species in a variety of habitats and circumstances. These include white-tailed deer (Odocoileus virginianus) (Erickson 1940; Krefting and Fletcher 1941), ruffed grouse (Bonasa umbellus) (Fisher, 1939; Frank, 1946), snowshoe hares (Lepus americanus) (Webb, 1942), songbirds (Kendeigh, 1944), and dead deer (DeBoer, 1947). Webb's approach for snowshoe hares was to use the mean perpendicular distance $\bar{x}$, derived from $\bar{r}$ and $\bar{\theta}$, the mean radial and angle measures, as an estimate of the effective strip width.

Hayne (1949) felt that estimates based on average flushing distances would underestimate population size, and proposed using the reciprocals or the harmonic mean of r as an estimate of the strip width. He assumed that each animal will flush if the observer approaches within a certain critical distance, and that the distance differs for each individual. His methods has been widely used.

Kelker (1945) was one of the first to examine line transect methods critically, and this led to his belt or strip transect method. For estimating deer densities, he counted only those animals within a pre-determine strip width and ignored animals outside the strip.

Hahn (1949) used a considerably different approach in an attempt to estimate strip width. He used a person to represent a deer, and measured the distance at which the person disappeared from view as he moved away from the transect line. From these measurements, he established visibility profiles in the different vegetation types encountered along roads in his study area, and thus was able to estimate the area in which animals might be seen during roadside counts.

During the 1950's and 1960's many field biologists used line transect methods but made few advancements toward assessment or improvement

of existing line transect estimators. Yapp (1956) presented a theoretical paper in which he attempted to develop a census methodology which took into account movements of animals prior to counting. Skellam (1958) reviewed Yapp's method, and further developed an unbiased estimator based on motion theory. As noted later by Seber (1973), however, the methods of Yapp and Skellam had little practical application because they required measurements unobtainable during normal line transect counts.

Robinette et al. (1954, 1956) provided insight into the relative precision of several estimators and the practical problems of counting inanimate objects. Their investigations into assessing numbers of dead deer and burlap sacks revealed that counts can have a considerable amount of negative or positive bias, depending on the environmental conditions and the estimator selected.

In the late 1960's, several advances in line transect theory were made. Gates et al. (1968), Eberhardt (1968) and Gates (1969) were among the first to develop a more statistically-rigorous approach. Using only perpendicular distances, Gates et al. (1968) based their estimator on the probability of detecting an animal along the transect. They used $g(x)$ to denote the probability of detection and proposed that $g(x)$ is exponential, $g(x) = \exp(-\lambda x)$, with the maximum likelihood estimate of λ is equal to $n-1/\sum x_i$. They based this estimator on the frequency distribution of perpendicular distances for grouse flushes in Minnesota which exhibited a negative exponential distribution. This estimator is restrictive because unless $g(x)$ is exponential, it can lead to badly-biased results. Gates (1969) then developed an estimator

for radial distances r , also based on the negative exponential distribution.

Eberhardt (1968) introduced a more general approach. He noted that the probabilities of detecting an animal decrease with increasing perpendicular distance, and that an appropriate model for the decreasing function is undefined. Rather than the negative exponential, he suggested adopting a more flexible model from a family of curves, either the power series or reversed logistic distributions. He developed an estimator based on the power series distribution.

The work of Gates and Eberhardt led to the development of a number of other line transect estimators. Frequency distributions of observations for a variety of animals in various types of vegetation were scrutinized and it gradually became clear that detection functions can assume a variety of shapes. Thus, more than one distribution must be considered for a particular animal and its habitat.

The half-normal distribution was suggested by Hemingway (1971) for Thomson's gazelle (Gazella thomsoni) in East Africa. Sen (1974) proposed a gamma distribution, a generalized form of the exponential distribution. The log-quadratic distribution provided the basis for an estimator developed by Anderson (1978), who attempted to find an equivalent to the Exponential Quadratic estimator. Quinn (1977) and Pollock (1978) independently proposed the generalized exponential distribution for $g(x)$, which, as noted by Gates (1979), included as special cases the exponential, half-normal and uniform distributions. In his computer program LINETRAN, Gates (1981) included an additional estimator based on the triangular distribution.

As noted by several investigators (Burnham and Anderson 1976; Seber 1973) estimators based on any underlying distribution will give unbiased estimates of population density if the assumptions of the underlying distribution are met. Departures from these assumptions can lead to badly-biased estimates.

In contrast to estimators based on parametric distributions, another approach was developed during the 1970's. Anderson and Pospahala (1970) used the line transect method to estimate densities of waterfowl nests in southern Colorado. They measured perpendicular distances of nests within a 16.5 ft strip and found that despite the narrow strip, frequencies of nests counted declined significantly near the limits of the strip. As a correction factor for the missed nests, they used a curvilinear regression equation. In their case, a quadratic equation performed best. This equation permitted a nest-density estimate to be calculated that was in no way dependent on an underlying distribution. Their paper laid the foundation for non-parametric approaches to density estimators.

Seber (1973) and Gross et al. (1974) also implicated the use of a distribution-free approach. Nevertheless, Burnham and Anderson (1976) first recognized the full potential and fundamental differences from parametric approaches. The non-parametric estimator of Burnham and Anderson (1976) required no assumptions about underlying distributions. It was an estimator based on perpendicular distances which required only that $G(0) = 1$, meaning that all animals on the transect line are counted. They also developed a modification of the Hayne estimator for radial distances which was not based on an underlying distribution.

The efforts of Burnham and Anderson led to the development of still other estimators. Crain et al. (1978) proposed an extension of the Fourier Series as an estimator. The Fourier Series estimator has since been shown to have robust properties with regard to variations in the underlying distribution and its use has been recommended over other transect estimators (Burnham et al. 1980).

Eberhardt (1978) recently developed a non-parametric estimator which is similar to that of Kelker (1945). It is based on grouped data, and uses only the two groups nearest the line.

Since their early development, efforts have been made to apply line transects to roadside counts (Nice and Nice 1921; Hosley 1936; Rasmussen and Doman 1943; Schrader 1944; Cronmiller and Fisher 1946; Taylor 1947; Hahn 1949). They were used mainly for white-tailed deer and mule deer (Odocoileus hemionus), and as index counts for bird species such as mourning doves (Zenaida macroura) and ringnecked pheasant (Phasianus colchicus).

Roadside counts of animals have taken three general forms. In the first, all animals are counted along the road transect and no distance measurements are made. Such counts reflect relative numbers and are used for comparisons with other areas or the same area at different times. The second approach involves establishing a fixed width or strip along one or both sides of the transect and counting all animals observed within that strip. Norton-Griffith (1978) discussed a variation of this where several fixed widths may be established to account for differences in vegetation or terrain along the transect. This method is most applicable to open country. The third is similar to Kelker's

(1945) belt transect except that all animals are counted and distances are measured to establish a visibility profile in the different vegetation types along the transect lines. Several variations have have been developed to measure profiles:

1. The average perpendicular distance of animals from the transect (Dasmann and Mossman 1962).
2. The disappearing distance of animals along a pre-established route (Hirst 1969), preferably for each vegetation type and for each species being counted.
3. The distance from the transect line to the point at which the frequency of observations begin to rapidly decline. That distance determines the effective strip width and observations made only within that width are included.

An additional method was attempted during this study, wherein the r and θ measures were made as done on foot transects.

Norton-Griffith (1978) noted that although roadside counts have been frequently employed in Africa and elsewhere, very little effort has been made to evaluate their accuracy. Criticisms of roadside counts involve bias in the random coverage of an area, and their attractiveness or avoidance of roads by animals (Norton-Griffith 1978; Gates 1979; Dasmann and Mossman 1962; Hahn 1949). Cronemiller and Fischer (1946), however felt that their roadside counts of white-tailed deer provided accurate density estimates, and Hirst (1969) showed that roadside disappearing distances for several species of African antelope gave reasonably-accurate population estimates.

Aerial transects have been widely used in Africa and elsewhere for counting large mammals. Density estimates are obtained from aerial transects by determining the strip width to be used prior to the count (Norton-Griffith 1978) and then tallying only those animals observed within the strip. Many sampling procedures have been used in aerial surveys but stratified random sampling is recommended (Jolly 1969; Jolly and Watson 1979).

Despite their wide acceptance, aerial counts have been shown consistently to be negatively biased, even for large mammals (Caughley 1977; Pienar et al. 1966; Jolly 1969b). There are many factors which affect the reliability of aerial estimates. Helicopters are recommended over airplanes, but even under the most favorable conditions, aircraft counts may provide only minimum population estimates.

STUDY AREA

Park W has been in existence since 1936. It is Niger's only national park and the one remaining locality with relatively-undisturbed upland and riparian vegetation. The park lies within the Sudan savanna zone and is international with portions also located in Benin and Upper Volta (Figure 4). The portion in Niger covers 2200 km², and lies between latitudes 11°05' and 12°35'N and longitudes 02°05' and 02°50'E. It is essentially a peneplain 250 m above sea level. The 750 mm isohyet and 35° isotherm pass through it. The Niger River, the only permanent flowing stream, forms the eastern boundary.

Annual rains begin between early April and early June, usually in May, and end in September/early October. The dry season has three distinct periods: warm and humid in October-November, relatively cool and dry from December through February, and hot in March-May. Wet season daily highs average 33°C.

The upland vegetation is mainly Combretum wooded savanna, with moderately dense woodlands and shrublands interspersed with small grassy openings. Riparian vegetation consists mainly of narrow bands of fringing forest. Annual fires burn approximately 70% of the park during the dry season. Most are set by park personnel during November and December to facilitate game viewing by tourists.

Park W has one of the most extensive road systems of West African parks. There are approximately 470 km of roads (Figure 5) which traverse

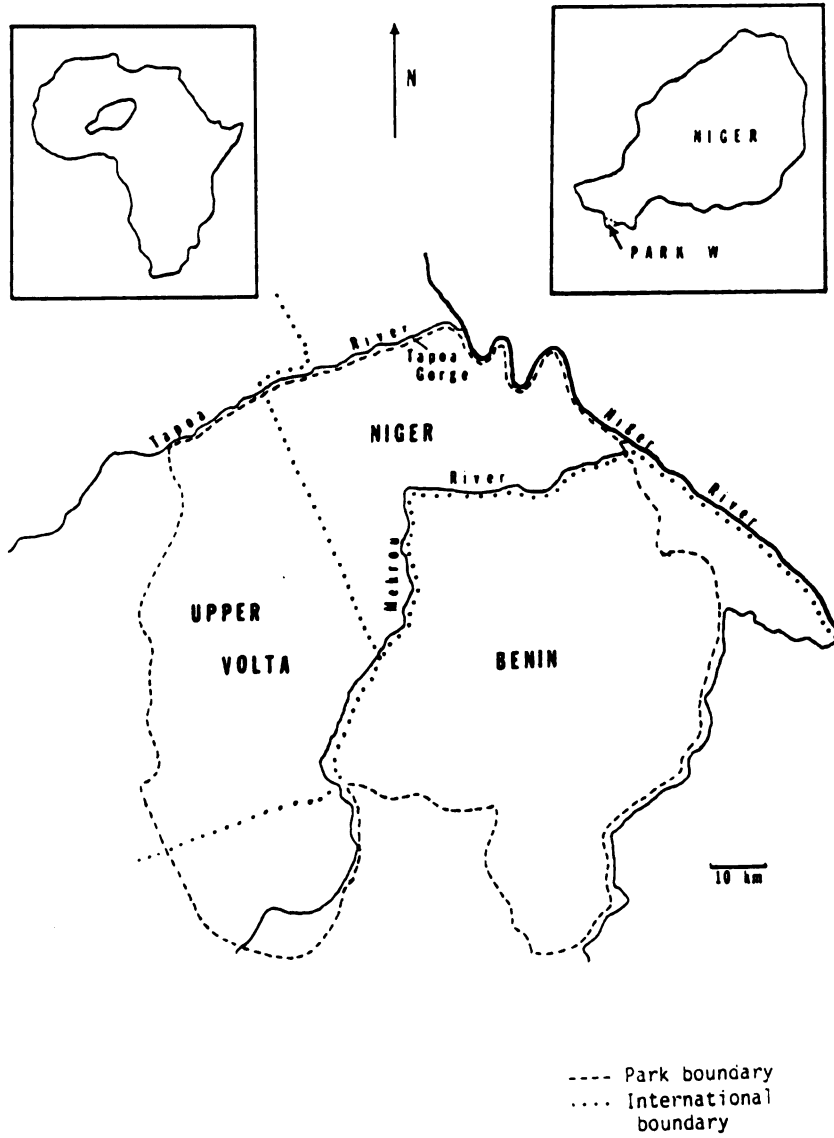


Figure 4. Map of Park W, Niger

representative types of vegetation and terrain. All roads are graded at the beginning of each dry season to permit passage by tourists. This is normally completed by December 1 of each year. Many portions of the road system become impassable soon after the first rains.

Time of Census

It was possible to conduct line transect counts in Park W from November to August. The period from mid-December to Mid-February, however, was considered best because daily high temperatures were moderate and visibility was comparatively good. Most fires were set by early December.

Counts during November were less desirable because not all areas of the park were accessible at that time and maximum visibility was only a few meters where grasses were unburned. The late-dry season also was not desirable because daily temperatures often reached 45°C (115°F) and field work became noticeably difficult. Animals responded to the heat by lying down and seeking shade making them more difficult to spot. A census during the late-dry season also ran the risk of being interrupted by rains. In 1976, for example, heavy rains arrived in mid-April. Many animals were concentrated along streams during the late dry season but quickly dispersed following the first substantial rains. The census was seriously affected. Counts during the rainy season were difficult, too, because many areas were inaccessible and visibility was significantly reduced.

Of the three major streams bordering Niger's Park W, the Niger is by far the largest (Figure 5). Its peak flow period occurs during

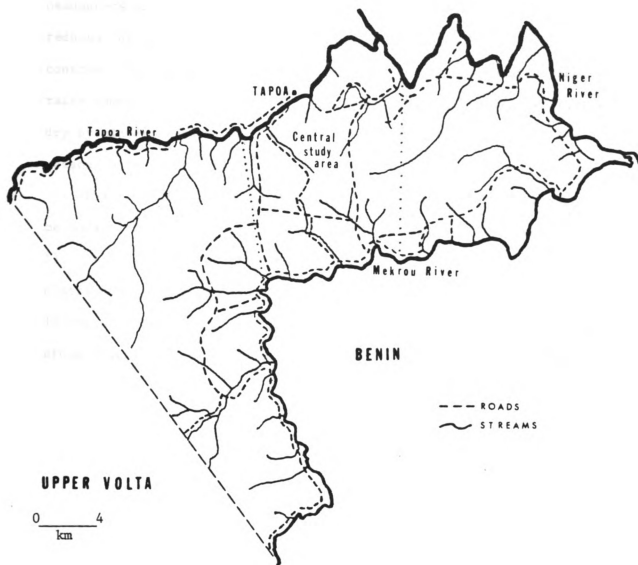


Figure 5. Boundaries, roads and major drainages in Park W, Niger.

the dry season (January-February), coincident with rainfall at the headwaters in the highlands of Guinea. The flow level is greatly reduced during the wet season. The Mekrou and Tapoa Rivers, in contrast, have seasonal flow for about five to six months after the rains commence. Except in the Tapoa Gorge, the Tapoa River is usually dry by mid-dry season, but numerous pools remain throughout the dry season in the Mekrou River.

For a detailed comparison of foot, roadside and aerial transect methods, the central portion of the park was selected for study (Figure 5). It is close to park headquarters in Tapoa, has a good road distribution and contains examples of most plant and animal communities in the park. In addition, it was probably the least affected by live-stock grazing and hunting, both illegal but prevalent in the park.

METHODS

Foot Transect Counts

Counts of animals were made during each mid-dry season (January-February) in 1976, 1977 and 1978. Counts were also attempted early and late in the dry season as well as during the wet season. The numbers of transects and distances walked were increased each year (Table 1). In 1978, the entire park was included in the survey.

Because of difficulties of access and of locating random starting points, complete randomization of transects was not possible. Road-side counts were made at the same time because of personnel and equipment limitations, and it was necessary to coordinate activities to maximize distances walked and minimize fuel and time wastages. Where possible, transect starting points were randomly located along roads or major rivers. Others were sited in representative habitats in a systematic manner designed to achieve time and fuel efficiency. It is believed that the foot transects (Figures 6-9) provided a representative coverage of the study area and total park.

Transects were normally traversed in cardinal directions, with a minimum of 1 km between transects to avoid duplications of observations. Most transects were walked between 0700 and 1100 hours. Usually, two persons were present on each transect. One served as observer/navigator and the other as observer/recorder. Transect distances were

Table 1. Numbers of transects and kilometers traversed during large mammal counts in Park W, Niger.

	<u>Central Study Area</u>			<u>Total Park</u>
	1976	1977	1978	1978
<u>Foot transects</u>				
Numbers	12	22	26	63
Total distances	76	160	208	760
<u>Roadside counts</u>				
Numbers	16	31	35	51
Total distances	776	1240	1200	2120

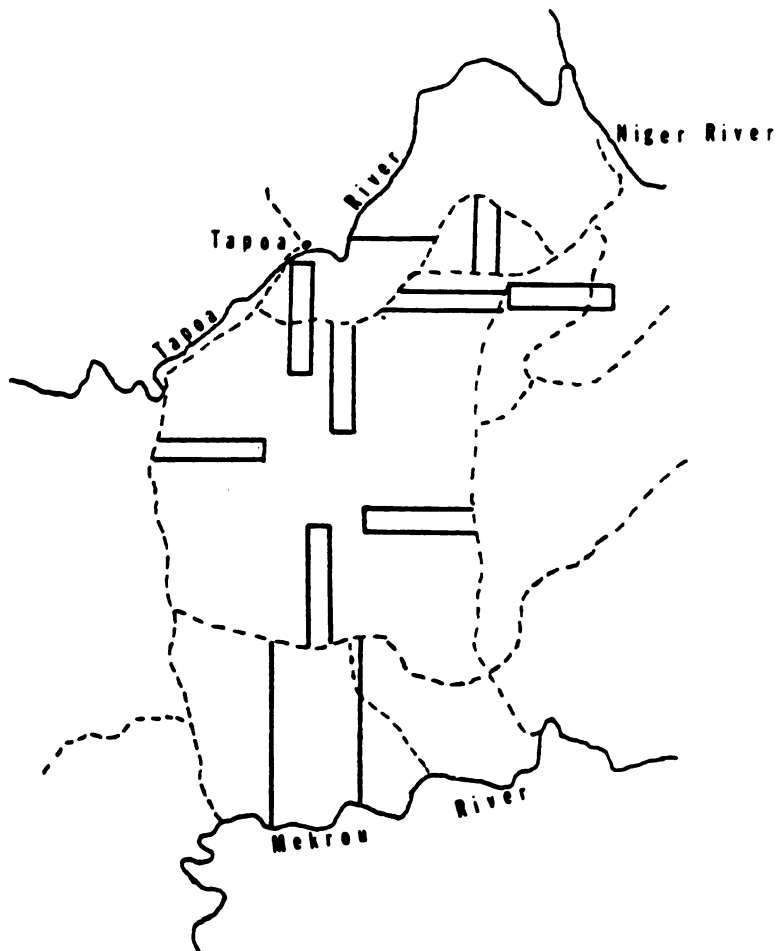


Figure 6. Locations of foot transects during the 1976 survey, Central Study Area, Park W, Niger.

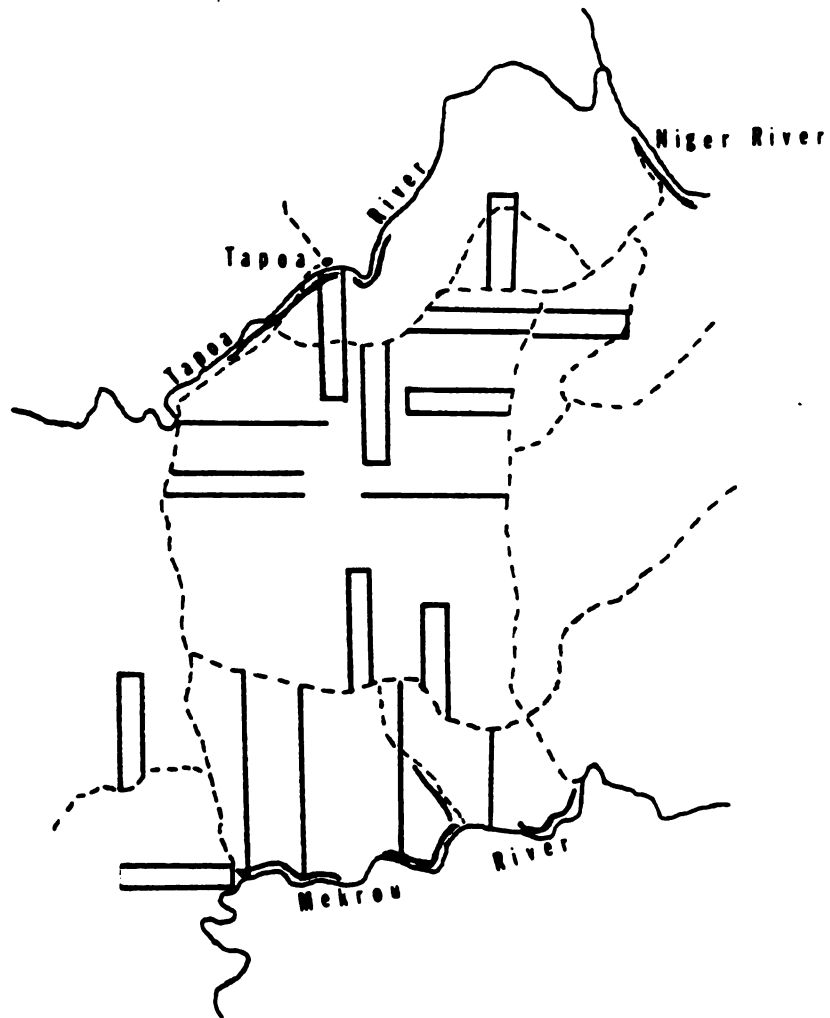


Figure 7. Locations of foot transects during the 1977 survey in Park W, Niger.

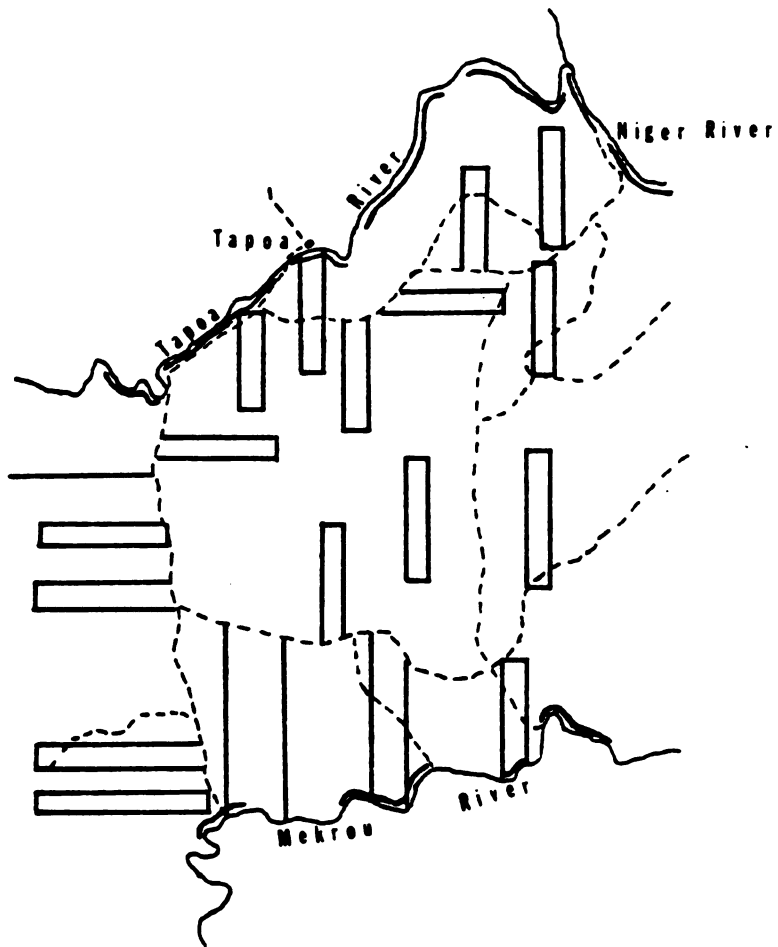


Figure 8. Locations of foot transects during the 1978 survey in Park W, Niger.

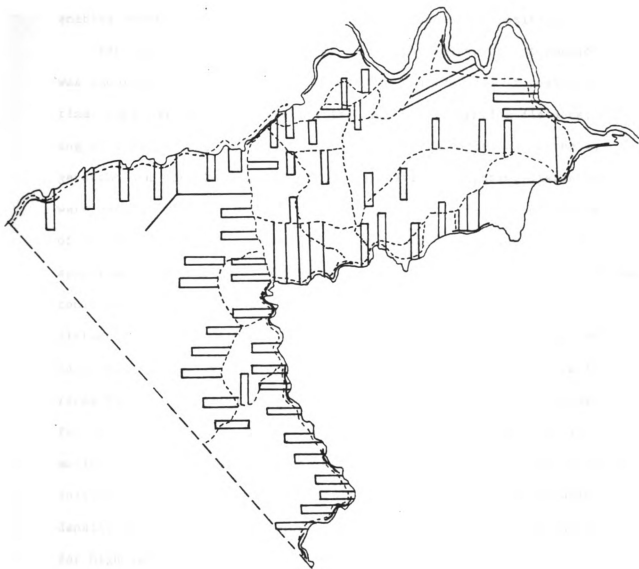


Figure . Location of foot transects during the park-wide survey of Park W, Niger.

determined by pacing and confirmed from topographic maps. Pacing enabled observations to be recorded on the transect by position.

For each observation along transects, the following information was recorded: species, number, sexes and relative ages if possible, time, location on the transect, animal activity, sighting distance, angle, disappearing distance, vegetation type, burn status of the vegetation and relative density of the vegetation. Sighting distances were defined as the number of meters from the observer to the center of a group. Group is defined here as one or more individuals. Disappearing distances were defined as the maximum distance that an observer could see the group. A basis for aiding judgements in disappearing distances was to estimate the maximum distance at which a group could have been spotted in vegetation of that type and density. A Mark IV range finder and pacing were used to measure distances and a compass for angles. In some instances, animals were not observed until in motion. For those observations, sighting distances and angles of their initial location were approximated or left unrecorded. The relative density of vegetation was recorded as 1 for low, 2 for medium and 3 for high density.

Roadside Counts

Roadside counts were carried out during the same time period as foot transects each year. Additional roadside counts were made during the early and late dry season, and also during the wet season until roads became impassable. Both morning and afternoon counts were made on each transect. Normally, two observers stood in the back of a

pickup truck which travelled between 15 and 25 km/hr. All park roads were traversed during the dry season but concentrated efforts were made in the central study area (Table 1). Transects along roads in the study area sampled approximately the same proportion of each vegetation type as did foot transects. In cases where an animal group did not voluntarily disappear, the vehicle proceeded along the road until a disappearing distance for the group could be obtained.

Aerial Counts

Aerial counts were made in February, 1977, and coincided with the locations and timing of foot and roadside counts made that month. Aerial censuses had been planned for 1976 and 1978 as well, but logistic complications prevented their completion.

A Bell 206 B Jet Ranger helicopter was employed for the aerial counts. All survey units (Figure 10) were sampled once. In high animal-density areas, three counts were made within a 3 day period. Air speed was maintained at 100 kph at an altitude of 100 m. The strip width sampled was 100 m on each side of the helicopter. Transects were a minimum of 2 km apart to avoid duplicate counts. Advantage was taken of natural landmarks such as roads and rivers to aid navigation and positioning of transects.

During the survey, one observer sat beside the pilot and two observers sat behind them. The pilot and forward observer assisted in spotting game while the rear observers both spotted and recorded. Desired strip widths for counting were established by marks placed on the aircraft windows while hovering over a measured and marked area on the ground.

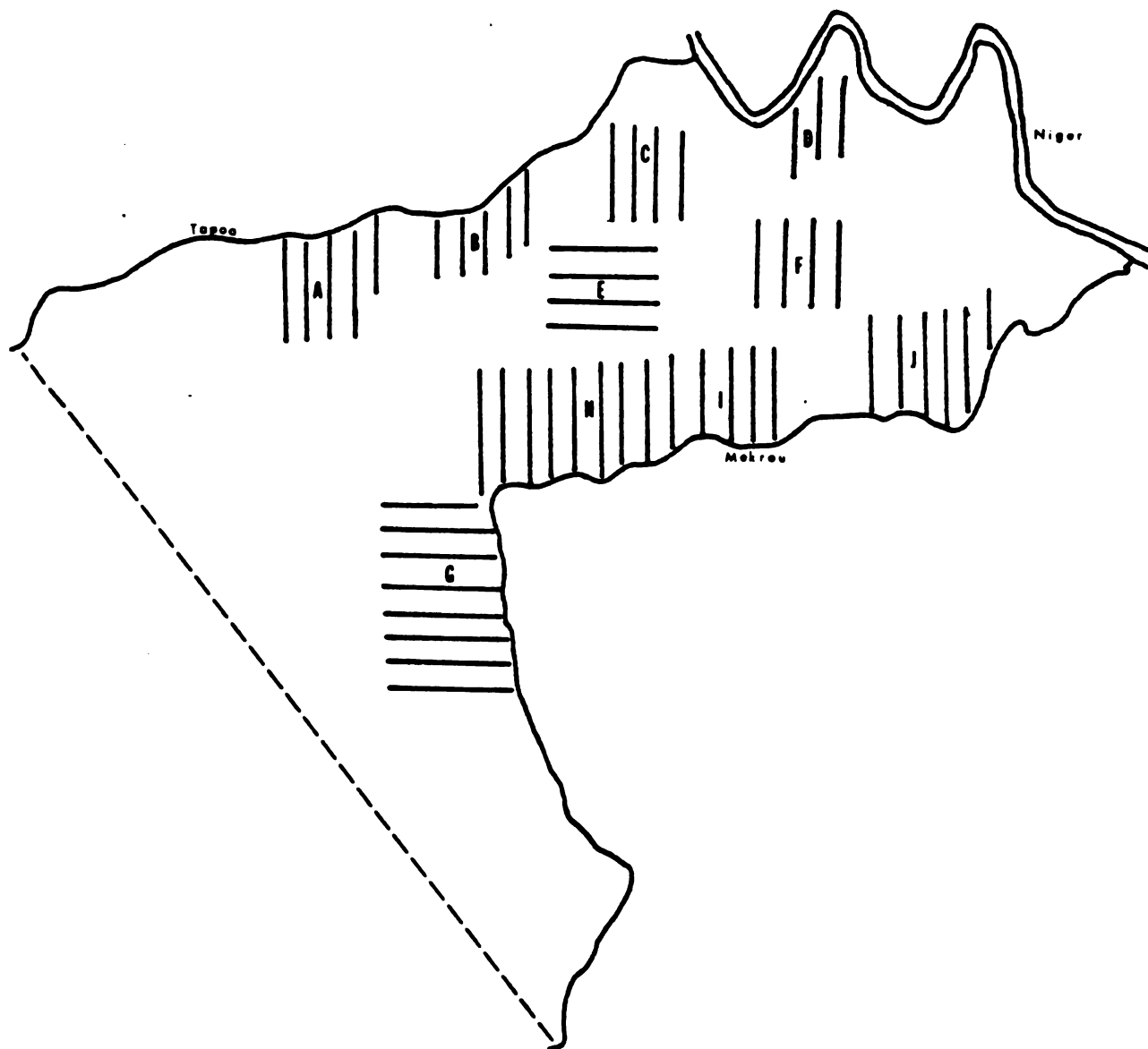


Figure 10. Locations of aerial transects in survey units a-j followed during the 1977 helicopter survey of Park W, Niger.

The study area was divided into two strata and the entire park into 5 strata according to relative animal densities as determined from ground counts.

Because these counts were intended to be used as a standard against ground counts, prior to and during the aerial counts, a serious effort was made to minimize bias. Five factors were specifically addressed as potentially biasing counts:

1. Animals visible but overlooked because of observer inefficiency.
2. Animals visible, but overlooked as the observer counted another group.
3. Animals concealed from view by vegetation.
4. Animals which moved out of the transect prior to counting.
5. Species misidentification.

There was no readily available check against these factors. For the first one, some measure of bias was obtained by comparing counts of the two observers on the right side.

Vegetation

A survey was made to determine the park's vegetation types and characteristics. The point center-quarter method (Cottam and Curtis 1956) was used to determine the species composition and density for woody vegetation. Sixty transects 100 meters in length consisting of 10 points each were established in the four types identified. From aerial photographs and after extensive ground verification, a vegetation map was prepared.

The extent of burned vegetation was estimated by point samples taken during the animal counts by foot transect and roadside counts. The point at the end of each 100 m transect was sampled to record whether it was burned or unburned. Along roads, the distance between points was 500 m.

Analysis of line transect data

The computer program LINETRAN developed by Gates (1981) served as the principal means of analyzing line transect data. With LINETRAN, the user has the option of specifying whether the data entered is truncated or untruncated, grouped or ungrouped, and can select one or more of 11 perpendicular distance and 4 radial line transect estimators. LINETRAN can also fit the data to the following distributions: half-normal, generalized exponential, triangular, polynomial, quadratic, and gamma distributions with $\alpha = 1.0$, $\alpha = 2.0$ or α variable. The test for the goodness of fit to the distributions is made by the Kolmogorov-Smirnov (K-S) statistic (Steele and Torrie, 1980). In addition, the cosine θ distribution of the measured angles (Hayne, 1949) optionally can be fitted and tested by chi square. For estimating variance, the user has the option of selecting the interpenetrating sample or specifying natural replications in time or space.

The original program LINETRAN was developed on an IMB computer. It required modification for compatibility with the CDC 6600 computer at Michigan State.

Evaluation of estimators

Criteria used for evaluating estimators included tests of goodness of fit to distributions on which certain estimators were based,

comparisons of relative density estimates with estimators of known bias, consistency of density estimates between species and between surveys and comparisons with results of aerial counts. The objective of these comparisons was to determine which estimators, if any, demonstrate consistent patterns between species and between surveys, and are generally useful for all species and habitats.

LINETRAN does not select the best or least biased estimator. The choice is entirely that of the investigator.

Species included in the analyses

Fourteen of the fifteen large mammal species (not including predators or primates) which occurred in the park were initially targeted for counting (Table 2). Observations later showed that topis, red-flanked duikers and red-fronted gazelles were rare. Estimation of their population densities was not feasible and they were omitted from the analyses.

Tests of Assumptions

The reliability of estimators can sometimes be determined by testing the assumptions on which they are based. Radial estimators are based on the assumption that the mean angle is approximately 32.7° . This can be tested by one of the two Z tests (Burnham et al. 1980). For $E(\theta) = 32.7^\circ$, the test statistic is

$$Z = \frac{n(\theta - 32.7)}{21.56}$$

where n is the number of observations.

A second test involves the $\sin(\theta)$, to show that it is an uniform

Table 2. Large mammal species in Park W, Niger whose populations were investigated in this study.

<u>Species</u>	<u>Scientific name</u>
Kob	<u>Kobus kob</u>
Waterbuck	<u>Kobus defassa</u>
Roan	<u>Hippotragus equinus</u>
Hartebeest	<u>Alcelaphus buselaphus</u>
Topi	<u>Damaliscus korrigum</u>
Buffalo	<u>Syncerus cafer</u>
Elephant	<u>Laxodonta africana</u>
Oribi	<u>Orebia ourebi</u>
Grimm's duiker	<u>Sylvicapra grimmia</u>
Red-flanked duiker	<u>Cephalophus rufilatus</u>
Bushbuck	<u>Tragelaphus scriptus</u>
Reedbuck	<u>Redunca redunca</u>
Warthog	<u>Phacochoerus aethiopicus</u>
Red-fronted gazelle	<u>Gazella rufifrons</u>

random variable on $0,1$. The test statistic is

$$Z = 12n (\bar{y} - 0.5) \quad \text{where } \bar{y} = \sin(\theta)$$

The other assumptions could not be directly tested. Instead, evidence from a variety of sources was used to determine if each assumption had been met.

Description of density estimators

Eighteen estimators of population density were included in the analysis. These estimators represent the majority of those developed and involve a wide range of mathematical approaches to density estimation. Several estimators including the King, Webb, and Dasmann-Mossman, have been largely replaced by others. They were included here, however, for comparative purposes.

Estimators based on perpendicular distances

Exponential Gates et al. (1968) developed the estimator

$$D_1 = \frac{\frac{1}{\bar{x}} (n-1)}{2L}$$

or in the $f(0)$ form, $D_1 = \frac{N \times \lambda}{2.0 L}$

where $\lambda = (N-1)/\Sigma(X)$, $\bar{x}$ is the mean perpendicular distance, n is the number of observations and L is the transect length. This parametric estimator requires that the detection function is negative exponential, and is sensitive to departures from this distribution.

Table 3. A list of the eighteen estimators evaluated in this study.

Name of estimator	Available in LINETRAN	Literature Source
<u>Perpendicular distances</u>		
Exponential	x	Gates et al. (1968)
Hemingway Normal	x	Hemingway (1971)
Quadratic	x	Anderson and Pospahala (1970)
Triangular	x	Gates (1981)
Generalized Exponential	x	Quinn (1977), Pollock (1978)
Spline	x	Gates (1981)
Polynomial	x	Anderson and Pospahala (1970)
Fourier Series	x	Burnham et al. (1980)
Eberhardt-Cox	x	Eberhardt (1978)
Kelker	x	Kelker (1945)
Dasmann-Mossman		Dasmann and Mossman (1962)
Webb		Webb (1942)
<u>Disappearing distance</u>		
Hahn	x	Hahn (1949)
<u>Radial distances</u>		
Geometric	x	Gates (1969)
Hayne	x	Hayne (1949)
Modified Hayne	x	Burnham and Anderson (1976)
Exponential	x	Gates (1969)
King		Leopold (1933)

Hemingway Normal Hemingway (1971) first proposed the half-normal distribution to fit observations based on perpendicular distances.

The general form of the detection function is

$$f(0) = \exp(ax)^2, \text{ where } a = \exp(-x^2/2)$$

For ungrouped, untruncated data, the form of the estimator is

$$D_2 = \frac{(\pi/2)^{1/2}}{\Sigma X^2 / n} \left(\frac{n - 0.8}{n} \right)$$

The form used in LINETRAN is $N/(L(\sigma^2(2\pi)))$, where $\sigma^2 = \Sigma(X^2/N)$

The underlying distribution must be approximately half-normal for density estimates to be unbiased.

Quadratic This estimator was proposed (Anderson and Pospahala, 1970) as a correction for bias caused by objects missed during strip transect counts. In this method, a quadratic curve is fitted to the detection function, and the intercept $b(0)$ is determined. The $b(0)$ is then used to estimate the density. The general form of the equation is

$$\hat{D}_3 = N \cdot b(0) / 2 * L * W(2)$$

where $W(2)$ is the width of the second class interval, $U(2) - U(1)$

Triangular For the case when the detection curve is approximately linear, this may be an appropriate estimator. The form of the estimator is

$$\hat{D}_4 = n / (2 * l * W)$$

where

$$W = x(\max)/2$$

Gates (1981) modified this equation somewhat because of its extreme sensitivity to outliers. He fits a straight line with the equation

$$Y = B(0) + B(1) * X + E$$

and uses the constrained least squares to obtain

$$D_4 = N * F(0) / 2 * L * W(2)$$

where $W(2) = U(s) - U(1)$ for grouped data, and

$W(2) = 1.0$ for ungrouped data, and

$F(0) = B(0)$.

Generalized Exponential This model is based on an exponential power series (Quinn 1977; Pollock 1978) and can assume a variety of detection function shapes. It has the general form

$$\hat{D}_5 = \exp \{ -(x/\beta)^\alpha \} \quad (\text{where } x, \alpha, + \beta > 0)$$

The model used in LINETRAN is

$$F(X) = \exp(-(X)\beta)^\alpha / (\beta * \omega 1.0 + 1.0/\alpha)$$

Spline This method was suggested by Gates (1979) as an alternative to the Kelker method. Gates (1981) noted that his procedure required the researcher to define an arbitrary distance, w , from the transect line in which all animals are seen. The spline method lets the data define that distance. LINETRAN does this by fitting a splining function

$$Y = \begin{matrix} B_0 & 0 \leq X \leq Z \\ B_0 + B_0(X-Z) & Z \leq X \end{matrix}$$

where Z is the point at which the detectability curve begins to decline (Figure 11) and B_0 is the average density of sighted animals to Z .

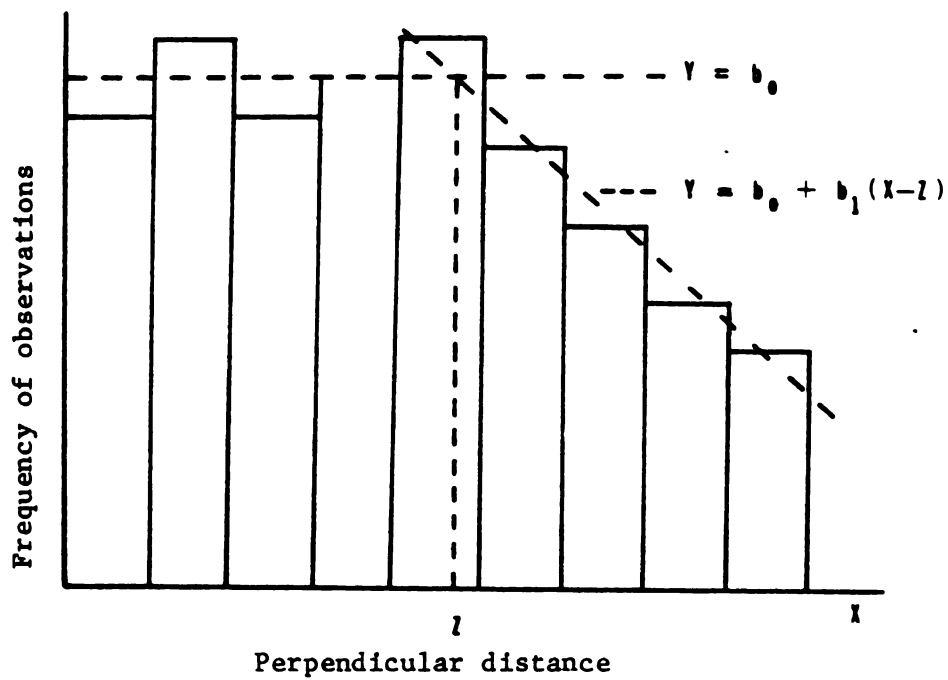


Figure 11. An example of a splining function using a hypothetical histogram.

The curve to the right of Z can be linear, quadratic or polynomial.

The form of the estimator is

$$\hat{D}_6 = \frac{B_o n}{2L w(2)}$$

where $w(2)$ is the width of the interval between Z and X.

Polynomial This estimator also is derived from the work of Anderson and Pospahala (1970). It takes the form

$$\hat{D}_7 = nF(0)/2L$$

where $F(0)$ is estimated by a polynomial of degree m ;

$$P(m) = B(0) + \sum_{j=1}^m (B(j)(x^2)^j) + \varepsilon$$

To avoid overfitting the data, an equation higher than the 6th degree is not permitted.

Fourier Series This non-parametric approach, developed by Crain et al. (1978) used the Fourier Series expansion of a probability density function over an infinite interval. Their estimator has the form:

$$\hat{D}_8 = \frac{n f(0)}{2L}$$

$$\text{where } f(0) = \frac{1}{W^*} + \sum_{k=1}^m \hat{a}_k$$

$$\text{and } \hat{a}_k = \frac{2}{nW^*} \sum_{j=1}^m \cos \frac{k\pi x_j}{W^*}$$

where W^* is the truncation point and $k = 1, 2, 3, \dots$. The stopping rule for the selection of m , the number of cosine terms in the Fourier Series, is

$$\frac{1}{W^*} \left(\frac{2}{n+1} \right)^{\frac{1}{2}} \geq |a_m + 1|$$

where $|a_m + 1|$ is the absolute value of $a_m + 1$

Kelker Index Kelker's (1945) model has as its detectability curve $g(x) = 1$ and has the basic form

$$\hat{D}_9 = n/2LW$$

where W is the cutoff point specified by the user within which all animals are likely to be seen.

Eberhardt-Cox This non-parametric estimator proposed by Eberhardt (1978) as based on the work of Cox (1969). It takes the form:

$$\hat{D}_{10} = (3N(1) - n(2)) / (4L(W(2)))$$

where $W(2)$ is the width of the second class interval.

Hahn Sometimes referred to as the "Hahn Cruise" or "Visibility Profile" method, Hahn (1949) proposed an estimator using distances in each vegetation type beyond which animals could no longer be easily detected,

$$\hat{D}_{11} = n/(2L\bar{x})$$

where $\bar{x} = \sum x_i / n$

Dasmann-Mossman For their density estimates, Dasmann and Mossman (1962) used mean perpendicular distances, $\bar{x}$, and

$$\hat{D}_{12} = n/2L\bar{x}$$

where $\bar{x}$ = the mean perpendicular distance of actual distance measures taken during the survey.

Webb Webb's (1942) method is a modification of the King method (see beyond) and is based on mean sighting angles and distances, where

$$\hat{D}_{13} = n / 2L\bar{r} \sin \bar{\theta}$$

where $\bar{r}$ is the mean radial distance, and $\bar{\theta}$ is the mean sighting angle.

Estimators based on radial distances

Geometric Gates (1969) proposed this estimator to "fill the void" because the geometric mean is always less than the arithmetic mean (King estimator) and greater than the harmonic mean (Hayne estimator). The Geometric estimator takes the form:

$$\hat{D}_{14} = n / (2L\bar{g})$$

where $\bar{g}$ is the geometric mean of sighting distances.

Hayne This is a basic method developed by Hayne (1949), where

$$\hat{D}_{15} = n / (2Lh)$$

and $h = n / \sum \frac{1}{r_i}$ is the harmonic mean of sighting distances

Modified Hayne Burnham and Anderson (1976) added a constant $C(2)$ to Hayne's formula to minimize bias. This modified version of Hayne's estimator has the form:

$$\hat{D}_{16} = C(2) n / 2Lh$$

where $h = n / \sum \frac{1}{r_i}$

and $C(2) = (1 - \Delta) + (\Delta(2/\pi))$,

and $\Delta = (\theta - 32.7^\circ) / (45^\circ - 32.7^\circ)$

This method requires that the average flushing angle be between 32.7° and 45° .

Exponential Where radial distances are distributed negative-exponentially $g(r) = r \lambda \exp(-\lambda r)$, the estimator from Gates (1969) is:

$$D_{17} = (2n - 1)/2L\bar{r}$$

where $\bar{r}$ is the arithmetic mean of the radial distances.

King This oldest estimator was developed by R. T. King but first published by Leopold (1933). It has the form:

$$D_{18} = n(1/\bar{r})/2L$$

Variances of density estimates

The variance of a density estimate can be obtained in several ways, depending on the sampling procedure and sample size. The following methods were evaluated for their applicability to density estimates in this study:

1. Interpenetrating sample variance. The interpenetrating sampling method (Cochran 1977) was designed to estimate variance from a single set of observations. Observations are randomly sampled after collection, and assigned to one of n subsamples. Densities are then estimated from each subsample, and the variance is determined from the densities of the individual subsamples.
2. Replicate samples Where separate density estimates D_i can be obtained from each transect line l , an estimator of $\text{var}(D)$

(Burnham et al. 1980) can be determined from

$$\text{Var}(D) = \frac{\sum l_i (D_i - D)^2}{L(R - 1)}$$

where D is the overall weighted density, L is the total transect length, and R is the number of replicate lines.

3. Indirect estimation of var(D) Burnham et al. (1980) noted that in the general estimation formula $D = nf(0)/2L$ both n and $f(0)$ are subject to sample variation. The $\text{var}(D)$ can be obtained indirectly by separate estimates of variances of $f(0)$ and n . The general equation is $\text{var}(D) = (D)^2 ((\text{cv}(n))^2 + (\text{cv}(f(0)))^2)$, where cv is the coefficient of variation.

$$\text{The variation of } n = \frac{L \frac{\sum_{i=1}^R \frac{n_i}{l_i} - \frac{n}{L}}{R-1}}{R-1}$$

4. Jackknife method. From a series of subsamples, the density is estimated by omitting, one at a time, the data from each subunit, and estimating the density from the remaining subunits. These densities are termed pseudovalues, P^1_i , and are used to estimate the average density where

$$P^1_i = LP - (L - l_i)P_i$$

These pseudovalues are then treated like R replicate estimators of density and are used to compute P_j and $\text{var}(P_j)$,

where

$$P_j = \sum_L P^1_i$$

and

$$\text{var}(P_j) = \sum \frac{(P^1_i - P_j)^2}{L(R - 1)}$$

If a stratified sampling scheme is desired, any of the above methods can be used to obtain within-stratum variance estimates.

Each of these methods of estimating variance was evaluated for application in this study. Estimation of variances from strata was not possible, however, because of the small sample sizes (including zero) from many of the strata. The jackknife method is appropriate for small sample sizes, but variance estimates by this method were so small that the author felt they did not realistically reflect the actual variability. For example, when coefficients of variation were between 40 and 50% for other methods, those of the jackknife method were usually less than 10%.

Indirect methods of variance estimation were of limited usefulness because variances of $f(0)$ have not been developed for each of the estimators. For large sample sizes, in consequence, the interpenetrating sample variance was employed, and for smaller sample sizes and density estimates from the central study area, replicate samples were used to estimate variances. It was recognized that replicate samples are undesirable for small sample sizes because reliable estimates may not exist.

Habitat preferences of large mammals were determined from density estimates of each species in each vegetation type. The ratio of estimated densities in each vegetation type and the estimated average density for the entire park gave a measure of selectivity for a habitat type. Values greater than 1.0 indicate a preference. Those less than 1.0 indicate that the animals did not utilize that habitat type in proportion to its abundance.

RESULTS

Vegetation

Though Park W contains many plant communities (Koster 1981), only the six major categories (Table 4) were considered for this study. Combretum shrublands together with Combretum woodlands comprised most of the park's vegetation (Table 4). Combretum woodlands were variable in height, density and composition, but consistently dominated by species of trees and shrubs of the genus Combretum and, to a lesser extent, by Terminalia. These woodlands were widely distributed in the park (Fig. 12), and generally comprised the intermediate vegetation between Combretum shrublands and riparian habitats. Shrublands dominated by Combretum species, occurred on well-drained ironpan soils. The distinction between woodlands and shrublands was not always obvious since tree species often assumed a shrub-like growth form on poorer soils. Riparian forest occurred as a narrow band along streams. They were composed of tall trees with a mostly-closed canopy and a dense understory of smaller trees and shrubs. Riparian woodlands were found on deeper soils adjacent to streams and often appeared as open parkland with a tall, dense grass cover. Riparian grasslands occurred in small patches along streams and in upland marshes. They were most common along the Niger River. Upland grasslands comprised openings in shrublands and woodlands.

Table 4. Characteristics of vegetation in Park W, Niger.

Vegetation	Percentage of total area	Average stem density/ha	Dominant species
Riparian grassland	1.3	78 <u>±</u> 8	Mimosa pigra Jardinia congoensis Sacciolepis africana Vetivera nigritana Sporobolus pyramidalis
Riparian forest	4.2	851 <u>±</u> 378	Diospyros mespiliformes Kegelia africana Anogeissus leocarpus Daniellia oliveri Mitragyna inermis Cola laurafolia Combretum micranthus Acacia ataxacantha
Riparian woodland	14.8	540 <u>±</u> 204	Diospyros mespiliformes Daniellia oliveri Anogeissus leocarpus Prosopis africana Pterocarpus erinaceus Terminalia avicennioides Tamarindis indica
Combretum woodland	37.4	898 <u>±</u> 368	Combretum nigricans C. glutinosum C. hypopilinum Crossopteryx febrefera Piliostigma reticulatum Combretum micranthum Guiera senegalensis
Combretum shrubland	39.7	364 <u>±</u> 306	Combretum micranthum C. nigricans C. glutinosum Guiera senegalensis Dicrostachys glomerata Securinega virosa
Upland grassland	2.6	242 <u>±</u> 92	Loudetia togoensis Microchloa indica Andropogon fastigiatus A. pseudapricus Acacia ataxacantha Combretum glutinosum

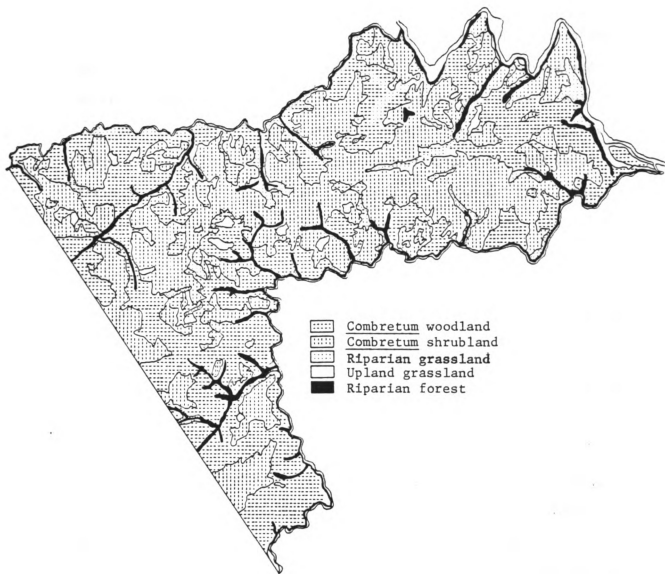


Figure 12. Vegetation map of Park W, Niger.

Distribution of Animals

Few of the large mammal species studied were ubiquitous in the park. Most species were more numerous in the central portion and along streams (Figs. 13 and 14). Roan, hartebeest, Grimm's duikers and warthog distributions covered the entire park. The principal factors believed to have affected animal distributions were vegetation, livestock, hunters and trappers, and water and fire. The influence of any one factor varied by animal and season.

Habitat Utilization

Patterns of habitat use as determined from foot transect counts (Table 5) indicated that each species preferences were unique. Warthogs were the most widely distributed animals, and were found in all habitat types. Only Grimm's duikers occurred regularly in upland grasslands and Combretum shrublands, whereas riparian and Combretum woodlands were often heavily utilized by most species. There was a strong association between kob, bushbuck and reedbuck density and the several riparian habitats. Those species were nearly always observed in or near riparian vegetation. While waterbucks also were distributed along streams, they were most often in Combretum woodlands near streams. The distributions of reedbucks was patchy because of the scattered occurrences of their preferred riparian grasslands. Within certain vegetation types, and within certain vegetation types, animals also displayed preferences for dense or open vegetation (Fig. 15). All species except bushbuck were rarely found in dense vegetation.

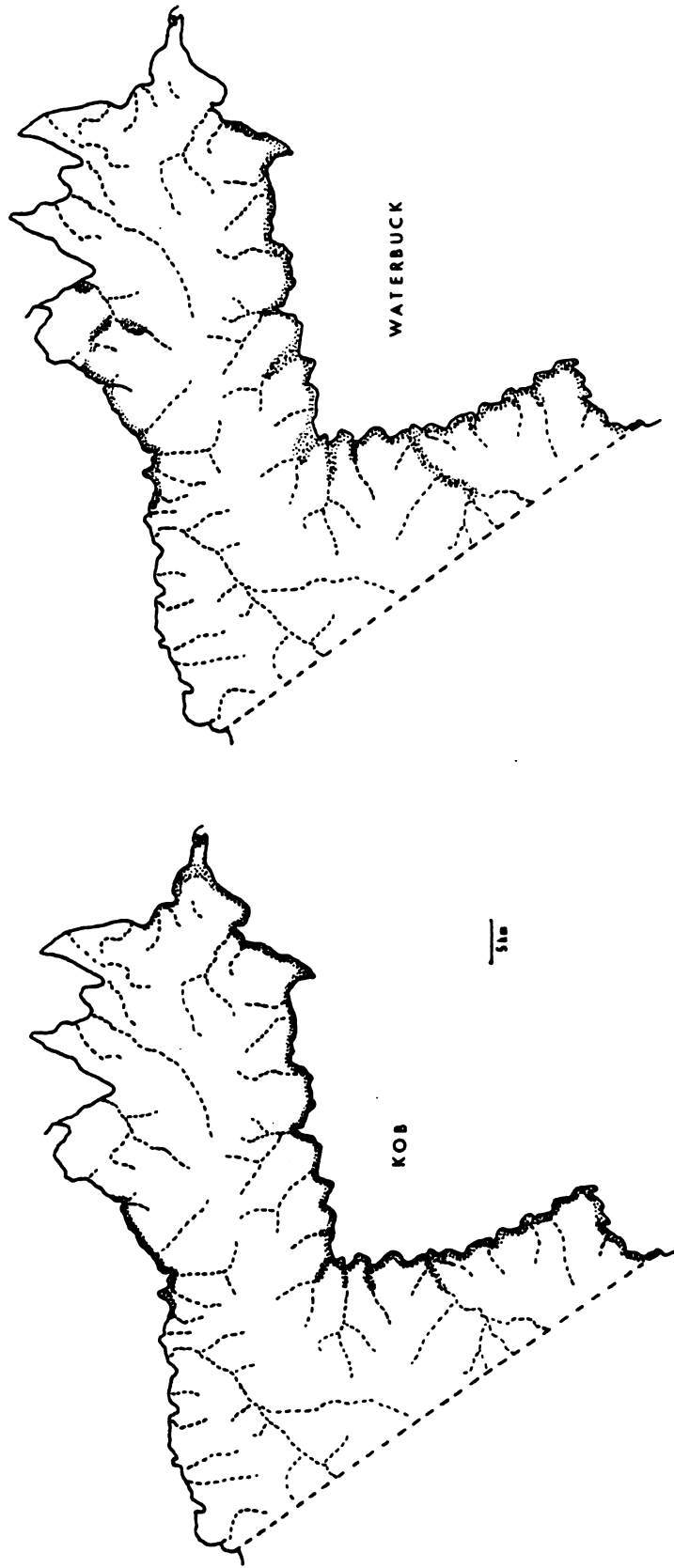


Figure 13a. Distributions of kob and waterbuck in Park W, Niger.

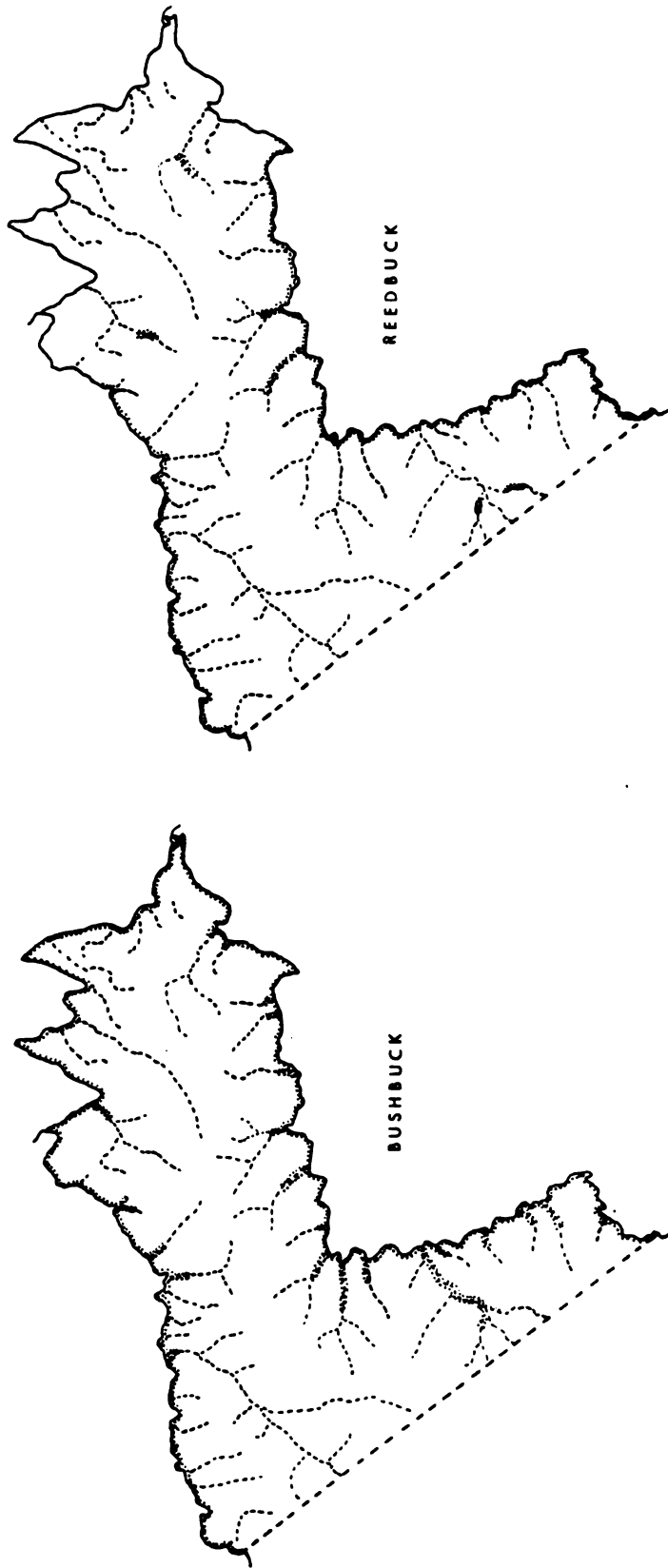


Figure 13b. Distributions of bushbuck and reedbuck in Park W, Niger.

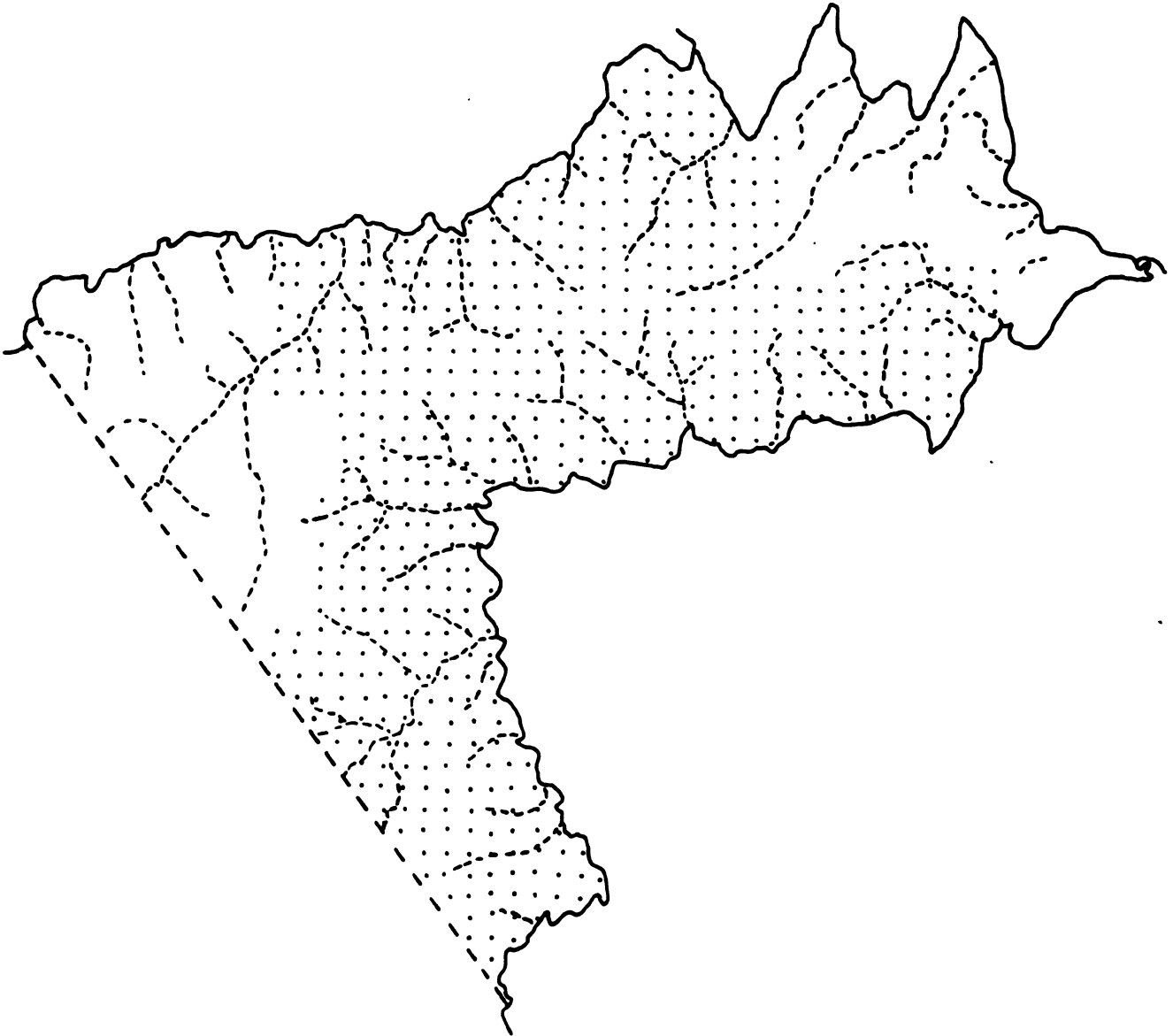
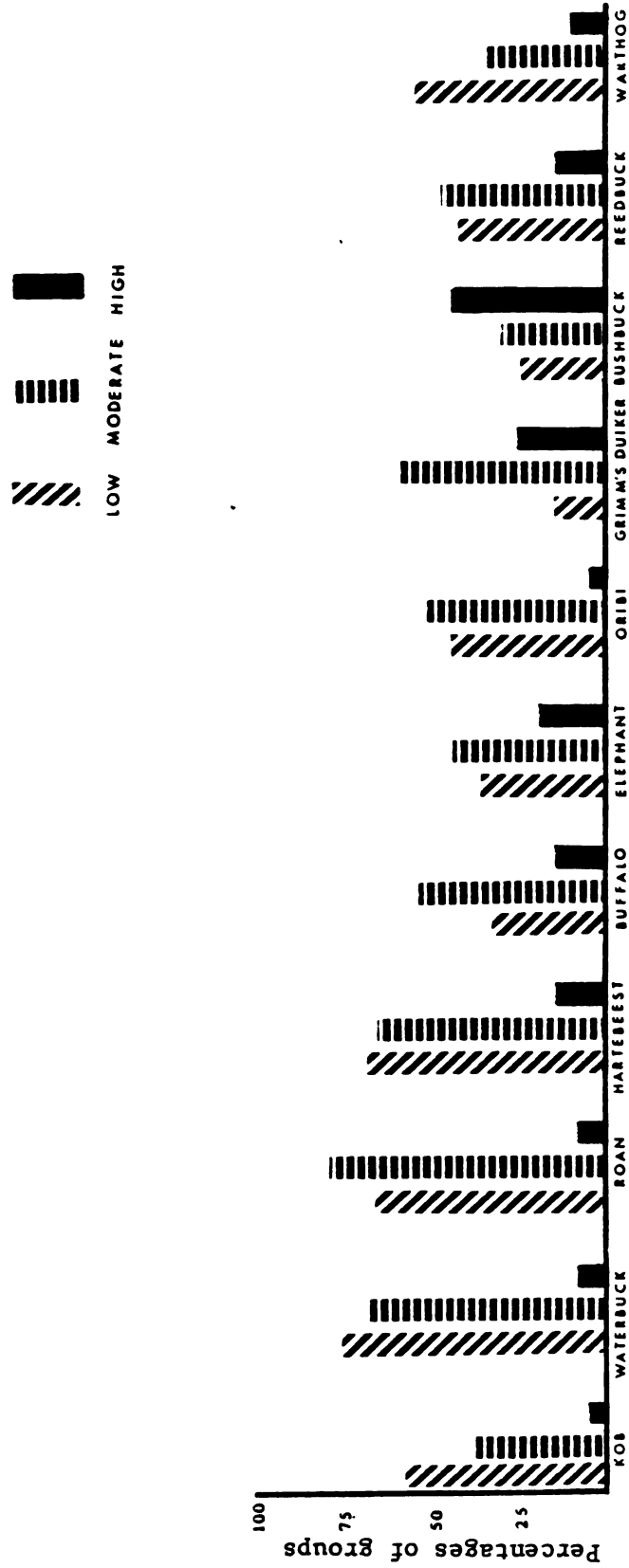


Figure 14. Distributions of buffalo and elephant in Park W, Niger.

Table 5. Selectivity indices of vegetation types of animals encountered during the censuses. A value greater than 1.0 indicates preference, and less than 1.0, partial or total avoidance.

Species	Riparian Grassland	Riparian Forest	Riparian Woodland	Upland Woodland	Shrubland	Upland Grassland
Kob	3.28	2.18	2.53	0.98	0.80	0.00
Waterbuck	0.20	0.00	4.04	1.94	0.00	0.00
Roan	0.00	0.00	3.39	1.64	0.22	3.45
Hartebeest	0.00	0.00	8.09	0.79	0.15	0.00
Buffalo	0.00	0.10	0.46	2.32	0.28	0.00
Elephant	0.00	2.33	0.48	1.96	0.48	0.00
Warthog	9.53	1.48	1.04	1.69	0.52	1.59
Oribi	0.00	0.00	0.69	1.40	0.78	0.00
Grimm's Duiker	0.00	0.00	0.26	0.62	1.36	0.87
Bushbuck	34.50	54.90	4.77	0.33	0.28	0.00
Reedbuck	224.10	3.25	5.12	0.63	0.00	0.00

Figure 15. Percentages of animal groups observed in low, moderate and high density vegetation during the 1976, 1977 and 1978 line transect counts in Park W, Niger.



Hunting and trapping

Hunting and trapping (snaring) of animals, though illegal in the park, frequently occurred along the park's perimeter and sometimes also in the interior. According to park wardens all species were affected, but elephants, buffaloes and the larger antelopes were the most sought-after.

Hunting was observed to have a profound effect on elephants. Following the wounding or death of an elephant, the remaining individuals or herds usually vacated the vicinity for a period. Populations of large mammals were noticeably reduced where hunters and trappers had easy access, and where frequent patrols were not possible (Fig. 16). In prime habitats along the Niger and lower Mekrou Rivers, for example, neither buffaloes nor elephants were observed during the entire study period.

Livestock

Livestock, mainly cattle and sheep, were commonly found along the Tapoa and Niger Rivers (Fig. 16) and less commonly in the interior of the park. The park was readily accessible to herders and their animals, and it contained attractive forage in an otherwise heavily-grazed region. Where villages occurred adjacent to the park, livestock could be found nearby in the park throughout the year. Along the Niger River, the heaviest livestock grazing period was the mid-to-late dry season when forage and water became scarce outside the park. An estimated 3,000 head were present during the February, 1977 aerial survey. Some sections along the Niger River

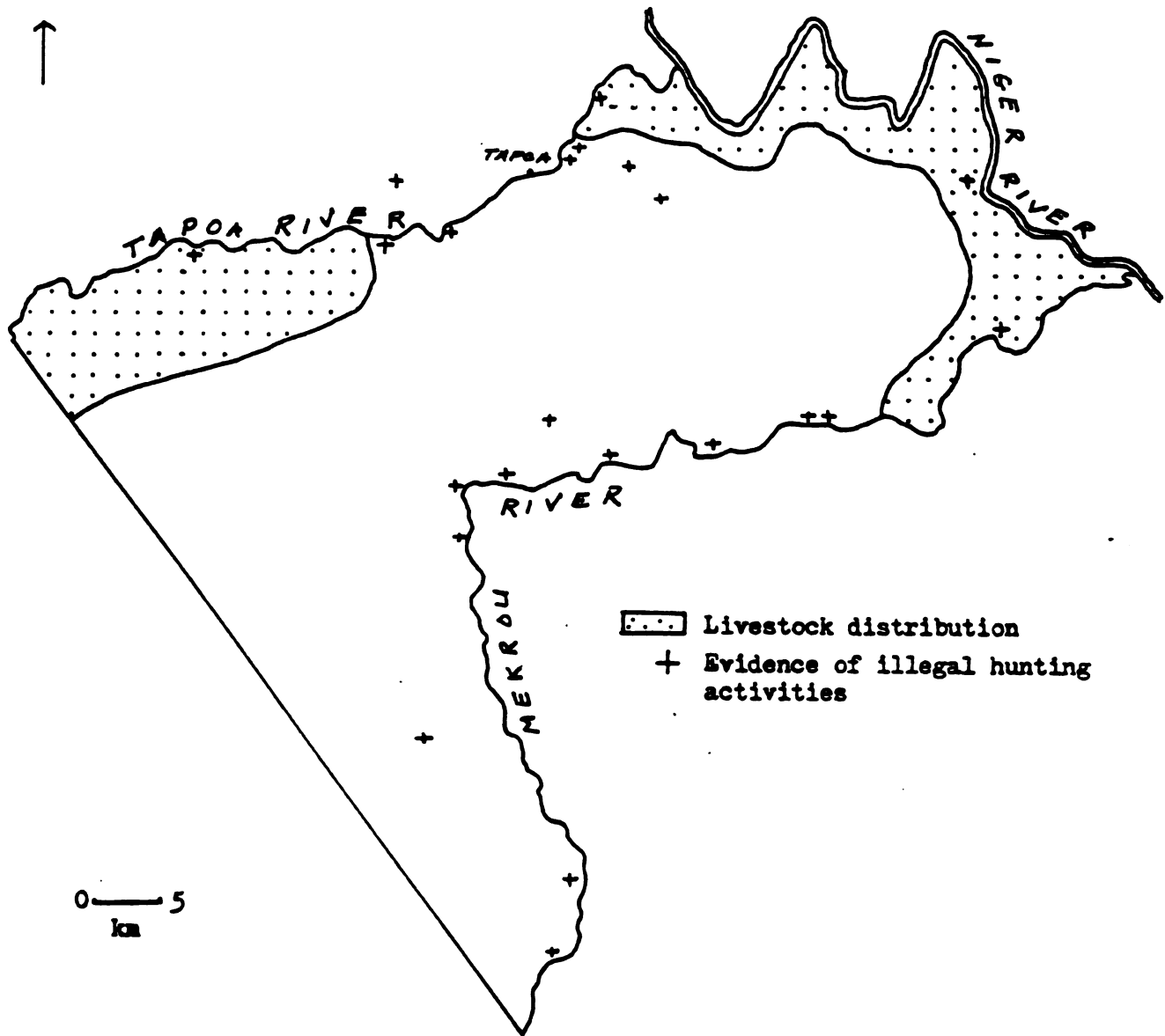


Figure 16. Approximate dry season distributions of livestock and locations of hunting incidences observed in Park W, Niger.

were grazed to the extent that soils were heavily trampled and left nearly devoid of vegetation. In all areas where both livestock grazing and hunting-trapping activities occurred, large mammals were virtually absent.

Water

The distributions of most large mammals appeared to be affected by water availability, but it was not always clear whether water, or the vegetation associated with water most-directly influenced animal distributions. Field observations indicated that all species except warthogs and Grimm's duikers drank water on a frequent basis. Water dependency was important in determining distributions of species associated with riparian habitats, kobs, waterbucks, reedbucks and bushbucks. The seasonal streams and most of the Tapoa River contained no water at the time of most censuses, and therefore, the occurrence of riparian species could be expected only along streams containing water or near waterholes. The degree to which all species required water strongly influenced their distributions, and consequently, population estimates.

A measure of the relationship between animals and water was obtained from the line transect data. Such transects were established perpendicular to streams. Since animal locations along transects were recorded, animal distances from known water sources could be plotted. For the four riparian species, numbers of observations declined rapidly as distance from water increased (Fig. 17). Approximately 90% of kob, bushbuck and reedbuck sightings were within 0.5 km of water. Hartebeests, buffaloes and oribis were also commonly

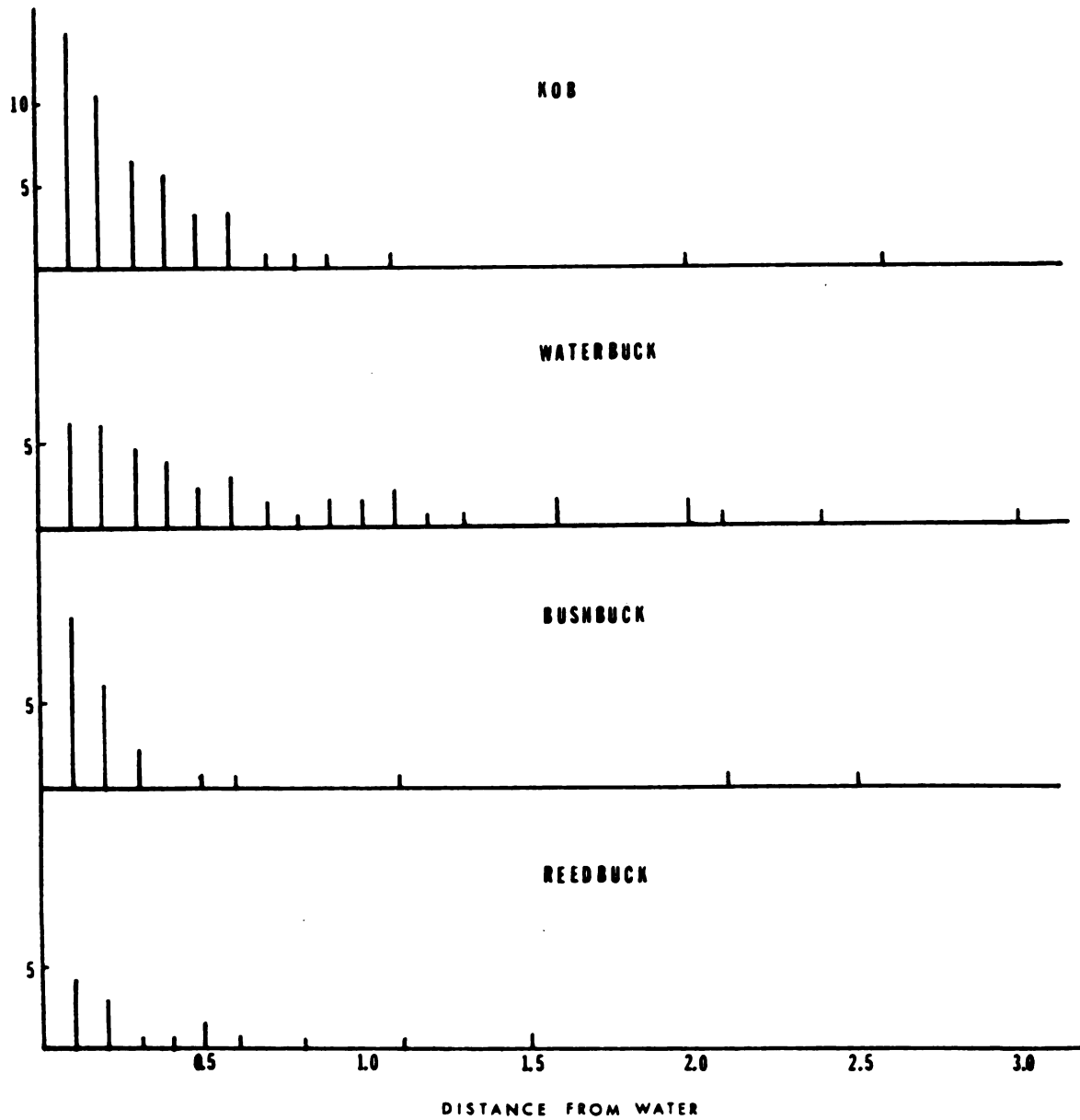


Figure 17. Numbers of observations of kobs, waterbucks, bushbucks and reedbucks made between a watersource and 3.0 km during foot transect counts from 1976-1978 in Park W, Niger.

encountered near water, though they were less restricted by water availability than the four riparian species.

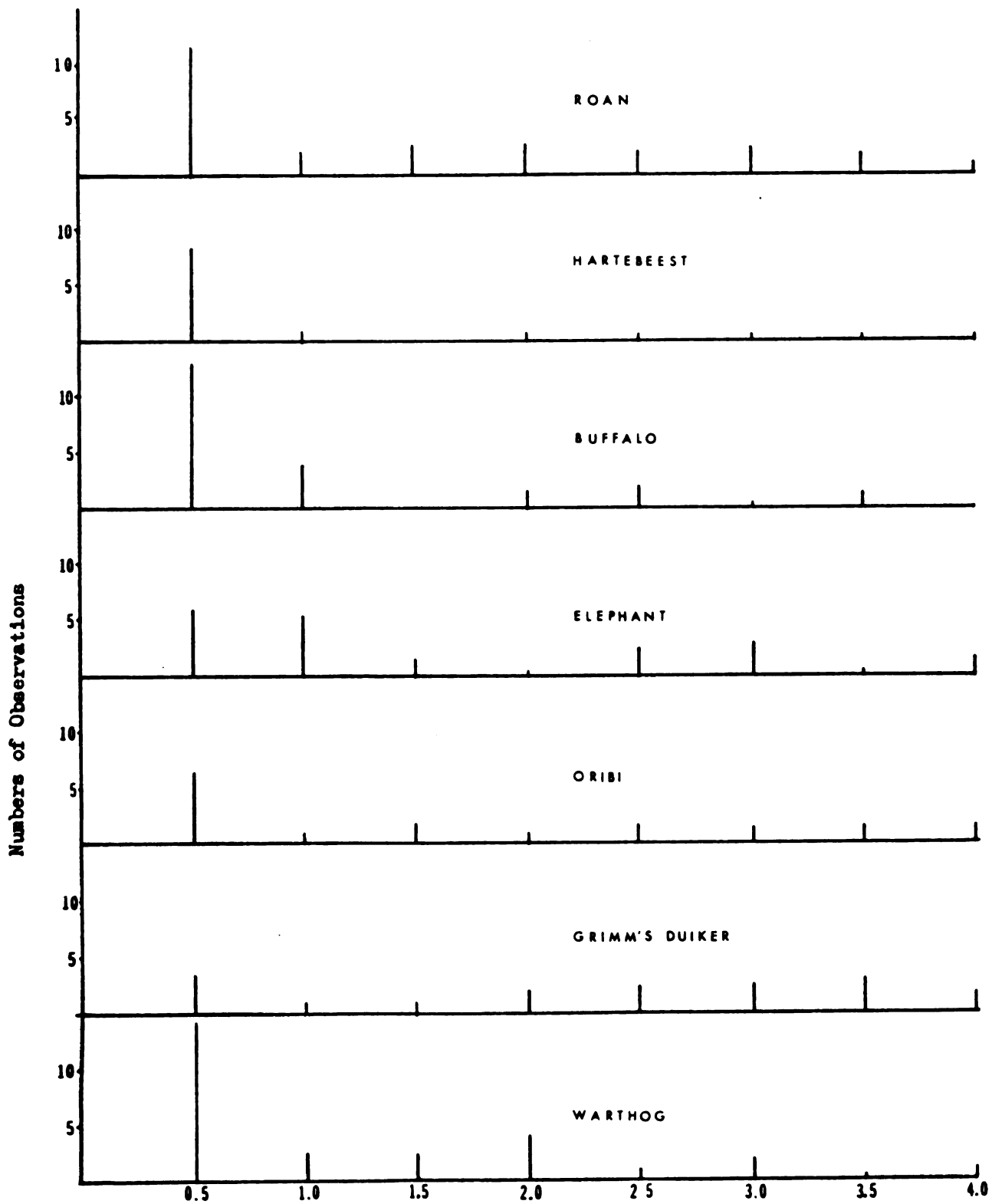
Roans, elephants, warthogs and Grimm's duikers were more evenly distributed along the transects (Fig. 18). This was expected for warthogs and Grimm's duikers since those two species can exist without free-standing water. Elephants and roans, though frequently seen at water, were apparently less likely to remain nearby after watering. Elephant and roan groups were observed as far as 8 km from water.

Bushbucks and reedbucks, though usually found within a few hundred meters of water, were not clearly water-dependent. Several sightings were made at considerable distances from water. Although other investigators have found these species to be in association with water (Odendaal and Bigalke 1979; Wilson and Child 1964; Holsworth 1972), it was not obvious in Park W whether water or vegetation restricted their distributions. Schoen (1971) showed that both species have little physiological adaptations to heat stress. He did not examine their water dependency, but it may be that they can exist for short periods without moisture.

Fire

The importance of fire in influencing animal distribution is probably less than that of vegetation and water, but all species exhibited tendencies to prefer burned or unburned areas. Because visibility was greater in burned areas and because vegetative types were unequally affected by fire, it was difficult to establish unbiased patterns of preference or avoidance for burned areas.

Figure 18. Numbers of observations of 7 large mammal species at $\frac{1}{2}$ km intervals between a watersource and 4.0 km during foot transect counts from 1976-1978 in Park W, Niger.



Yet when percentages of observations were compared with total areas burned each year, certain patterns emerged.

Several species were consistently observed in burned areas in approximately the same proportions as the total area burned, whereas other species were found in greater or lesser proportions (Table 6). Species such as oribi and hartebeest evidently were attracted to the green flush of perennial grasses which occurred after burning whereas bushbuck and reedbuck sought unburned areas. In areas burned during the mid-dry season, herbaceous vegetation was almost totally consumed and the green flush was minimal. These areas were mostly avoided by animals.

For later use in estimating the population sizes of riparian species, their presence or absence along all streams was recorded. Kobs and waterbucks were mainly restricted to the Niger, Mekrou and Tapoa Rivers, whereas buckbucks and reedbucks also were found along many of the small seasonal streams (Table 7). Nearly the entire distance of each stream had been visited during the study, yet bushbucks and reedbucks were not often seen. It is questionable whether these species were indeed absent. They were secretive during the day and flush only when closely approached. They may have been missed. Kobs and waterbucks, conversely, were quite visible and their distributions were more easily verified.

Aerial Counts

During aerial counts, attempts were made at counting all large mammal species. But because of difficulties in spotting the

Table 6. Percentages of the total vegetation burned and percentages of animals occurring in burned vegetation in Park W, Niger.

	1976	1977	1978
Percentage of <u>vegetation burned</u>	68%	76%	71%
<u>Species</u>			
Kob	68	73	81
Waterbuck	58	77	80
Roan	88	83	81
Hartebeest	88	82	94
Buffalo	55	73	68
Elephant	33	48	36
Oribi	93	96	88
Warthog	83	87	72
Grimm's duiker	63	81	82
Bushbuck	38	27	46
Reedbuck	35	43	44

Table 7. Distributions of riparian species along streams in Park W, Niger, as determined from ground surveys in 1976, 1977 and 1978.

Stream	Total kilometers	Estimated kilometers occupied			
		Kob	Waterbuck	Bushbuck	Reedbuck
Mekrou	141	141	141	141	141
Niger	73	15	5	73	+
Tapoa	78	19	19	78	60
Dyerikomoso	8	-	-	1	-
Bata	4	-	?	1	3
Nyafarou	6	2	2	1	2
Gomandi	18	-	-	1	2
Diamonpinga	10	-	-	1	1
Kiba	4	-	-	1	4
Tyeri Fouanou	3	-	-	1	2
Kibatyerou	4	-	-	1	-
Bossegata Gorou	4	-	-	1	-
Boguel	5	-	-	1	1
Bonkogou	9	-	-	1	9
Hari Kwara	1	1	2	2	-
Anana	8	3	6	6	8
Doundou	5	2	2	1	1
Kidyopienaga	3	1	1	1	1
Kargaougwa	9	3	3	1	1
Tyeri	5	-	-	1	-
Kirimkouandi	7	3	3	1	1
Kpenmoana	6	3	3	1	-
Meydyaga	8	3	8	8	8
Samboanli	8	-	-	4	4
Soanda	10	-	-	4	4
Otem Fouanou	6	1	1	1	-
Layar Gorou	5	1	1	1	-
Moussiemou	6	-	-	1	-
Tyalkoey	8	-	-	1	-
Borofwanou	20	-	-	1	-
Ousmandyoari	8	-	-	1	-
Dyodyonga	4	-	-	1	-
Ouskwafwanou	9	-	?	1	-
Filimaze	6	-	-	1	-
Mamasse Gourou	3	-	-	1	-
Tapoa Gorge	2	1	1	1	-
Totals	514	181	198	344	253

- Species absent

? Species present but not on a regular basis

+ Not observed but likely occurs

smaller antelopes, only counts of elephants, buffaloes, roans, hartebeests, waterbucks and kobs were included.

On the basis of information obtained during ground surveys, the park was divided into five strata (Fig. 19). Strata 2 and 4 corresponded to the study area which was intensively sampled by foot and roadside counts.

The results of the aerial survey (Tables 8 and 9) reflected those factors which influence animal distributions. Strata 1 and 3, for example, which were most accessible to herders and hunter-trappers, had considerably lower density estimates of elephants than other strata. And in stratum 3, which is bordered by the Niger River, animals were mainly found along the lower Mekrou River.

Separate estimates were calculated for buffaloes in bachelor male groups and those in breeding herds. Bachelor males occurred in groups of 1 to 11, whereas breeding herds ranged in size from 12 to 160. Density estimates for breeding herds represented group densities. Population estimates can be obtained by multiplying group density by the mean group size, 40.

As a check on whether smaller groups were more likely than large groups to be overlooked by observers, a comparison was made with group sizes determined from ground counts made during the same time period. Comparisons between small, intermediate and large groups revealed that for all species differences between frequencies of group sizes were not significant (Table 10).

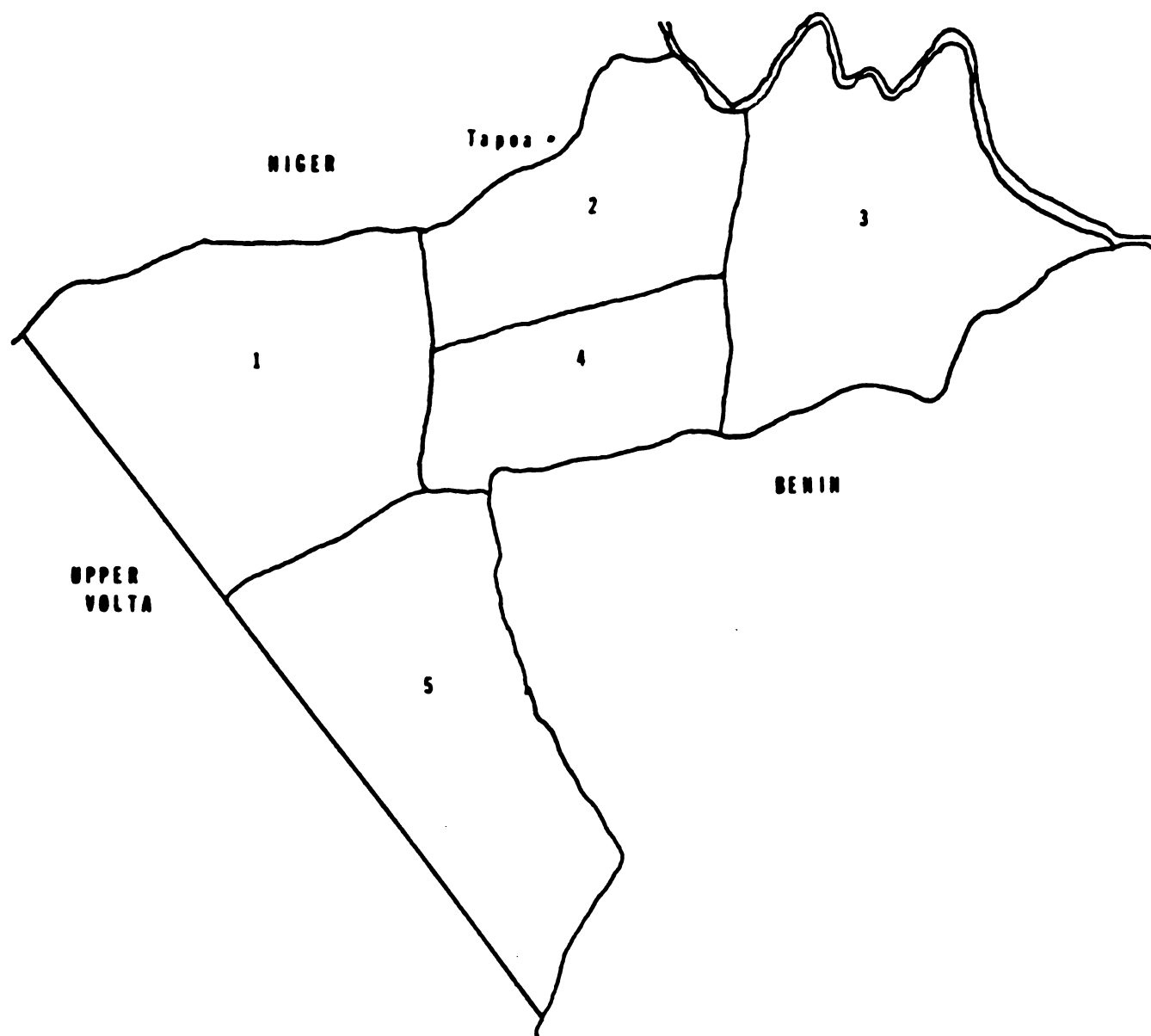


Figure 19. Designated strata used to estimate animal densities from the 1977 aerial transects in Park W, Niger.

Table 8. Density estimates of large mammals in Park W from the park-wide aerial census. Densities are in numbers/km².

Species	Strata					Average Density	Total Population Estimate
	1	2	3	4	5		
Kob	0.000	0.000	0.021	0.089	0.075	0.047	101 ± 68
Waterbuck	0.000	0.164	0.146	0.270	0.439	0.177	402 ± 194
Roan	0.000	0.069	0.020	0.412	0.312	0.120	286 ± 177
Hartebeest	0.173	0.385	0.043	0.081	0.015	0.123	262 ± 152
Buffalo (T)	0.000	0.027	0.021	0.019	0.015	0.020	43 ± 27
Buffalo (B)	0.057	0.069	0.065	0.358	0.222	0.141	295 ± 145
Elephant	0.056	0.290	0.020	1.419	0.733	0.359	768 ± 266

T = Breeding herds of buffalo. Estimates are for herd density.

B = Bachelor herds.

Table 9. Density estimates of large mammals in the central study area from aerial transect counts.

Species	Strata		Total Density	Population Estimate
	1	2		
Kob	1.680	0.724	1.100	53 $\pm$ 40
Waterbuck	0.544	0.800	0.972	103 $\pm$ 66
Roan	0.060	0.571	0.259	141 $\pm$ 87
Hartebeest	0.340	0.090	0.244	133 $\pm$ 146
Buffalo (T)	0.027	0.019	0.024	13 $\pm$ 11
Buffalo (B)	0.069	0.410	0.200	109 $\pm$ 48
Elephant	0.290	1.429	0.728	397 $\pm$ 144

T = Breeding herds of buffalo. Estimates for for herd density

B = Bachelor herds

Table 10. Comparisons of group sizes as determined from ground and aerial counts during February, 1977, in Park W, Niger. Values represent numbers of observations in each group size class.

Species		Group sizes				Chi-square values
		1	2-3	4-6	7+	
Kob	Ground	22	29	5	5	2.70 ns
	Aerial	6	7	4	0	
Waterbuck	Ground	7	18	14	5	0.84 ns
	Aerial	7	11	6	4	
Roan	Ground	21	5	7	15	1.50 ns
	Aerial	12	2	2	4	
Hartebeest	Ground	4	6	5	5	1.18 ns
	Aerial	1	5	4	1	
Buffalo	Ground	4	5	4	7	1.25 ns
	Aerial	10	6	7	15	
Elephant	Ground	2	1	4	9	0.00 ns
	Aerial	3	2	6	15	
Warthog	Ground	5	18	6	0	0.67 ns
	Aerial	1	5	3	0	

Results of the study area and park-wide surveys

During the preliminary foot transect survey in the central study area, only 8 of 14 large mammal species were observed (Table 11). Because of the small sample sizes, variances and coefficients of variation were large (Table 12). Required sample sizes projected from this survey were extremely large, even at the 20% coefficient of variation level. Subsequent observations in the park indicated that topi, red-fronted gazelle and red-flanked duiker occurred in very low numbers. They were omitted from further consideration in this study.

During the 1977 survey, although sampling efforts were doubled and all species were observed, the numbers of observations of each species were still small (Table 11). In spite of the large number of transects, required sample sizes were unrealistically large. The positioning of transects parallel to streams resulted in a relatively insignificant increase in sightings of riparian species.

In 1978, the study area was nearly saturated with foot transects, but numbers of observations were still small for most species (Table 11). Several factors were responsible for the few encounters. First, relative densities of animals were low, especially in upland woodlands and shrublands. Second, the uneven distribution of animals affected the sampling intensity of the different species. Since some species were widely distributed and others clumped near water, efforts to obtain estimates for all species required that all areas be sampled and not just the high density areas. Third, visibilities in all vegetation types were limited over most of the park. In many areas, observers could see no more than 50 m and often less.

Table 11. Numbers of observations made during the 1976, 1977 and 1978 foot transect counts in the central study area in Park W, Niger.

Species	1976		1977		1978	
	Number of Observations	Total No. Observed	Number of Observations	Total No. Observed	Number of Observations	Total No. Observed
Kob	2	6	5	13	6	16
Waterbuck	3	10	3	7	5	10
Roan	3	20	6	17	5	15
Hartebeest	0	-	1	6	4	22
Buffalo	3	13	3	6	4	7
Elephant	0	-	2	46	4	40
Oribi	2	4	6	8	7	17
Grimm's duiker	2	2	5	5	10	11
Bushbuck	1	1	4	4	10	14
Reedbuck	0	-	1	2	4	8
Warthog	4	15	5	18	5	11

Table 12. Density estimates, coefficients of variation and required sample sizes for foot transect counts made in the central study area in 1976, 1977 and 1978 in Park W, Niger.

Species	Density*	1976			1977			1978				
		cv	ss	L	Density	cv	ss	L	Density	cv	ss	L
Kob	1.316	61.5	19	722	0.877	36.3	17	528	1.429	47.8	34	221
Waterbuck	0.877	57.4	27	670	0.772	34.8	9	484	0.893	35.0	15	119
Roan	0.138	58.1	25	641	0.210	112.1	188	5017	0.124	48.4	29	1097
Hartebeest	* *				0.053	110.7	31	4901	0.074	63.0	40	1856
Buffalo	0.215	54.7	15	570	0.062	72.9	40	2123	0.061	55.6	31	1445
Elephant	* *				0.035	37.0	7	547	0.112	56.2	32	1759
Oribi	0.157	34.9	6	231	0.140	41.3	26	682	0.238	53.6	50	1345
Grimm's duiker	0.271	64.6	10	792	0.487	34.8	15	484	0.527	54.4	81	1384
Bushbuck	0.714	98.8	24	1854	1.600	86.8	75	3011	2.250	19.2	9	52
Reedbuck	* *				1.200	110.7	31	4902	1.183	35.7	13	86
Warthog	0.369	59.6	36	675	0.211	25.2	8	254	0.210	41.9	22	925

*Density is in numbers/km²

cv = coefficient of variation

ss = required sample size for a cv of 20%

L = required transect length for a cv of 20%

* * = none observed during the survey

Fourth, individuals of most species tended to occur in groups. Encounters with groups were less likely than if animals occurred singly. The combination of these four factors translated into low probabilities of encounters with groups.

Though numbers of observations were small, groups observed per kilometer walked were consistent between years. Density estimates, therefore, were relatively similar for the three years.

The results of the 1978 park wide survey were similar to those in the central study area with respect to distance and angle measures and density estimates. The number of groups counted were roughly proportional to the distances walked. The number of observations of any species, though, did not exceed 36 (Table 13). The recommended minimum number of observations for line transect estimators is 40 (Burnham et al. 1980). This figure was impossible to attain for many species unless the park had been saturated with transects. Furthermore, for species which occurred in large groups such as roans and hartebeests, the majority of the population would need to be counted.

Because the number of observations for any one survey was small, observations were pooled into a single sample for the purpose of evaluating estimators (Table 14). The objective was to detect patterns and relationships between estimators with a larger data set, because estimators perform better with larger numbers of observations. Following these analyses, individual surveys were reviewed to determine whether general patterns found for larger data sets held true for the smaller number of observations encountered during actual surveys.

Table 13. Results of the 1978 park-wide foot transect count in Park W, Niger.

Species	Number of observations	Total No. observed	Density	cv	ss	L
Kob	25	72	1.240	26.3	114	146
Waterbuck	17	64	1.402	38.4	181	283
Roan	19	46	0.231	39.6	176	2046
Hartebeest	8	51	0.025	19.5	-	-
Buffalo	10	19	0.120	42.6	86	2300
Elephant	6	51	0.057	43.6	208	1766
Oribi	21	38	0.310	27.4	90	1014
Grimm's duiker	23	25	0.845	31.2	63	1390
Bushbuck	17	23	3.151	10.9	-	-
Reedbuck	20	30	4.842	41.6	112	341
Warthog	36	92	0.449	42.3	411	3408

Density is in km^2

cv = coefficient of variation in percent

ss = required sample size for a 20% coefficient of variation

L = required transect length for a 20% cv

Table 14. Basic measures of the combined foot transect counts of 1976, 1977, and 1978 in Park W, Niger. Distances are in meters.

Species	Sample size	Mean perpendicular distance	Mean disappearing distance	Mean sighting distance	Mean angle
Kob	63	30.04 *	99.70	57.46	33.37
Waterbuck	61	30.15	96.41	71.64	27.30
Roan	64	37.52	101.60	83.08	30.84
Hartebeest	27	44.10	115.72	80.40	35.19
Buffalo	60	29.15	92.40	58.97	33.07
Elephant	12	39.53	115.00	73.50	34.58
Oribi	70	32.06	95.04	66.77	30.14
Grimm's duiker	66	12.08	48.05	23.15	34.24
Bushbuck	50	13.34	48.40	22.54	40.04
Reedbuck	50	15.30	53.14	25.40	41.28
Warthog	64	32.60	77.80	57.60	36.60

*meters

Evaluations of estimators

A comparison of density estimates from the 18 estimators (Table 15) demonstrates, as also found by other investigators, that they may give widely differing results. Inferences about estimates of population density may vary greatly, depending on which estimator is selected. On closer examination of the estimators, however, certain patterns emerge.

Among the estimates based on perpendicular distances, the Dasmann-Mossman and Webb estimators consistently gave the highest estimates or nearly so. The Hahn estimator, conversely, nearly always gave the lowest estimate. Several estimators typically gave estimates which were between the highest and lowest ones, including the Hemingway Normal, Quadratic, Triangular, Generalized Exponential, Polynomial, Fourier Series and all those estimators based on grouped data.

Among the radial estimators, only the Geometric and King estimators gave estimates which were consistently between the high and low estimates. Estimates from the Exponential estimator were always higher than other radial estimators and all perpendicular distance estimators except the Dasmann-Mossman. In general, the rank relationship between radial estimators was in ascending order: King < Geometric < Hayne and Modified Hayne < Exponential. The Hayne and Modified Hayne estimators both yielded consistently high estimates.

There was a strong tendency for estimators based on grouped data to give similar values which were moderate in ranking. For kob, the overall range of estimates was roan 3.16 to 10.88/km², whereas for estimates based on grouped data, the range was 6.36 to 7.35/km².

Table 15. Comparisons of density estimates from pooled foot transect counts in Park W, Niger, from 1976-1978.

Estimators	Kob	Water- buck	Roan	Harte- beest	Buffalo	Ele- phant	Oribi	Grimm's duiker	Bush- buck	Reed- buck	Warthog
<u>Perpendicular distances</u>											
(untruncated, ungrouped)											
Exponential	10.32**	7.48	8.40	2.95	10.12	1.39	10.76	26.91	14.46	14.56	9.65
Hemingway Normal	6.92	5.05	5.93	1.90	6.59	0.98	7.24	18.41	9.11	10.49	5.94
Quadratic	5.43	5.35	5.05	5.68	5.19	4.64	5.39	6.62	4.05	6.86	5.87
Triangular	6.22	4.52	4.40	7.25	5.42	3.30	5.51	7.05	4.24	7.66	6.50
Generalized Exp.	6.02	4.19	3.77		6.59	0.89	6.10	15.14	9.69	7.17	
Polynomial	3.72	3.68	4.42	4.73	5.48	1.50	5.19	7.09	3.70	8.65	5.27
Fourier Series	6.38	4.63	3.34	0.85	6.46	0.93	6.69	12.52	10.39	7.61	6.66
Dassman & Mossman	10.49	10.12	8.53	3.06	10.29	1.52	10.92	27.32	14.76	14.85	9.82
Webb	9.97	6.98	7.51	2.91	9.32	1.44	10.44	26.72	13.58	13.56	9.32
(untruncated, grouped)											
Kelker	6.38	3.97	3.77	1.54	6.15	*	6.29	13.51	9.42	5.91	5.90
Eberhardt-Cox	6.93	3.87	3.09	1.54	6.53		6.57	13.51	10.93	5.02	6.51
Splined	6.38	4.08	4.44	1.54	6.15		6.29	13.51	9.42	6.79	5.90
Polynomial	6.49	3.83	3.77	1.82	6.70		6.12	11.39	10.81	4.50	6.60
Quadratic	6.05	4.13	4.32	1.50	5.91		6.32	14.26	8.52	7.05	5.31
Triangular	6.98	5.01	5.46	1.74	6.73		7.45	17.91	9.33	9.30	5.80
<u>Disappearing dist.</u>											
Hahn	3.16	2.38	3.15	1.17	3.25	0.52	3.68		4.07	6.80*	4.11

Table 15. (cont'd.)

Estimators	Kob	Water- buck	Roan	Harte- beest	Buffalo	Ele- phant	Oribi	Grimm's duiker	Bush- buck	Reed- buck	Warthog
<u>Radial distances</u>											
Geometric	6.12	3.68	4.23	1.85	6.00	0.87	5.74	18.32	9.87	9.67	7.30
Hayne Const. Rad	6.95	4.64	4.72	2.03	7.20	0.92	6.50	29.09	11.42	10.62	14.10
Modified Hayne	6.82	5.39	4.98	1.88	7.13	0.87	1.99	27.77	8.94	7.93	12.50
Exponential	10.88	6.35	7.64	3.30	10.09	1.57	10.41	28.29	17.29	17.72	11.02
King	5.48	3.20	3.85	1.68	5.09	0.82	5.24	14.26	8.73	8.95	5.56
<u>Perpendicular distances</u> (truncated, ungrouped)											
Exponential	5.50	4.61	0.19	1.32	8.07	*	5.76	15.20	10.68	0.28	8.66
Quadratic	5.44	5.56	5.12	3.97	5.41		5.66	6.90	4.19	7.33	6.05
Triangular	5.35	4.62	4.27	1.22	5.93		5.65	8.43	4.35	9.47	6.44
Polynomial	4.62	4.02	4.21	1.20	4.14		4.65	9.05	4.66	10.31	5.60
Fourier Series	6.72	4.64	4.18	1.27	6.58		6.64	12.62	10.91	6.32	6.96
(Truncated, grouped)											
Hemingway Normal	7.64	5.30	4.64	2.08	7.91	*	8.04	17.89	10.84	5.52	7.40
Quadratic	6.61	4.43	4.24	1.66	6.66		6.86	15.09	9.42	6.79	6.18
Polynomial	6.75	4.35	4.10	1.94	7.30		6.76	12.64	10.91	6.99	6.77
Kelker	6.38	3.97	3.77	1.54	6.15		6.29	13.51	9.42	5.91	5.90
Eberhardt-Cox	6.94	3.87	3.09	1.54	6.53		6.57	13.51	10.93	5.02	6.51
Splined	6.38	4.08	4.44	1.66	6.15		6.76	12.64	10.91	6.99	6.77

*Too few observations to group the data.

**Densities are in numbers/km².

As an aid for evaluation, density estimates were ranked from 1, the lowest estimate, to the highest (Table 16). Though this did not necessarily reveal information concerning bias, it did aid in exposing patterns among estimators. For each species, there was a wide range of values. There also tended to be a group of estimates with similar values and which were approximately between the highest and lowest values. Examples of this range in values have been shown for buffalo, waterbuck and kob by plotting frequency histograms of density estimates (Fig. 20). For those species, there is a clumping of estimates near some central value and several estimates which are somewhat higher or lower. A plot of density estimates and confidence limits for kob further illustrates this range of values (Fig. 21). The lowest and highest values are markedly below and above the cluster of moderate values. Unfortunately, it could not be assumed that the median value had the least bias. In reality, none or several of the values between the highest and lowest may have relatively small bias.

Based on these results, estimators could be further categorized to illustrate relationships between density estimates. Values of low (L), low to moderate (L-M), moderate (M), moderate to high (M-H) and high (H) were assigned to estimates based on their values relative to other estimates (Table 17).

It is evident from Table 17 that not all estimators are consistently low, moderate or high. Among estimators based on ungrouped data, only the Dasmann-Mossman, Webb and Exponential estimators, are always high, the Hahn estimator always low, and the Hemingway-Normal, Generalized Exponential, Geometric and Fourier Series nearly

Table 16. Rankings of density estimators for pooled foot transect counts in Park W, Niger.

Estimator	Species											Total
	Water- buck	Roan	Harte- beest	Buffalo	Ele- phant	Oribi	Grimm's duiker	Bush- buck	Reed- buck	Warthog		
<u>Perpendicular Dist.</u>												
Exponential	6	11	1	17		6	11	12	1	15	81	
Hemingway Normal	14	15	18	10		16	14	7	17	5	117	
Quadratic	3	19	17	4		7	2	2	11	6	89	
Triangular	4	12	12	5		5	3	3	14	8	68	
Generalized Exp.	7	8	5	11		8	10		10	12		
Polynomial	2	6	9	2		2	4	4	16	3	52	
Fourier Series	11	13	8	9		12	5	11	6	11	91	
Dassman & Mossman	19	21	21	20		20	16	18	20	17	188	
Webb	18	20	19	18		18	15	17	19	16	175	
(Grouped data)												
Kelker	9	5	4	7		9	7	9	5	4	65	
Eberhardt-Cox	15	4	2	8		11	7	9	5	4	80	
Splined	9	7	13	7		9	7	9	7	4	78	
Polynomial	12	9	7	15		13	6	14	1	10	107	
Quadratic	10	10	11	12		14	9	8	8	7	96	
Triangular	17	16	14	16		17	12	13	4	14	137	
<u>Disappearing Dist.</u>												
Hahn	1	1	3	1		1	1	1	2	1	15	
<u>Radial distances</u>												
Geometric	8	2	10	9		3	13	10	15	13	89	
Hayne Const. Rad.	16	14	15	13		10	19	16	18	20	155	
Modified Hayne	13	18	16	10		15	17	6	12	19	139	
Exponential	20	17	20	17		19	18	19	21	18	188	
King	5	3	6	8		3	8	5	13	2	56	

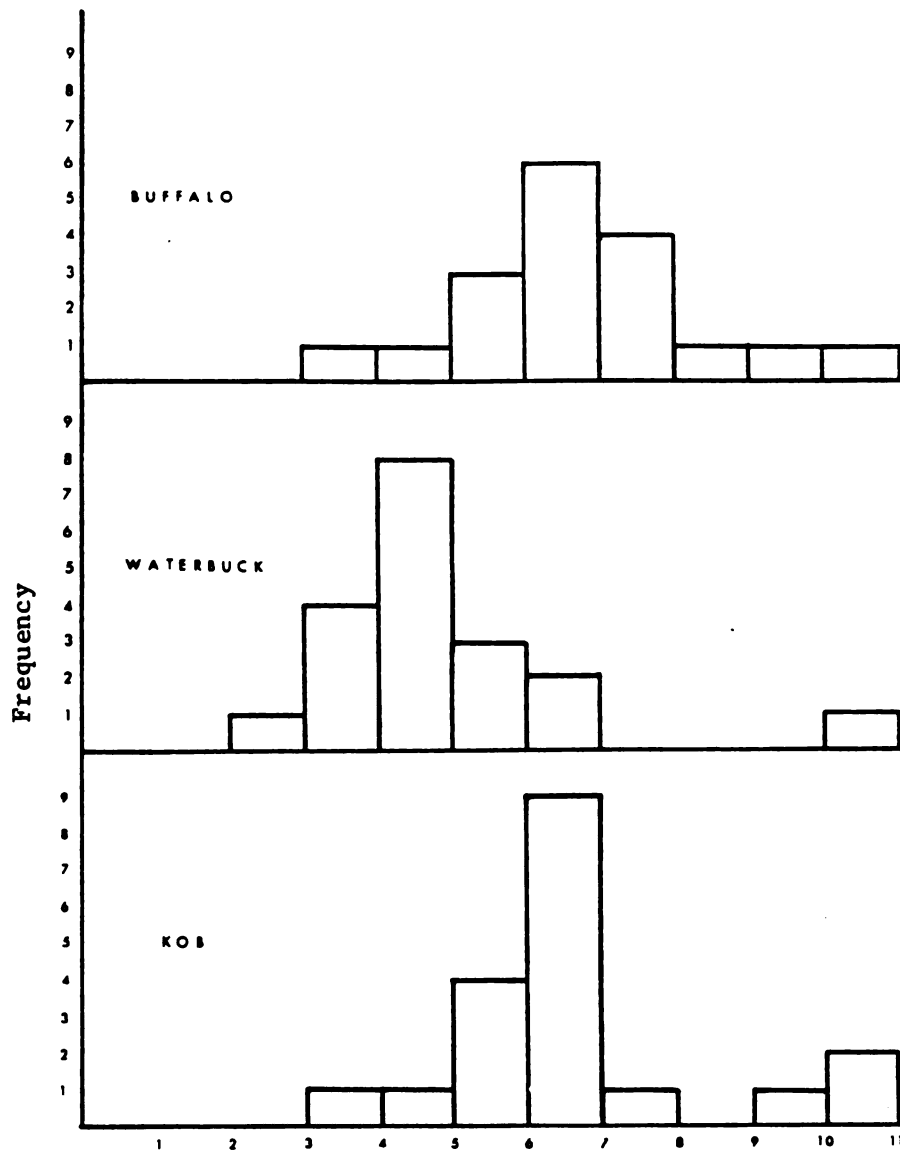


Figure 20. Frequencies of density estimates for buffalo, waterbuck and kob as based on the pooled foot transect data.

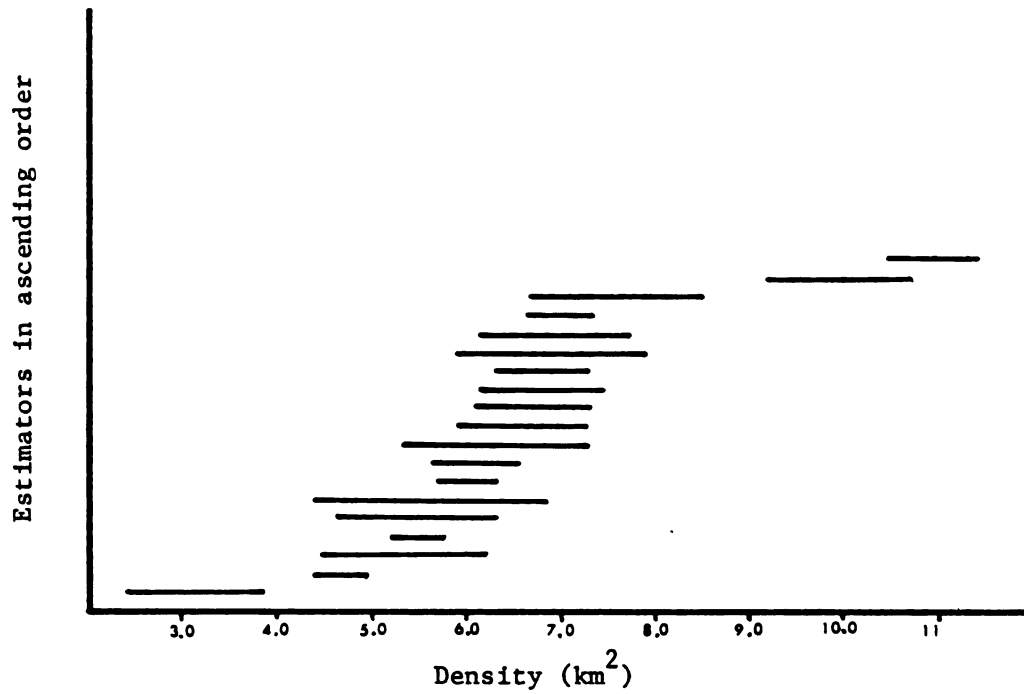


Figure 21. Density estimates and confidence limits for kob from the pooled foot transect data set in ascending order.

Table 17. Relative values of density estimates from the pooled foot transect data for foot transects in Park W, Niger.

Estimator	Kob	Water- buck	Roan	Harte- beest	Buffalo	Ele- phant	Oribi	Grimm's duiker	Bush- buck	Reed- buck	Warthog
Exponential	L-M	M	L	L	H	H	M	M	M	L	H
Hemingway Normal	M-H	M	M	M	M-H	M	H	M-H	M	M	M-H
Quadratic	M	M-H	M-H	H	M	H	M	L	L	M	M
Triangular	M	M	M	L	M	L	M	L	L	M-H	M
Generalized Exp.	M	M	M	M	M	M	M	M	M	M	M
Polynomial	L	M	M	L	L	L	L-M	L	L	M-H	M
Fourier Series	M	M	M	L	M	M	M	M	M	M	M
Dasmann-Mossman	H	H	H	H	H	H	H	H	H	H	H
Webb	H	H	H	H	H	H	H	H	H	H	H
Kelker	M	M	M	M	M	M	M	M	M	M	M
Eberhardt-Cox	M	M	L	M	M	M	M	M	M	M	M
Splined	M	M	M	M	M	M	M	M	M	M	M
Polynomial	M	M	M	M	M	M	M	M	M	M	M
Quadratic	M	M	M	M	M	M	M	M	M	M	M
Triangular	M	M	M	M	M	M	M	M	M	M	M
Hahn	L	L	L	L	L	L	L	L	L	L	L
Geometric	M	L-M	M	M	M	M	M	M	M	M	M
Modified Hayne	M	M	M-H	M	M	M	L	H	M	M	M
Hayne Const Rad.	M	M	M	M	M	M	M	H	H	H	H
Exponential	H	H	H	H	H	H	H	H	H	H	H
King	M	L	M	M	L-M	M	L-M	M	M	M	L-M

always moderate. All estimators based on grouped data are consistently moderate. The relative values of the remaining estimators are considerably less consistent. Estimates from the Exponential (x) estimator, for example, are very low or very high for several species.

The effects of truncation on density estimates varied from none to great. Only the Exponential, Quadratic, Triangular, Polynomial, Fourier Series, Kelker, Spline and Eberhardt-Cox estimators are influenced by truncation (Gates 1981). The exponential estimator was very sensitive to truncation. The truncated estimate was usually much lower and more in-line with other estimators. The Splined, Kelker and Eberhardt-Cox estimators were virtually unaffected by truncation. Density estimates from the Fourier Series, Quadratic and Polynomial estimators increased slightly with truncation, while estimates of the Triangular estimator were decreased by a large amount. The overall effect of truncation was to raise or lower untruncated estimates to more moderate values.

Comparisons with other studies

For those estimators which were consistently higher or lower than others, it was of interest to know whether they over- or underestimated population densities. Fortunately, there have been several simulation and field studies in which the population size was known (Table 18). Several estimators in those studies consistently exhibited negative or positive bias. The Webb and Exponential estimators, which yielded the highest estimates from the pooled data, were found in other studies to overestimate true population sizes. The King estimator usually gave low estimates in this study

Table 18. Tendencies of estimators toward positive or negative bias as determined from studies on populations of known size.

Estimator	Literature Source						
	1	2	3	4	5	6	7
Exponential, Gamma				+	+	+	+
Hemingway Normal			0	0			
Quadratic			0				
Generalized Exponential			0				0
Polynomial			0				
Fourier Series			0				
Dasmann and Mossman -				+			
Webb				+	+	+	
Kelker		-		0	0,+		
Hahn		-		+			
Geometric						-	+
Hayne				+,0			
Exponential, Gamma				+	+		
King				-	-	-	

1. Dasmann and Mossman (1962)
2. Hirst (1969)
3. Burnham et al. (1980)
4. Evans (1975)
5. Robinette et al. (1974)
6. Gates (1969)
7. Quinn (1977)

- = negative bias
 0 = small bias, either direction
 + = positive bias

and in several independent investigations was found to be negatively biased. Most other estimators examined displayed little bias or were not consistent in the direction of bias.

The prediction by Kranz (1973) and the results of a field study by Evans (1975) indicated that the Hahn procedure overestimated densities were not confirmed by this study. For each species in Park W, the Hahn estimator gave estimates which were below all others, often by a considerable amount.

Goodness-of-fit tests to detection functions

A basic requirement for parametric estimators is that the detection function of perpendicular or radial distances closely match that of a known distribution. A calculated value that is larger than the suprema (critical value) indicates that the observed distribution significantly differs from the expected. If the underlying distribution is significantly different from the expected, the estimator based on that expected distribution may be biased.

Goodness-of-fit tests applied to the detection functions revealed that for each species there were several distributions which were not significantly different from the detection function (Table 19). For perpendicular distances, fitting the exponential distribution with $\alpha = 1.0$. In several cases, it provided the best fit. Values for the half-normal distribution were all well below the suprema for each species, indicating that the detection functions were all approximately half-normal. Fits to the generalized exponential distribution were not significantly different for seven species, but highly significantly for four others. These poor fits,

Table 19. Goodness of fit tests to distributions for pooled foot transect data.

Distributions	Kob	Water- buck	Roan	Harte- beest	Buffalo	Ele- phant	Oribi	Grimm's duiker	Bush- buck	Reed- buck	Warthog
<u>Radial estimators</u>											
Gamma, a variable	.084	.808*	.092	.154	.125	.215	.098	.087	.090	.081	.075
Gamma, a = 2	.131	.178*	.206*	.240	.084	.263	.200	.091	.156	.207*	.080
<u>Perpendicular estimators</u>											
Half-Normal	.100	.078	.170	.232	.098	.126	.081	.110	.167	.193	.100
Triangular	.132	.116	.112	1.606*	.215*	.969*	.172*	.437*	.457*	.111	.091
Gamma, a = 1	.159	.132	.201*	.208	.117	.099	.277*	.154	.180	.226*	.069
Generalized exp.	.080	.054	.984*	.963*	.098	.142	.054	.096	.980*	.980*	.096
Gamma a variable	.044	.100	.117	.193	.074	.166	.089	.102	.131	.108	.056
<u>Non-parametric goodness of fit tests</u>											
Quadratic	.213*	.184*	.250*	.278*	.255*	.628*	.142	.089	.059	.478*	.188*
Polynomial	.048	.278*	.277*	.044	.249*	.068	.135	.050	.016	.410*	.186*
Test Criterion	.173	.176	.171	.267	.177	.410	.164	.169	.194	.194	.171

* Significant at the 95% confidence level.

however, may reflect problems encountered with the program LINETRAN rather than the data. Tests to the Triangular distribution indicated poor fits in five of the 11 species.

The usefulness of the Quadratic and Polynomial estimators was indicated by goodness-of-fit tests against their respective equations. Values for the quadratic distribution were non-significant for three of the 11 species, though several of these had values only slightly above the suprema. Similarly, fits to the polynomial distribution were non-significant for only five of the 11 species.

Goodness-of-fit tests with radial distances indicated that distributions for all species were exponential when the α = variable was used. For $\alpha = 1.0$, fits to four of the species were significantly different from the K-S criterion.

Goodness-of-fit tests were useful for explaining the variability of some estimators such as the Triangular and Quadratic. The wide range of density estimates for the Triangular estimator, for example, was probably due to the lack of triangularity of the detection function. For hartebeest, this estimator yielded an estimate considerably higher than all others. The goodness-of-fit test to the triangular distribution for hartebeest was significantly different from the critical value. Similar variability in density estimates was found for Grimm's duiker and bushbuck when poor fits were obtained for the triangular distribution. When goodness-of-fit tests to the triangular were non-significant, as with warthog, estimates were moderate.

These results reflected the general pattern for many estimators, in that when the goodness-of-fit tests indicated close agreements, the estimator based on that distribution tended to yield moderate density estimates.

The value of goodness-of-fit tests in selecting a single best parametric estimator appeared to be limited. For each species, usually several distributions were not significantly different from the detection function of a species. With kob, for example, fits to the half-normal, triangular, exponential and generalized exponential distributions were all below the test criterion. The estimators based on these distributions, however, gave different estimates ranging from 5.50 to 7.63/km². The fit to the exponential distribution for radial distances and the polynomial also gave non-significant results. While estimates from all those estimators were moderate in ranking and between the highest and lowest estimates, certainly not all of these estimates are unbiased. These estimates were relatively close to each other, but different enough to be of ecological importance. Thus, the value of goodness-of-fit tests as a basis for selecting an estimator is questionable. This is especially true for the Exponential estimator for radial distances, which was higher than most other estimators whether or not the detection function was exponential. It could only be concluded that if a goodness of fit tests indicates a good fit, the estimator based on that distribution will give a moderate but not necessarily unbiased estimate.

Tests of angle measures

Goodness-of-fit tests to the Cosine θ distributions were significant for all species except roan (Table 20), indicating that angle measures were not made uniformly over the sighting radius. This may be attributed to observer's methods of searching for animals along the transect. They concentrated on the area directly in front of them. If so, fewer observations would be made at the larger angles.

Table 20. Values for tests to determine the applicability of radial estimators for pooled foot transect data in Park W, Niger.

Species	Critical value:	Cosine Theta 12.59	Tests	
			$E(\theta) = 32.7$ 1.96	$E(\sin \theta) = 0.5$ 1.96
Kob		24.67**	0.24	1.38
Waterbuck		24.02**	1.59	1.12
Roan		5.59	0.69	0.35
Hartebeest		*	0.60	1.37
Buffalo		23.60**	0.13	1.23
Elephant		*	0.30	0.81
Oribi		19.87**	0.99	1.82
Grimm's duiker		46.39**	0.47	1.76
Bushbuck		19.47**	2.41**	3.51**
Reedbuck		23.9**	2.81**	3.91**
Warthog		13.96**	1.45	2.67**

*Too few observations were available to fit the Cosine Theta distribution.

** Significant at the 95% level.

Despite the few observations made at the larger angles, mean sighting angles were close to the theoretical 32.7° except for reedbuck and bushbuck (Table 20). Similarly, the test for whether the $\sin \theta = 0.5$, was significant for only bushbuck, reedbuck and warghog. These results indicate that radial estimators are useful for most species.

Hahn estimator

Compared to other estimators, the Hahn consistently yielded estimates which were low (See Table 15). In most cases, those estimates were 25% to 50% lower than moderate ones and usually 2 to 3 times lower than the highest estimates. The Hahn estimator was always ranked lower than the King estimator. The only instances in which the Hahn was not the absolute lowest was when other estimates, usually those from the exponential (x), were completely out-of-line with all others.

These results were in direct contrast with findings in other studies. Evans (1975), working with white-tailed deer in Texas, reported that both in theory (as found by Kranz, unpublished thesis) and in practice, the Hahn method overestimated population densities. Hirst (1969) found the Hahn method to yield nearly unbiased estimates of a blusbok (Damaliscus dorcas) in South Africa. Other investigators (Lamprey 1964, Sihvonen 1977, Van Lavieren and Bosch 1977) felt that disappearing distances gave reliable results.

Comparisons between the King and Hahn estimators in Sihvonin's study on antelopes in Upper Volta revealed that the Hahn estimator was always lower than that of King. An examination of disappearing distances in this study, however, indicated that the Hahn method, as applied here, was subject to several biases which will be discussed below.

Comparisons of frequency distributions

For the Hahn estimator to have yielded unbiased estimates, all animals between the observer and the disappearing distance should be detected. With the live populations of animals, it was not possible to directly test whether or not animals were missed. An examination of frequency histograms of perpendicular, radial and disappearing distances of each species, though was informative. For each species, there were marked differences between the three histograms (Fig. 22). Perpendicular distances at which the animals were seen declined rapidly as distances from the transect line increased. Apparently, fewer animals were seen at the further distances. Frequencies of disappearing distances, by contrast, were often the highest at approximately the maximum perpendicular distances, while radial distance frequencies usually peaked somewhere between the two. These results imply that disappearing distances overestimated the area in which all animals could be seen, and in all probability, underestimated group densities. This discrepancy between perpendicular and disappearing distances was especially large for bushbuck, reedbuck and Grimm's duiker.

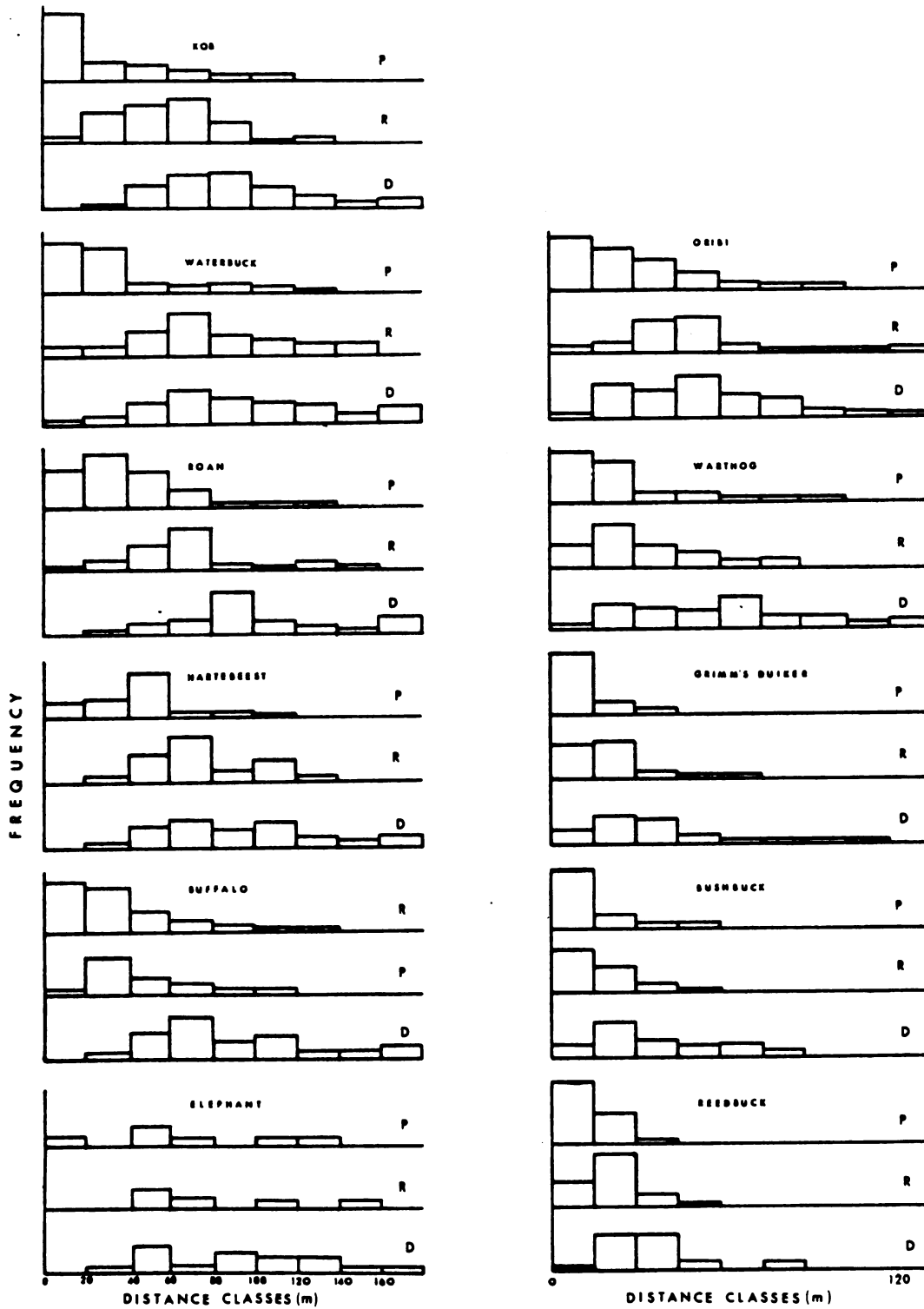


Figure 22. Comparisons between perpendicular (P), radial (R), and disappearing (D) distances from pooled foot transect data.

There are several possible explanations for the scarcity of detection at the longer disappearing distances. First, it was noticeably more difficult to spot animals as distances from the transect line increased. Vegetation usually did not abruptly conceal animals. Instead, visibility gradually declined as the distance and amount of obstructing vegetation increased. At the longer distances, it was often possible to see only parts of animals. Under those circumstances, even an experienced observer might miss such an animal while scanning the vegetation. When the observer was watching animals disappear and thus knew the animal was present, the observer might have considered that animal to be easily observable. It was quite possible that disappearing distances overestimated the effective area because it is easier to follow a moving animal through the brush than to spot it at that same distance.

A second factor was that of response behavior. Some species may have used open vegetation as escape cover, and so were visible at a greater-than-average distances. Thirdly, habitat preferences may have distorted the mean disappearing distances. The vegetation in which animals occurred most often may not have been representative of their visibilities in the average vegetation type. This appeared to have been true for waterbucks and oribi which avoided dense vegetation. Possibly, bias due to this factor was not large, however, since disappearing distances of the larger mammals were similar to those of smaller species even though their preferred habitats differed.

A fourth factor involved the manner in which observers scanned vegetation for animals. Ideally, the two observers on foot transects

should have scanned an area from the transect line to the point of maximum visibility at 90° on both sides of the line as well as the entire area in front of them (Fig. 23). An examination of the sighting angles recorded, however, revealed that comparatively few observations were made between 75° and 90° . Furthermore, the mean angle should have been near 45° if the entire area had been scanned equally well. Instead, most mean angles were considerably below 45° , indicating that sighting efforts were directed more toward the central portion of the transect than the sides.

A fifth factor was fire. Approximately two-thirds of the park was burned annually, and most species demonstrated either a preference for or an avoidance of burned areas (see Table 6). Visibilities in burned areas were considerably greater than those in unburned vegetation (Table 21). As a result, mean visibilities were based not only on relative proportions of habitat use, but also the proportions of burned areas traversed, and thus, may have been further biased.

Biases from these five factors was minimized to some extent in other studies (Hahn 1949, Lamprey 1964). These authors measured the disappearing distances of an assistant who walked at right angles to the transect lines. Where a sufficient number of distances along transects were thus averaged, the total area sampled could be calculated. This was also done during this study, but regrettably those data were lost while in air transit. In recalling the distance measures, however, they were quite similar to those obtained by the actual measurements of disappearing animals.

It was felt that a visibility profile, as determined from disappearing distances of an assistant, was subject to biases from the

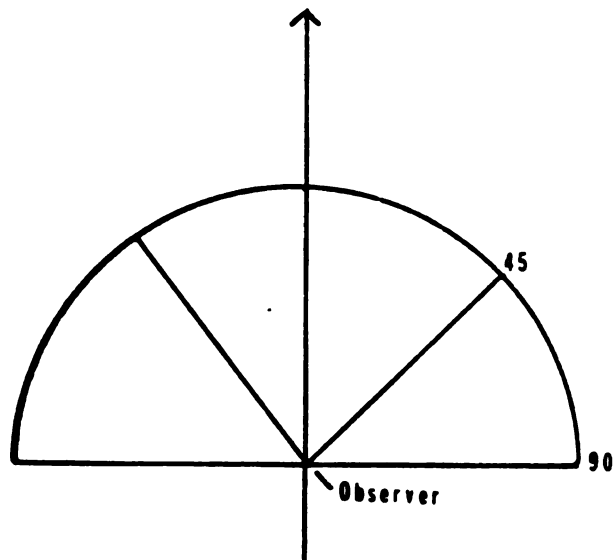


Figure 23. Sighting radius for observers when the detection of exposed animals depends on scanning the vegetation.

Table 21. Comparisons of mean disappearing distances in meters of species in burned and unburned vegetation during the 1976-1978 foot transect counts in Park W, Niger.

Species	Unburned	Burned
Kob	76	90
Waterbuck	91	109
Roan	97	107
Hartebeest	92	109
Buffalo	82	110
Elephant	76	114
Oribi	81	101
Warthog	56	86

several factors discussed above. It was, for example, likely that a moving person in dense cover was easier to observe than spotting an animal at that distance. Also, as assistants moved, there was a tendency to select a "path" through the vegetation, especially when thorny shrubs were encountered. This would result in longer distance-measures, a problem which was not reported in other studies.

Comparisons of distance measures for similar sized species.

A common application of the Hahn method in Africa has been to make observations of similar-sized species, and combine the data into a common visibility profile. This has been based on the premise that the larger the animal, the greater the distance at which it could be seen, and that animals of similar size disappeared at approximately the same distance. This was the case in this study for many species (Table 22), but some did not fit this pattern. Elephants and oribis, the largest and smallest species studied for example, had nearly the same mean disappearing distance per vegetation type. This was mainly because oribis were commonly observed in clearings and open woodlands whereas elephants were often in dense vegetation and sought concealment cover when detected. Large species including roan, hartebeest, waterbuck and buffalo also had similar profiles in woodlands and shrublands (Table 22), in spite of their dissimilar coloration, size and habitat preferences.

Correlation coefficients between animal size (shoulder height) and perpendicular, sighting and disappearing distances indicated no significant difference between those measures (Fig. 24). Habitat preferences undoubtedly influenced these results. Most species utilized habitats in which visibilities were similar. Too, the vegetation

Table 22. Disappearing distances of similarly sized large mammal species by vegetation type, Park W, Niger.

Vegetation Type	Species							
	Kob	Waterbuck	Roan	Hartebeest	Buffalo	Elephant	Oribi	Warthog
Riparian Grassland	127	143	105	165	189	*	*	105
Riverine Forest	45	*	*	*	*	*	*	41
Riparian Woodland	89	106	100	103	110	90	96	67
Upland Woodland	88	101	112	101	107	93	104	87
Shrubland	87	111	105	93	91	100	100	70
Upland Grassland	*	*	*	*	*	*	144	140

* No disappearing-distances were determined in this vegetation type.

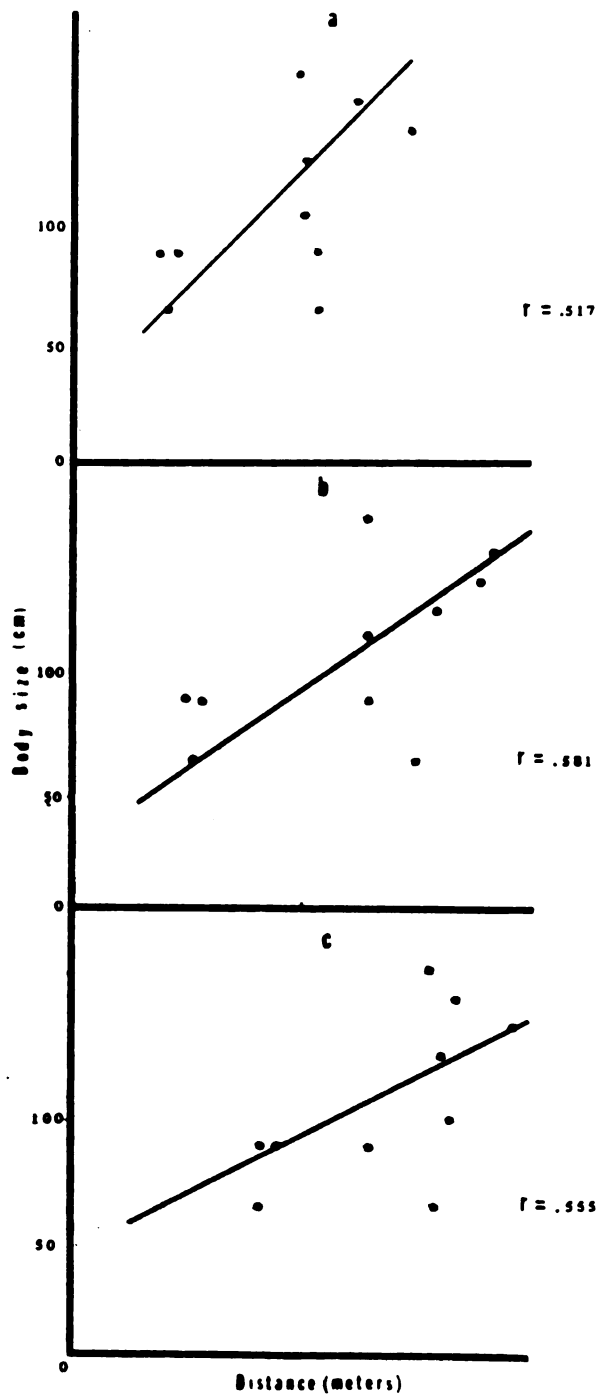


Figure 24. Correlations between body size and mean perpendicular (a), sighting (b), and disappearing (c) distances for the pooled foot transect data.

was not stratified in a manner such that smaller animals were less visible at the further distances. In many areas, the vegetation above 1.5 m was more dense than it was near the ground, and the smaller animals could be observed at longer distances.

Efficiency of estimators

Comparisons of coefficients of variation (Table 23) showed considerable differences in variability between estimators. No estimator consistently had a low or high coefficient of variation.

Park-wide survey

To determine if patterns were consistent for smaller sample sizes, analyses applied to the pooled foot-transect data were performed similarly on the results of the park-wide survey. The patterns among estimators were similar to those of the pooled data set despite the smaller sample sizes (Table 24). The Hahn estimators, as expected, generally gave the lowest density estimate and had the lowest overall ranking. The King estimator, too, consistently had low rankings. The Webb and Dasmann-Mossman estimators consistently ranked high.

The Fourier Series estimators, surprisingly, tended to give low estimates rather than moderate ones as found in the pooled results. In several instances, the Fourier Series estimates were lower even than the King and Hahn results. Other notable differences involved the Quadratic and Exponential estimators which yielded some estimates that were among the highest. The Quadratic ranked even higher than the Webb estimator (Table 25). The Exponential also ranked higher than the Webb estimator and achieved the same rank as the Dasmann-Mossman estimator.

Table 23. Comparisons of percent coefficient of variation for estimators from truncated, pooled foot transect data in Park W, Niger.

Estimator	Kob	Water- buck	Roan	Harte- beest	Buffalo	Oribi	Grimm's duiker	Bush- buck	Reed buck	Warthog
Exponential	30.4	7.5	15.2	42.2	17.3	18.1	14.9	54.1	14.8	22.0
Hemingway Normal	28.4	11.1	12.5	52.5	18.2	18.8	14.5	58.5	12.1	20.5
Quadratic	6.8	24.3	13.1	17.3	4.3	6.1	15.0	6.0	42.1	10.8
Triangular	11.1	2.0	47.6	63.6	24.4	5.3	4.3	26.3	22.4	8.2
Generalized Exp.	32.7	6.2	16.4		13.4	13.5		46.8	5.4	
Polynomial	8.7	49.8	20.1	84.2	20.4	32.9	64.0	38.2	34.5	30.3
Fourier Series	44.9	16.5	31.8	37.2	15.0	16.4	16.0	48.3	25.1	20.6
Kelker	36.6	2.18	55.5	29.7	10.3	15.6	31.0	32.9	28.9	20.6
Eberhardt-Cox	43.2	19.3	10.2	3.2	3.2	14.6	58.0	9.0	53.2	27.0
Splined	36.6	27.0	47.1	47.9	30.4	15.6	31.0	43.1	25.1	22.9
Polynomial*	40.4	11.6	42.3	44.7	18.1	13.3	10.1	45.5	34.7	22.8
Quadratic*	30.8	6.2	33.8	39.8	11.0	17.3	22.6	45.3	18.7	19.2
Triangular*	26.4	11.9	24.9	41.4	13.8	18.6	16.2	56.2	14.0	16.6
Hahn	25.7	24.4	6.9	26.3	14.0	5.7	#	#	#	9.7
Geometric	13.2	15.9	15.7	30.0	16.8	11.2	22.8	68.4	18.5	21.8
Hayne Const. Rad.	15.9	4.4	18.8	31.2	20.7	10.1	35.9	66.1	20.9	50.3
Modified Hayne	27.5	15.3	23.6	26.0	28.2	14.7	30.8	48.3	32.1	51.7
Exponential**	11.2	21.2	13.8	31.7	13.9	11.9	16.1	43.1	16.8	13.5

* Based on grouped data.

**Based on radial distances.

Not calculated for animals which flush.

Table 24. Density estimates from the 1978 park-wide survey in Park W, Niger.

Estimators	Kob	Water- buck	Roan	Harte- beest	Buffalo	Ele- phant	Oribi	Grimm's duiker	Bush- buck	Reed- buck	Warthog
(Perpendicular)											
Exponential	1.775	0.501	0.204	0.104	0.165	0.012	0.451	0.711	5.227	6.000	0.680
Hemingway Normal	2.861	2.236	0.343	0.085	0.140	0.061	0.386	1.194	5.827	2.894	0.444
Quadratic	6.768	6.208	0.596	0.664	0.817	0.059	0.737	0.849	6.854	5.294	0.878
Triangular	4.196	1.803	0.256	0.245	0.758	0.011	0.111	0.834	4.362	4.817	0.733
Generalized exp.	7.046	1.697	0.263	0.056	0.148	0.049	0.263	0.962	3.996	6.254	0.770
Polynomial	4.998	1.714	0.150	0.458	0.733	0.054	0.210	0.831	4.024	4.768	0.856
Fourier Series	2.691	1.730	0.190	0.070	0.095	0.049	0.317	0.819	4.556	1.618	0.308
Dasmann-Mossman	4.345	3.250	0.477	0.119	0.220	0.095	0.547	1.796	8.361	5.294	0.779
Webb	3.943	3.013	0.450	0.114	0.200	0.093	0.509	1.731	7.516	5.259	0.757
Grouped data											
Kelker	2.643	*	0.195	*	*	*	0.260	0.929	*	3.100	0.494
Eberhardt-Cox	3.083		0.146				0.211	0.072		4.573	0.669
Splined	2.643		0.195				0.260	0.929		1.280	0.495
Polynomial	2.822		0.228				0.321	1.033		2.338	0.453
Quadratic	2.841		0.210				0.290	1.004		2.872	0.507
Triangular	3.475		0.195				0.317	1.156		3.200	0.591
(Disappearing)											
Hahn	1.240	1.010	0.145	0.061	0.092	0.046	0.250	0.460	2.384	2.214	0.359
(Radial)											
Geometric	2.247	1.795	0.252	0.073	0.148	0.062	0.334	1.203	5.214	4.151	0.651
Hayne Const. Rad	2.545	2.564	0.281	0.063	0.181	0.067	0.372	1.944	5.643	5.084	1.823
Modified Hayne	2.716	2.941	0.264	0.076	0.159	0.057	0.319	1.865	4.407	4.467	1.625
Exponential	3.908	2.711	0.453	0.133	0.229	0.104	0.608	1.659	9.430	6.152	0.886
King	1.997	1.402	0.231	0.071	0.120	0.057	0.310	0.845	4.842	3.151	0.449

*Insufficient number of observations to group the data.
 Densities are in numbers of groups per km².

Table 25. Rankings of density estimates from low to high from 1978 park-wide survey, Park W, Niger.

Estimator	Kob	Water- buck	Roan	Harte- beest	Buffalo	Ele- phant	Oribi	Grimm's duiker	Bush- buck	Reed- buck	Warthog
Exponential	2	1	6	9	6	2	15	2	15	7	12
Hemingway Normal	11	9	15	8	3	8	14	13	6	10	3
Quadratic	19	15	19	15	13	7	19	7	17	11	18
Triangular	16	8	11	13	12	1	1	5	13	4	15
Generalized exp.	20	4	12	1	4	4	6	9	19	2	14
Polynomial	18	5	3	14	11	5	2	4	12	3	17
Fourier Series	7	6	4	4	2	4	9	3	2	6	1
Dasman-Mossman	17	14	18	11	9	12	17	17	17	13	16
Webb	15	13	16	10	8	11	16	16	16	12	13
Grouped Data											
Kelker	6	*	5	*	*	*	5	8	7	*	6
Eberhardt-Cox	12		2				3	10	11		11
Splined	6		5				5	8	1		7
Polynomial	9	8					11	12	4		5
Quadratic	10		7				7	11	5		8
Triangular	13		5				9	12	9		9
(Disappearing)											
Hahn	1	2	1	2	1	3	4	1	3	1	2
(Radial)											
Geometric	4	7	10	6	4	9	12	14	9	8	10
Hayne Const. Rad.	5	10	14	3	7	10	13	19	14	9	21
Modified Hayne	8	12	13	7	5	6	10	18	10	5	20
Exponential	14	11	17	12	10	13	18	15	18	14	19
King	3	3	9	5	3	6	8	6	8	7	4

*There were too few observations to group the data.

These differences may have been a result either of small sample sizes or of properties of the detection functions.

Relative values of estimators

The relative values of estimators reveal that there is more variability among density estimators for the park-wide survey than for the pooled data set (Table 26). Only the Hemingway-Normal and Geometric estimators always yield moderate estimates. As with the pooled data set, the Hahn estimator is always low and the Dasman-Mossman, Webb and Exponential (r) estimators are always high. Other estimators, except the King and Modified Hayne, which are quite variable.

There are sufficient observations to group the data for only 6 of the 11 species, and a complete evaluation of these is not possible therefore. It is noteworthy, however, that with the smaller sample sizes of the park-wide survey, these estimators are much less consistent.

Goodness-of-fit tests

Results of goodness-of-fit tests were similar to those for the pooled data set except for the poor fits obtained for the quadratic and polynomial distributions (Table 27). The suprema for most species were rarely below the K-S criterion. As for the pooled data, estimators based on distributions which were not significantly different from the assumed distribution yielded results which tended to be moderate in ranking.

There were not enough observations to fit the cosine theta distribution, but the tests for the sighting angles were not significant for any species (Table 28), when determining if measured angles were significantly different from 32.7° . The test to determine whether the

Table 26. Relative values of density estimates from the 1978 park-wide data for foot transects in Park W, Niger.

Estimator	Kob	Water- buck	Roan	Harte- beest	Buffalo	Ele- phant	Oribi	Grimm's duiker	Bush- buck	Reed- buck	Warthog
Exponential	L-M	L	M	L	M	L	M	M	M	H	M
Hemingway Normal	M	M	M	M	M	M	M	M	M	M	M
Quadratic	H	H	H	H	H	M	H	M	M	H	H
Triangular	M-H	M	M	H	H	L	L	M	M	M-H	M-H
Generalized Exp.	H	M	M	L	M	L	L	M	M	H	M-H
Polynomial	H	M	L	H	H	L	L	M	M	M	H
Fourier Series	M	M	L-M	L-M	L	L	M	M	M	L	L
Dasman-Mossman	H	H	H	H	H	H	H	H	H	H	M-H
Webb	H	H	H	H	H	H	H	H	H	H	M-H
Kelker	M		M					M		M	M
Eberhardt-Cox	M		L				L	L		M-H	M
Splined	M		M				L	M		L	M
Polynomial	M		M				M	M		L	M
Quadratic	M		M				M	M		M	M
Triangular	M		M				M	M		M	M
Hahn	L	L	L	L	L	L	L	L	L	L	L
Geometric	M	M	M	M	M	M	M	M	M	M	M
Modified Hayne	M	M-H	M	M	M	M	M	H	M	M-H	H
Hayne Const Rad.	M	H	M	M	M	M	M	M-H	M	M	H
Exponential	H	H	H	H	H	H	H	H	H	H	H
King	L-M	L-M	M	L-M	L-M	M	M	M	M	M	M

Table 27. Results of goodness-of-fit tests to selected distributions from the 1978 park-wide survey in Park W, Niger.

	Kob	Water- buck	Roan	Harte- beest	Buffalo	Ele- phant	Oribi	Grimm's duiker	Bush- buck	Reed- buck	Warthog
Test criterion:	.290	.363	.278	.555	.430	.608	.267	.267	.304	.321	.230
<u>Distributions</u>											
(Radial)											
Gamma, α variable	.075	.152	.091	.136	.228	.216	.117	.141	.156	.156	.079
Gamma $\alpha = 2.0$	.117	.119	.191	.298	.248	.263	.230	.125	.211	.228	.084
(Perpendicular)											
Half-normal	.068	.146	.199	.220	.198	.182	.147	.101	.352*	.176	.164
Triangular	.433*	.132	.270	3.515*	1.017*	.369	.102	.202	.237	.134	.632*
Gamma $\alpha = 2.0$	.399*	.971*	.953*	1.000*	.215	1.000*	1.000*	.399*	.222	1.000*	.110
Generalized Exp.	.913*	.933*	.960*	.714*	.183	.833*	.963*	.082	.196	.947*	.063
Gamma α variable	.111	.160	.087	.122	.183	.215	.113	.134	.194	.125	.063
(Non-parametric estimators)											
Quadratic	.498*	.753*	.718*		.526*	1.063*	.743*	.029	.328*	.358*	.320*
Polynomial	.429*	.751*	.684*		.004	1.000*	.648*	.024	.101	.290	.206

*Significant at the 95% confidence level.

Table 28. Test statistics on angle measurements to determine the validity of radial estimators.

Species	$E(\theta) = 32.7^{\circ}$	$E(\sin \theta) = 0.5$
Kob	0.335 *	0.116
Waterbuck	0.401 *	0.470 *
Roan	0.383 *	1.212 *
Hartebeest	0.237 *	2.810 *
Buffalo	0.312 *	1.137
Elephant	0.354 *	0.984 *
Oribi	0.529 *	1.962 *
Grimm's duiker	0.282 *	1.008 *
Bushbuck	0.431 *	1.572 *
Reedbuck	0.550 *	2.714 *
Warthog	0.535 *	1.933 *

*Significant at the 95% confidence level

$\sin \theta$ equal 0.5, however, was significant for oribi, reedbuck and hartebeest, indicating that for those 3 species in this study, radial estimators may not be appropriate.

Comparisons of density estimates in the central study area

Patterns in density estimates from the 1976, 1977 and 1978 surveys in the central study area were somewhat different to those for either the park-wide survey or pooled data set (Tables 29-31). Three estimators, the Quadratic, Triangular and Polynomial, gave estimates which were often considerably higher than other estimators, often by ten times or more. The Fourier Series estimator often gave results as low or lower than the Hahn estimator. The variability of these estimators with small sample sizes was not surprising because a true detection function may not exist and consequently unbiased estimates of $f(0)$ may not exist.

Among the radial estimators, the sequential relationship was similar to that of the pooled data set, but density estimates were moderate rather than high (Table 32). All estimators, however, generally followed the same ranking patterns as for the pooled data and park-wide survey.

The relative values of estimators (Table 33) were fairly constant between the pooled data set, park-wide survey and three surveys in the central study area. The Geometric estimator was the only consistently moderate one, though the Hemingway-normal, Generalized Exponential, Fourier Series and Hayne estimators were usually moderate.

Comparisons between years in the central study area

Comparisons of density estimates between the three annual surveys in the central study area (Tables 29-31) revealed that for most species

Table 29. Density estimates from the 1976 foot transect counts in the central study area in Park W, Niger.

Estimate	Kob	Water-		Roan	Buffalo	Oribi	Grimm's		Bushbuck	Warthog
		buck	buck				duiker	duiker		
Exponential	2.690	1.862		.332	.391	.147	.587		1.153	1.001
Hemingway-Normal	2.315	1.773		.324	.387	.230	.859		1.205	1.061
Quadratic	*	*		3.815	3.682	*	1.082		6.793	*
Triangular	21.00	17.583		.028	.313	3.916	.279		3.697	4.414
Generalized Exp.	2.063	1.915		.254	.308	.242	.817		1.515	1.036
Polynomial	7.359	8.683		.382	.481	*	*		*	1.764
Fourier Series	.588	.639		.294	3.28	.110	.274		1.513	.669
Dasman-Mossman	3.074	1.863		.332	.587	.294	1.175		3.027	1.333
Webb	3.041	1.859		.362	.487	.284	1.201		3.022	1.338
Hahn	1.316	.877		.138	.215	.157	.271		.714	.369
Geometric	1.986	1.434		.255	.303	.157	.741		1.189	.661
Modified Hayne	1.526	1.137		.318	.253	.154	.645		.516	.901
Hayne Const. Rad.	1.993	1.440		.263	.304	.157	.752		1.189	.807
Exponential	3.713	2.618		.411	.504	.235	1.096		1.189	.996
King	1.980	1.429		.165	.302	.114	.731		2.381	.566

* Estimates from the Quadratic and Polynomial estimators were not possible for very small sample sizes.

Table 30. Density estimates from the 1977 foot transect and 1977 aerial counts in the central study area in Park W, Niger.

Estimator	Kob	Water- buck	Roan	Harte- beest	Buffalo	Ele- phant	Oribi	duiker	Bush- buck	Reed- buck	Warthog
Exponential	2.338	1.708	.431	.065	.182	.097	.262	1.023	2.970	5.106	.425
Hemingway Normal	2.083	1.502	.369	.059	.176	.069	.300	.882	1.995	5.427	.409
Quadratic	*	*	2.581	*	1.014	*	*	3.248	17.35	6.339	1.490
Triangular	8.059	9.715	1.327	.595	1.219	.231	4.304	1.314	10.28	2.932	1.768
Generalized Exp.	2.148	1.425	.297	.071	.166	.062	.305	.767	7.290	5.556	.326
Polynomial	3.193	3.520	.640	.217	.492	.105	1.879	2.112	21.990	.365	.462
Fourier Series	.486	0.098	.193	.050	.059	.065	.055	.806	4.644	.967	.252
Dasmann-Mossman	2.671	1.952	.518	.074	.242	.106	.394	1.278	3.960	7.660	.566
Webb	2.416	1.975	.485	.071	.189	.101	.321	1.247	3.524	3.808	.453
Hahn	.877	.772	.210	.053	.062	.035	.140	.487	1.600	1.200	.211
Geometric	1.445	1.004	.277	.068	.070	.061	.181	.723	4.575	1.339	.264
Modified Hayne	1.385	1.087	.332	.012	.104	.061	.191	.766	5.826	2.456	.337
Hayne Const. Rad.	1.498	1.020	.312	.068	.079	.064	.189	.768	7.358	1.633	.312
Exponential	2.615	1.852	.451	.128	.123	.110	.172	1.215	3.944	1.714	.397
King	1.395	.988	.246	.068	.070	.101	.140	.675	2.254	3.808	.227
Aerial	0.496	0.293	0.044	0.039	0.076	0.069					

*Sample sizes too small to obtain an estimate

Table 31. Density estimates from the 1978 foot transect survey in the central study area in Park W, Niger.

Estimator	Kob	Water- buck	Roan	Harte- beest	Buffalo	Ele- phant	Oribi	Grimm's duiker	Bush- buck	Reed- buck	Warthog
Exponential	2.552	2.351	.370	.117	.244	.261	.499	2.923	3.861	3.356	.523
Hemingway Normal	1.872	1.988	.325	.121	.286	.137	.458	.506	2.807	3.222	.506
Quadratic	5.634	*	2.780	.260	*	.464	*	2.499	10.760	5.122	2.174
Triangular	.030	8.980	1.324	.551	.718	.167	4.473	1.646	3.190	2.151	.408
Generalized Exp.	1.565	2.010	.302	.128	.202	.123	.395	1.642	2.061	2.591	.363
Polynomial	.089	3.720	.989	.075	.304	.210	1.504	2.638	12.030	1.726	2.764
Fourier Series	1.388	.666	.333	.058	.104	.131	.412	1.754	2.441	1.976	.425
Dasmann-Mossman	2.835	2.644	.462	.156	.325	.284	.599	3.288	4.344	3.934	.729
Webb	3.00	2.105	.402	.157	.321	.269	.526	2.948	3.613	4.472	.655
Hahn	1.429	.893	.124	.074	.061	.112	.238	.527	2.250	1.183	.210
Geometric	2.936	1.240	.414	.101	.182	.163	.328	2.116	3.310	2.118	.359
Modified Hayne	1.594	1.241	1.437	.080	.176	.123	.305	3.194	3.685	2.305	.561
Hayne Const. Rad.	3.708	1.299	1.871	.102	.184	.129	.343	3.266	4.698	2.210	.471
Exponential	4.492	2.237	.391	.176	.314	.220	.573	3.070	4.386	3.571	.521
King	1.429	1.184	.217	.101	.179	.153	.313	1.625	2.323	2.041	.289

*Too few observations to obtain an estimate

Table 32. Rankings of density estimates from the 1976, 1977 and 1978 foot transect counts in Park W, Niger.

Estimator	Kob			Waterbuck			Boon			Hartebeest			Buffalo			Elephant			Oribi			Grimm's duik.			Bushbuck			Reedbuck			Warthog					
	76	77	78	76	77	78	76	77	78	76	77	78	76	77	78	76	77	78	76	77	78	76	77	78	76	77	78	76	77	78						
Exponential	11	8	9	9	9	7	10	9	6	4	5	7	10	9	8	4	7	11	3	7	9	4	9	10	3	4	10	4	10	11	8	10	10			
Manningway Normal	10	6	7	7	8	8	9	8	5	4	8	9	8	9	9	6	4	6	9	8	10	8	6	5	2	5	11	10	10	9	8	10	9	8		
Quadratic	15	15	15	15	14	14	15	15	13	13	13	15	14	15	13	14	13	4	14	11	15	7	12	13	14	8	6	14	15	5	6	14	15	5		
Triangular	15	14	14	15	15	1	14	12	12	12	14	7	15	14	12	8	11	15	15	3	14	2	11	12	6	8	6	14	15	5	6	14	15	5		
Generalized Exp.	9	3	3	11	7	9	4	5	3	3	7	9	6	7	7	3	2	8	10	6	9	3	3	7	10	1	12	9	9	6	4	12	9	9	6	4
Polynomial	15	4	5	13	13	13	12	13	11	11	3	11	13	10	9	9	9	13	10	9	10	9	14	15	1	1	13	12	15	1	1	13	12	15		
Fourier Series	1	2	2	1	1	1	7	1	4	2	1	8	1	2	5	4	1	1	7	2	7	4	6	9	4	2	3	4	3	6	2	3	4	3	6	
Deomann & Moorman	13	11	10	12	11	10	11	10	9	10	14	11	13	13	10	13	10	12	10	13	13	15	10	7	11	14	13	12	13	13	14	13	12	13	13	
Mobb	12	12	12	8	10	12	11	12	9	8	11	12	10	12	8	12	9	11	11	14	12	12	9	5	8	9	14	11	11	12	9	14	11	11	12	
Mahn	4	1	1	2	5	4	2	2	1	2	2	1	2	1	1	1	5	2	1	1	1	1	1	2	1	2	3	2	1	1	1	1	1	1	1	
Geometric	7	5	6	5	3	6	5	4	9	6	5	4	3	5	2	7	5	4	4	7	4	5	4	8	7	4	5	3	4	3	4	5	3	4	3	
Modified Mayne	5	9	9	3	6	5	8	7	13	1	4	2	5	3	2	2	4	6	2	5	5	13	1	10	9	7	8	6	7	11	7	8	6	7	11	
Mayne Conat. Rad.	8	10	10	6	11	10	6	6	14	6	6	5	4	6	4	3	5	5	5	8	6	14	4	11	13	5	7	5	5	7	5	7	5	5	7	
Exponential	14	11	13	12	4	3	13	10	7	10	12	13	11	11	11	10	7	8	10	12	11	11	4	6	12	6	12	7	8	9	6	12	7	8	9	
King	6	7	4	4	2	2	3	3	2	6	2	3	3	4	8	6	2	3	3	3	6	2	8	8	9	4	3	1	2	3	2	3	1	2	3	2

Table 3). Relative values of density estimates from the 1976, 1977 and 1978 foot transect counts in Park V, Niger.

Estimator	Job			Waterbuck			Rees			Marriehout			Buffalo			Elaphant			Oribi			Grimm's duiker			Rushbuck			Reedbuck			Warthog		
	1976	1977	1978	1976	1977	1978	1976	1977	1978	1976	1977	1978	1976	1977	1978	1976	1977	1978	1976	1977	1978	1976	1977	1978	1976	1977	1978	1976	1977	1978	1976	1977	1978
Exponential	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M
Marquay Normal	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M
Quadratic	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M
Triangular	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M
Generalized Exp.	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M
Polynomial	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M
Fourier Series	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M
Daniels & Newman	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M
Lebb	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M
Mahon	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L
Geometric	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M
Modified Wayne	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M
Wayne Const. Rad.	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M
Exponential	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M
King	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M

* None observed during survey

L = estimates were low in relation to all others

M = estimates were moderate in relation to all others

H = estimates were high in relation to all others

L-H = estimates were low to moderate

M-H = estimates were moderate to high

I = had no definite pattern and values were of the extreme

estimates from individual estimators were relatively close. For kob, estimates from the Exponential (x) estimator from 1976, 1977 and 1978 were 2.690, 2.338 and 2.552 /km² respectively. Density estimates for a species in a given year, however, were quite variable. The range between the highest and lowest estimates for kob in 1978, for example was 0.030 to 5.634 /km². This disparity between estimates was considerably greater than those of the park-wide survey and pooled data set. The apparent cause was small sample sizes. The detection functions for small samples were irregular and did not necessarily correspond to any of the assumed distributions. Fitting a polynomial or quadratic equation to a few observations can lead to badly-biased and erratic density estimates.

The rankings of estimators by species for the three annual censuses were relatively constant (see Table 32), though patterns were somewhat different than those found in larger data sets. Estimates of the Triangular and Quadratic estimators, for example, though much higher in ranking than in the pooled data set, were consistently high, not only between years, but between species.

Comparisons of foot and aerial transect counts

It was originally anticipated that aerial counts would provide standard for comparison with ground counts. The results indicate, however, that this may be true only for buffaloes and elephants. Density estimates only of those two species were similar for aerial and foot transect counts (see Table 30). The aerial estimate of elephant groups fell midway between the Hahn and Dasmann-Mossman estimators, and was equal to the Hemingway-Normal, a consistently moderate estimator.

Aerial estimates for buffaloes also fell between the highest and lowest estimates, but was closer to the lowest one.

Density estimates from aerial counts of hartebeests (see Table 30) were slightly below the Hahn estimate from the 1977 foot transect counts, but those of roans, waterbucks and kobs were considerably below it. From evidence presented earlier, it appeared that the Hahn estimator yielded underestimates of density. Aerial counts too, therefore, underestimated densities of the four antelope species.

The two species for which foot and aerial estimates were similar were the two largest and most visible from the air. It was possible, but unlikely that elephants, which mostly occurred in groups of 6 or more, were missed during aerial counts. Similarly, few buffaloes were probably missed since they seldom occurred in cover with a dense canopy and were mostly in groups. The four antelope species, however, were more difficult to locate from the air, especially when they remained stationary as the aircraft passed over. It was possible that some animals were missed.

The consistency between estimates from the three annual counts also may be significant in comparing foot and aerial counts. Though variable, the lower range of ground estimates was considerably higher than the aerial counts. Thus it appears that aerial counts were useful mainly for buffaloes and elephants, but that foot transect counts were equally useful for those species and served as a reliable general indicator of animal density.

Tests of Assumptions

An evaluation of the underlying assumptions of the estimators gave a general indication of their reliability and usefulness. From this

study, assumptions ii and iii, the independence of individual sightings and the avoidance of duplicate counting appeared to have been met.

Only rarely was a group of animals sighted as the result of the activities of another group and those sightings could be and were excluded from the results. By plotting all observations on a map, it became apparent that no group had been counted more than once. This indicated that the minimum distance of 1 km between transects was adequate.

Animals were not randomly distributed in the study area as required in assumption i, but it was felt that the systematic coverage of the study area provided an accurate reflection of mean densities. The positioning of transects perpendicular to streams and proportional sampling in low and high density areas seemed to compensate for the tendency of animals to congregate near water. Those transects which were positioned parallel to streams to obtain estimates of the riparian mammal species, however, in all likelihood did not provide meaningful density estimates. They were not used for determining density estimates.

Assumption iv, that each animal or group is seen in the exact position it occupied when startled, must have been violated to some degree for each species. By recording the activity of groups when first noticed, however, some measure of the validity of this assumption could be made. A large percentage of sightings of oribis, roans and Grimm's duikers was made only after groups had moved (Table 34). Only buffaloes and reedbucks tended to have all groups spotted in their first positions. It is possible, nevertheless, that some buffalo and reedbuck groups moved away from the transect line prior to detection. The large percentage of oribis running when first encountered reflected their wariness and the difficulty in spotting them before they moved. Grimm's duikers,

Table 34. Activities of animals when first spotted and their responses after detection during all foot transect surveys in Park W, Niger. Values are in percentages of the total seen.

Species	Activity when spotted				Response		
	Standing	Walking	Running	Lying down	Remained	Walked away	Ran
Kob	61	18	3	18	10	47	43
Waterbuck	40	40	4	16	8	63	29
Roan	46	27	18	9	13	44	43
Hartebeest	50	38	12	0	13	38	49
Buffalo	75	12	0	13	14	64	22
Elephant	55	36	9	0	9	55	36
Oribi	28	16	28	28	11	11	78
Grimm's duiker	10	7	21	62	0	7	93
Bushbuck	22	4	13	61	4	5	91
Reedbuck	8	5	0	87	4	5	91
Warthog	32	26	10	32	11	30	59

which usually flushed from thickets, were secretive and were observed attempting to sneak away undetected. These observations indicate not only that there were errors as a result of movements in measurements of angles and radial distances, but also that some groups, which might have been observable from the transect line, could have moved off prior to detection.

The high percentage of groups which ran after being encountered by an observer also reflected the shyness of many species and the potential for not seeing groups (Table 34). Species which normally flushed (bushbuck, reedbuck and Grimm's duiker) characteristically sought hiding-cover after flushing. On two known occasions, bushbucks were flushed prior to being seen by the observer. They were heard moving through the brush and identified by their characteristic "bark". Undoubtedly, other bushbucks were not detected and probably groups of other species similarly moved ahead of or away from observers prior to detection, especially when in dense cover.

Because of their docile nature, it was unlikely that many kobs, waterbucks or buffaloes moved far enough to go undetected along transects. Complete accuracy in measurement, however, cannot be certain.

Assumption v, that distance and angle measurements are made without bias, must have been violated at least to the degree that animals moved toward or away from transect lines prior to detection. For the oribis this was an important factor but for other species it was not believed significant. Assumption v was also violated, however, where observers tended to round measurements to the nearest five meters or five degrees. In this regard, the use of rangefinders for recording distances presented difficulties in obtaining exact readings, especially

where large animal groups were seen. It was not always possible to determine the center of a group when it was widely-scattered.

Several other assumptions were implicit in all methods. Where animals occurred in groups of 2 or more, for example, it was assumed that the size of the group had no effect on detection. To test this assumption, correlation coefficients were determined for relationships between group size and distance measures (Table 35). None were found to be significant between group size and sighting, perpendicular or disappearing distances except for hartebeest, bushbuck and reedbuck. Significant correlations determined for bushbuck and reedbuck were caused by several sightings of groups of 3 individuals at long distances. The latter correlations are not considered to be important because most individuals of these species occur singly or in groups of two. The correlation for hartebeest, too, was of questionable importance because of the small number of hartebeest groups encountered. In general, for this study it is believed that the assumption that group size has no effect on distance measures was met.

Another assumption was that the countability or sightability of animals remained constant during the counting period. This implies that animal behavior should not affect counts. Activity profiles for each species, though showed that animal activity changed appreciably by time during the day (Fig. 25). During the early morning hours, most animals were active but, as temperatures increased, animals usually sought shade or cover. Responses to rising temperatures varied from none and remaining in the open to resting in thickets or seeking shelter in excavated holes, as with warthogs. Individuals of some species including bushbuck, reedbuck and Grimm's duiker, normally

Table 35. Correlation coefficients for relationships between group size and distance measures for the pooled foot transect data.

Species	Perpendicular Distances	Sighting Distances	Disappearing Distances
Kob	.011	.081	.077
Waterbuck	.096	.023	.103
Roan	.158	.101	.132
Hartebeest	.365	.608*	.742*
Buffalo	.041	.039	.068
Elephant	.311	.192	.231
Oribi	.068	.115	.325
Grimm's duiker	.403	.218	.057
Bushbuck	.698*	.592*	.345
Reedbuck	.485*	.396	.187
Warthog	.024	.054	.092

*Significant at the 95% level.

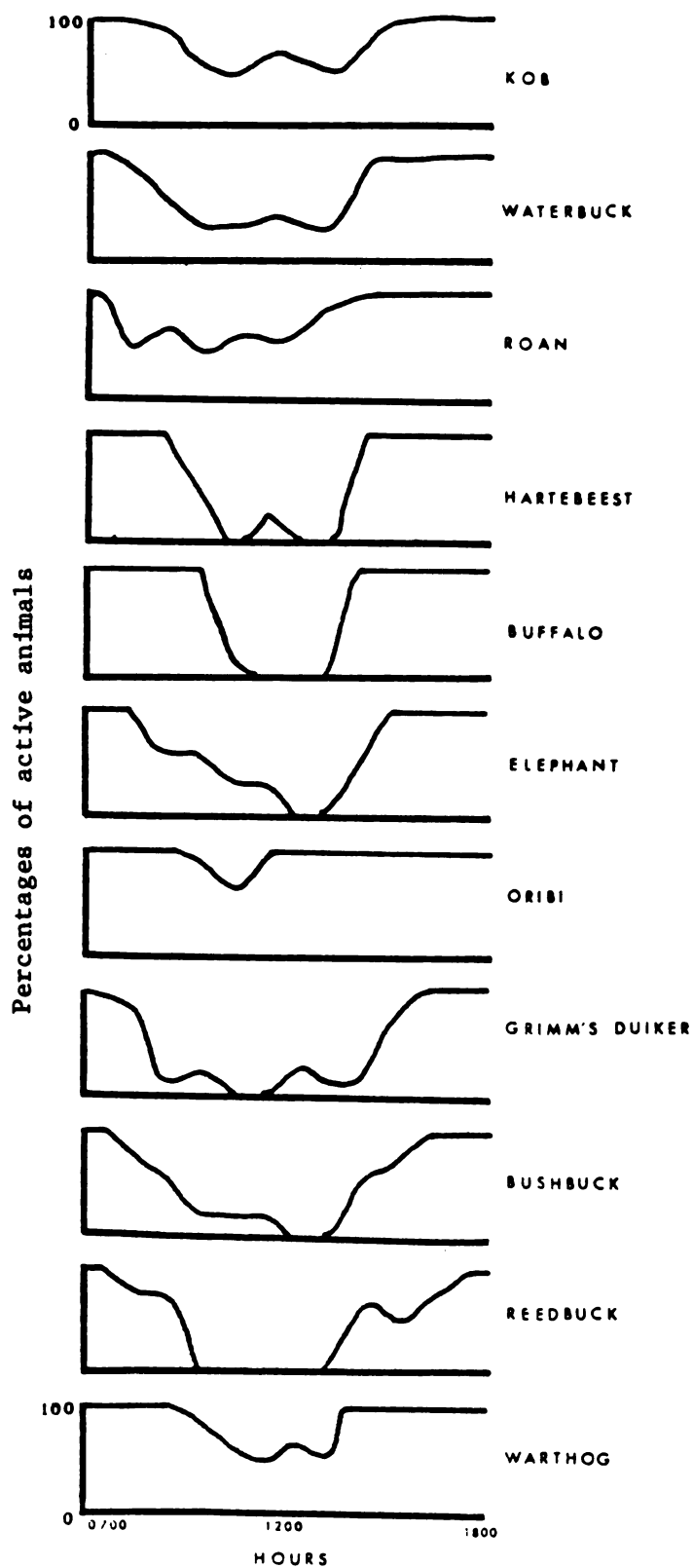


Figure 25. Percentages of animals active during 0700 and 1900 hours from January to February in Park W, Niger.

hid in dense cover during the day, often as early as 0800 hours. During the course of walking transects, therefore, the mode of detection changed from that of spotting active animals to one of detecting resting individuals, usually as a result of some response of an animal. The detection function certainly was altered, this may have adversely affected density estimates. For example, the mean sighting and perpendicular distances of active bushbucks were 71.5 and 52.8 m respectively, whereas for inactive groups the respective mean distances were 22.3 and 12.0 m. Similar patterns were evident for reedbuck, Grimm's duikers and warthogs but was less evident for other species. For any one species, therefore, there can be at least two detection functions.

Despite these uncertainties, animals were actually encountered at roughly the same rate throughout the counting period. Sighting rates per unit time walked were surprisingly constant for all species (Table 36). In this study, the assumption that all individuals of a species are equally visible to the observer throughout the course of an animal census appears valid. It is acknowledged that the validity of this acceptance is open to further review.

Evaluation of Transect Locations

Transects positions parallel to streams yielded higher density estimates for kob, bushbuck and reedbuck but lower estimates for waterbucks than those which were perpendicular to streams. To help determine whether these differences were real or because of differences in sighting distances, the number of groups seen per kilometer walked were compared.

For all species except kob, mean numbers observed per kilometer of riparian transect were significantly different from those of perpendicular transects at the 90% level (Table 37). Bushbuck and reedbuck

Table 36. Number of observations per unit time walked during the 1976, 1977 and 1978 foot transect counts in Park W, Niger.

Species	Time (am)				
	8-9	9-10	10-11	11-12	12-1
Kob	.16	.10	.09	.10	.15
Waterbuck	.11	.06	.05	.06	.07
Roan	.09	.13	.08	.08	.19
Hartebeest	.00	.03	.02	.04	.04
Buffalo	.08	.11	.11	.09	.06
Elephant					
Oribi	.11	.13	.06	.12	.11
Grimm's duiker	.02	.09	.14	.15	.07
Bushbuck	.09	.06	.09	.04	.19
Reedbuck	.04	.00	.09	.12	.11
Warthog	.11	.14	.16	.19	.19

Table 37. Comparisons between mean numbers of groups observed per kilometer walked for transects positioned parallel and perpendicular to streams during the 1978 foot transect counts in Park W, Niger.

Species	Riparian Transects	Perpendicular ¹ Transects	Perpendicular ² Transects
Kob	0.215	0.146*	
Waterbuck	0.062	0.188**	
Bushbuck	0.207	0.038***	0.076**
Reedbuck	0.241	0.094***	0.189*

¹Mean density based on 1.0 km from streams

²Mean density based on 2.0 km from streams

* Significant at the 60% level.

** Significant at the 90% level.

***Significant at the 95% level.

numbers were compared using both 1.0 km and 0.5 km as the maximum distance at which all or most individuals were likely to be seen. The greatest discrepancy occurred with bushbucks, which were usually found in or adjacent to riparian forests. Fewer waterbuck groups were observed along riparian transects because that species ranges further into the savanna and usually avoids dense riparian vegetation.

Differences in density estimates between riparian and perpendicular transects may be attributed to the distributions of riparian species with respect to water. Concentrations of kobs, bushbucks and reedbucks decreased as the distance from water increased (Fig. 26). Transects positions parallel to a stream therefore sample only a particular density of any one species.

Results: Roadside Counts

To provide a larger sample for evaluation, data from the 1976, 1977 and 1978 roadside counts were combined into one pooled data set. Grimm's duikers, bushbucks and reedbucks were not included in the analyses. Because of their secretive diurnal habits, few observations could be made on those species from vehicles.

As compared to pooled foot transect data, sample sizes for the pooled roadside counts are larger for each species. The pooled angle and distance measures are comparable to those of foot transects, except for several species where mean angles are somewhat larger (Table 38). Density estimates exhibit a wide range of values, as did foot transect estimates, though ranges here are slightly less extreme (Table 39). Patterns in relationships between roadside count estimators are similar to those reported for foot transects, especially regarding those

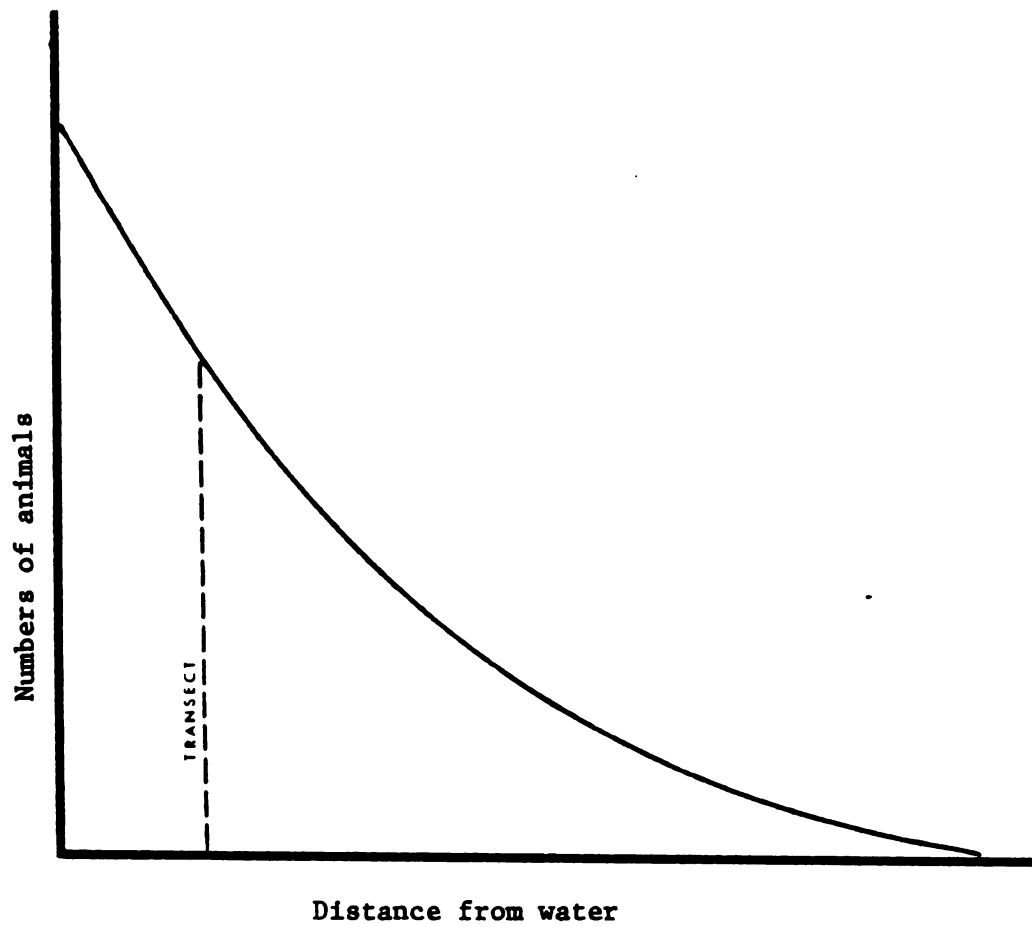


Figure 26. Diagrammatic representation of the decreasing concentrations of animals from a stream and the relative position of a transect positioned parallel to a stream.

Table 38. Basic measures of pooled data from roadside counts recorded during the 1976-1978 censuses in Park W, Niger.

Species	Number of observations	Mean angle	Mean perpendicular distance*	Mean sighting distance	Mean disappearing distance
Kob	121	39.2	39.7	68.1	90.6
Waterbuck	81	37.0	42.1	71.5	104.6
Roan	93	33.2	40.0	82.6	104.3
Hartebeest	61	37.8	38.9	67.9	100.2
Buffalo	52	43.3	45.1	71.3	102.1
Elephant	42	40.7	40.1	73.7	83.8
Oribi	78	36.7	40.7	70.9	84.9
Warthog	79	38.9	35.2	60.8	82.3

*Distances are in meters.

Table 39. Density estimates from the 18 estimators from pooled data of roadside counts in Park W, Niger.

Estimator	Kob	Waterbuck	Roan	Hartebeest	Buffalo	Elephant	Oribi	Warthog
<u>(Ungrouped data)</u>								
<u>Perpendicular distance</u>								
Exponential	1.776	.653	.069	.077	.015	.015	.137	.220
Half-Normal	2.004	.578	.255	.158	.109	.110	.184	.223
Quadratic	1.171	.563	.175	.158	.129	.154	.188	.165
Triangular	1.304	.525	.180	.138	.088	.092	.176	.161
Generalized Exp.	1.934	.568	.141	.100	.071	.100	.168	.192
Polynomial	1.200	.501	.180	.075	.010	.099	.141	.131
Fourier Series	1.253	.346	.177	.106	.079	.088	.118	.138
Dasmann & Mossman	3.048	.916	.362	.231	.156	.163	.274	.340
Webb	2.811	.896	.320	.216	.144	.136	.263	.313
<u>Disappearing distance</u>								
Hahn	1.354	.368	.131	.090	.78	.069	.117	.146
<u>Radial distance</u>								
Geometric	2.044	.696	.193	.149	.117	.099	.176	.236
Modified Hayne	1.935	.958	.212	.145	.098	.084	.181	.258
Hayne Const. Rad.	2.392	.958	.212	.145	.098	.084	.181	.317
Exponential	3.539	1.073	.348	.262	.196	.175	.312	.392
King	1.77	.540	.175	.132	.099	.089	.157	.197

Table 39. (cont'd.)

Estimator	Kob	Waterbuck	Roan	Hartebeest	Buffalo	Elephant	Oribi	Warthog
(Grouped data)								
<u>Perpendicular distance</u>								
Kelker	1.607	.610	.114	.143	.074	.067	.120	.197
Eberhardt-Cox	1.425	.763	.033	.157	.066	.037	.084	.204
Splined	1.607	.610	.195	.143	.083	.098	.157	.197
Polynomial	1.692	.562	.094	.148	.078	.089	.151	.204
Quadratic	1.797	.617	.170	.149	.084	.089	.156	.224
Triangular	2.160	.685	.227	.166	.098	.123	.196	.275

estimators which characteristically yield high or low estimates. The Webb, Dasmann-Mossman and Exponential (r) estimators are always high, while the Hahn estimator is always low (Table 40). Yet estimates of the Hahn estimator are seldom the lowest, however, because of the erratic nature of several other estimators which sometimes yield very low estimates which are out-of-line with all others. The Exponential (x), Polynomial (ungrouped) and Eberhardt-Cox estimators, for example, are moderate in some cases but extremely low in others.

A tight grouping of estimates based on grouped data, as found for foot transect data, is evident in roadside counts only for kobs, waterbucks, hartebeests and buffaloes. The large variability among density estimates for the other four species is caused mainly by extreme estimates from the Triangular and Eberhardt-Cox estimators, respectively.

Among the radial estimators, the Exponential estimator is always the highest and the King always the lowest (Table 40). The sequential relationship between estimators in ascending order is King < Geometric < Modified Hayne < Hayne Constant Radius < Exponential, which coincides with that for foot transect data. Only the Geometric estimator is always moderate (Table 41), though the King estimator is moderate for 6 of the 8 species, and never as low as the Hahn estimator. A comparison of sequential rankings (Table 40) between pooled foot and roadside transect data shows the similar patterns between the two data sets. Two exceptions include the Fourier Series estimator, which is moderate for foot transects and low for roadside counts, and the King estimator, which is ranked much lower for foot transects. The relative values (Table 42) for estimators also are usually the same for the two data sets.

Table 40. Rankings of estimates from pooled roadside transect data in Park W, Niger.

Estimator	Kob	Waterbuck	Roan	Hartebeest	Buffalo	Elephant	Oribi	Warthog	Total
Exponential	9	11	2	2	2	1	5	9	41
Hemingway-Normal	14	9	15	14	13	15	15	10	105
Quadratic	1	7	8	15	15	19	16	5	86
Triangular	4	4	9	7	10	10	12	4	60
Generalized Exp.	12	8	5	4	4	14	11	6	64
Polynomial	2	3	9	1	1	13	6	1	36
Fourier Series	3	1	8	5	7	5	3	2	34
Dasmann & Mossman	19	16	18	19	18	20	20	17	147
Webb	18	15	16	18	17	18	19	15	136
Hahn	5	2	4	2	5	4	2	3	27
Geometric	15	13	10	11	14	12	13	12	90
Modified Hayne	13	17	12	9	11	6	14	13	95
Hayne Const. Rad.	17	19	13	17	16	16	18	16	132
Exponential	20	18	17	20	19	21	21	18	154
King	10	5	7	6	12	7	9	7	63
Kelker	7	9	2	8	5	3	4	7	45
Eberhardt-Cox	6	14	1	13	3	2	1	8	48
Splined	7	9	11	8	8	11	10	7	71
Polynomial	8	6	3	10	6	8	7	8	56
Quadratic	11	10	6	12	9	9	8	11	76
Triangular	16	12	14	16	11	17	17	14	117

Table 41. Relative values of estimates from pooled roadside counts in Park W, Niger.

Estimator	Kob	Waterbuck	Roan	Hartebeest	Buffalo	Elephant	Oribi	Warthog
Exponential	M	M	L	L	L	L	M	M
Hemingway Normal	M	M	M	M	M	M	M	M
Quadratic	L	M	M	M	M	H	M	L-M
Triangular	L	M	M	M	L-M	M	M	L-M
Generalized Exp.	M	M	L-M	L-M	L	M	M	M
Polynomial	L	M	M	L	L	M	M	L
Fourier Series	L	L	M	L-M	L	M	L	L
Dasman-Mossman	H	H	H	H	H	H	H	H
Webb	H	H	H	H	H	M-H	H	H
Hahn	L	L	L	L	L	L	L	L
Geometric	M	M	M	M	M	M	M	M
Modified Hayne	M	M	M	M	M	M	M	M
Hayne Const. Radius	M	H	M	M	M	M	M	H
Exponential	H	H	H	H	H	H	H	H
King	L-M	M	M	M	M	M	M	M
Kelker	M	M	L	M	L	L	L	M
Eberhardt-Cox	M	M	L	M	L	L	L	M
Splined	M	M	M	M	L	M	M	M
Polynomial	M	M	L	M	L	M	M	M
Quadratic	M	M	M	M	L	M	M	M
Triangular	M	M	M	M	M	M	M	M

Table 42. Rankings and relative values of the totals for all species for pooled foot and roadside transect data in Park W, Niger.

Estimator	Foot		Roadside	
	Rank	Value	Rank	Value
Exponential	9	I	4	I
Hemingway Normal	15	M-H	16	M-H
Quadratic	10	I	13	I
Triangular	5	L-M	8	L-M
Generalized Exponential	6	M	10	M
Polynomial	2	L-M	3	I
Fourier Series	12	M	2	L-M
Dasmann and Mossman	19	H	20	H
Webb	18	H	19	H
Hahn	1	L	1	L
Geometric	10	M	14	M
Modified Hayne	18	I	15	M-H
Hayne Constant Radius	17	M-H	18	M-H
Exponential	20	H	21	H
King	3	L-M	9	M
Kelker	4	M	5	L-M
Eberhardt-Cox	8	M	6	L-M
Splined	7	M	11	M
Polynomial	14	M	7	M
Quadratic	13	M	12	M
Triangular	16	M	17	M-H

The main differences are for estimators such as the Fourier Series and King in which a slight shift occurs from L to L-M or M to M-H.

Hahn estimator

The Hahn estimator has the lowest overall ranking (Table 42), but there is less discrepancy between the Hahn and moderate estimates than for foot transects. For several species, density estimates of the Hahn are only slightly below moderate values, and below estimates from the Dasmann-Mossman and Webb estimators by a factor of about two rather than three.

Frequency histograms of perpendicular, sighting, and disappearing distances are very similar to those for pooled foot transect data, with the exception of more sightings made at longer distances (Figs. 27a and b). This may be because it is easier to concentrate on spotting animals while riding. Consequently, the discrepancy between estimates based on sighting and perpendicular distances and the Hahn estimator is reduced. Based on a comparison between perpendicular and disappearing distances, however, the Hahn estimator in all likelihood still underestimates population density from roadside counts. Few animals were initially spotted at the points where they disappeared. This indicates that during roadside counts, observers can totally concentrate on spotting animals even though it is more difficult to locate animals than to follow them to the limits of visibility.

Goodness-of-fit tests to detection functions

Goodness-of-fit tests to detection functions follow patterns similar to those determined for foot transect data (Table 43). Radial distances are nearly always distributed negative exponentially, with

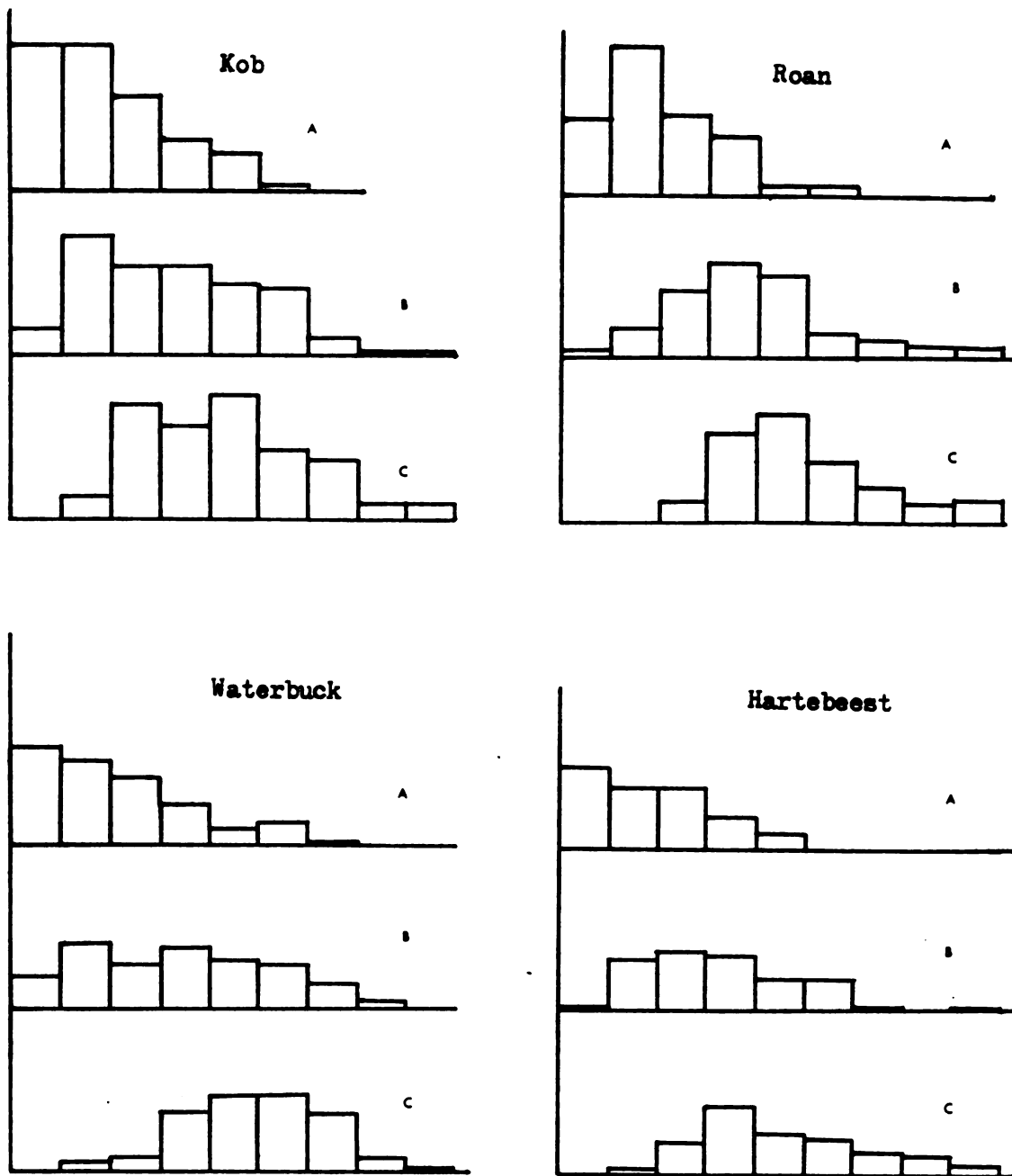


Figure 27a. Histograms of perpendicular (a), sighting (b) and disappearing (c) distances of the pooled roadside count data of kob, waterbuck, roan and hartebeest.

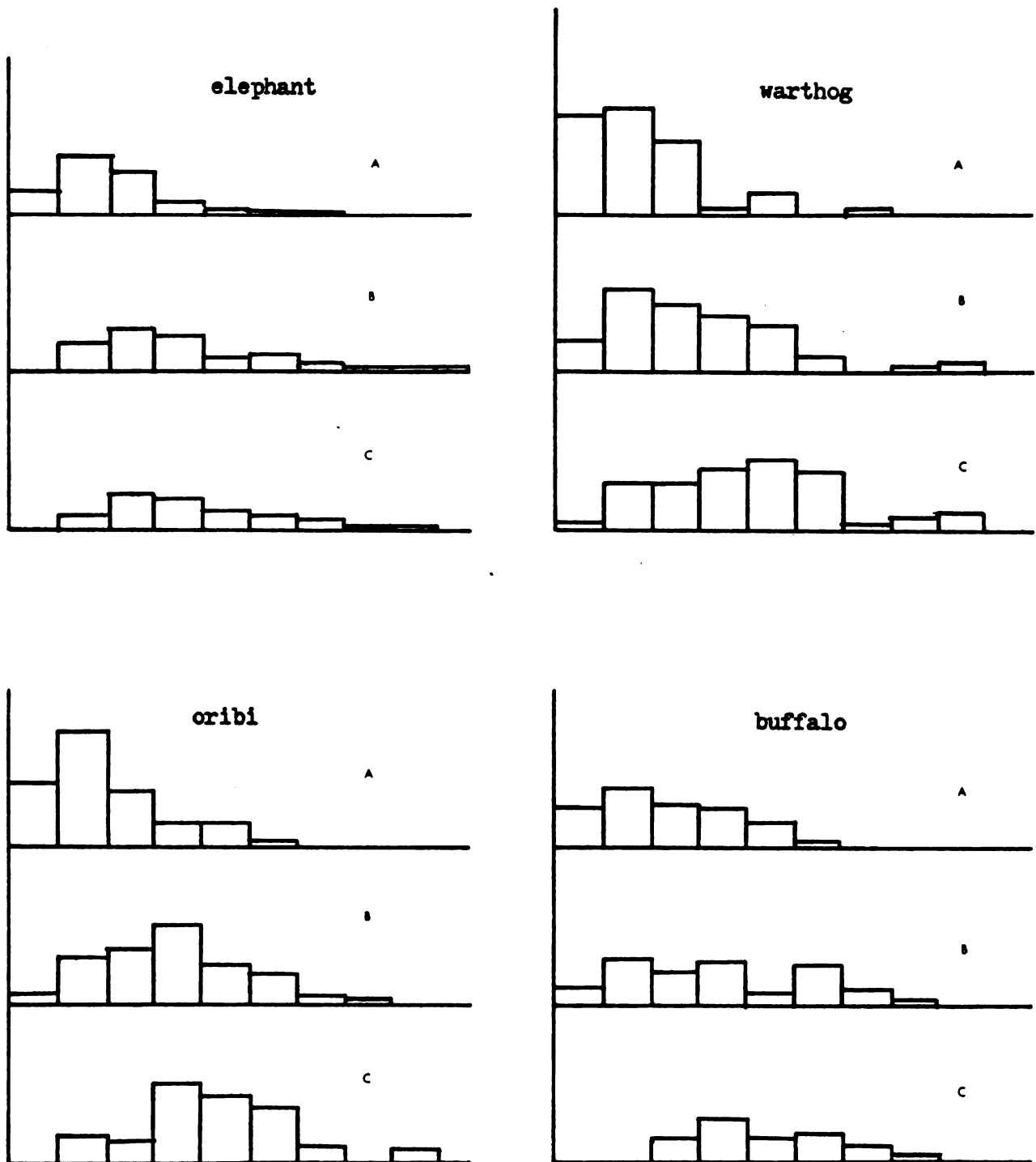


Figure 27b Histograms of perpendicular (a), sighting (b) and disappearing (c) distances of the pooled roadside count data of buffalo, elephant, oribi and warthog.

Table 43. Values of goodness-of-fit tests to specified distributions for pooled roadside count data in Park W, Niger.

	Kob	Waterbuck	Roan	Hartebeest	Buffalo	Elephant	Oribi	Warthog
K-S criterion:	.124	.152	.142	.176	.190	.212	.155	.154
<u>Distribution</u>								
Gamma, α variable	.098	.129	.083	.056	.102	.084	.060	.055
Gamma, $\alpha = 2.0$	.101	.111	.158*	.119	.087	.127	.134	.103
Half Normal	.063	.092	.169*	.139	.142	.139	.107	.081
Triangular	.235*	.128	.181*	.099	.119	.401*	.090	.205*
Gamma, $\alpha = 1.0$	.227	.149	.647*	.459*	.813*	.789*	.292*	.245*
Generalized Exp.	.992*	.095	.989*	.984*	.962*	.976*	.987*	.987*
Gamma, α variable	.062	.114	.049	.125	.095	.078	.058	.056
Quadratic	.042	.186*	.068	.315*	.445*	.460*	.202*	.145
Polynomial	.059	.250*	.035	.330*	.423*	.496*	.213*	.074

*Significant at the 95% confidence level.

α = variable usually giving the best fit. Among the perpendicular distance distributions, consistently good fits are evident for both the half-normal and gamma distributions with α = variable. The suprema for the triangular, generalized exponential and gamma with α = variable distributions often exceed the critical value. Similarly, fits to the polynomial and quadratic distributions are significantly different for five of the eight species.

As indicated earlier for foot transect data, poor fits to certain distributions may explain why estimates are unusually high or low. With roadside counts, this cause and effect is less evident. When suprema for the triangular distribution are significantly above the critical value, density estimates are still moderate. Only for the Quadratic and Polynomial estimators do goodness-of-fit tests aid in explaining erratic estimates.

Frequency distributions

The most obvious characteristic of frequency distributions of pooled roadside count data was the fewer observations in the first distance class as compared with the second (Fig. 28). The skewed distributions were likely caused by avoidance of roads by animals, presumably because of vehicle disturbance. This avoidance of roads is more clearly illustrated by examining the detection functions between the transect line and 40 m, the point where most frequencies of sightings rapidly declined. For nearly every species, there were fewer observations in the first 10 m than the next three sighting classes (Fig. 28). For oribis, the detection function is the reverse of the expected shape. Despite the skewed distributions, the suprema for those species are

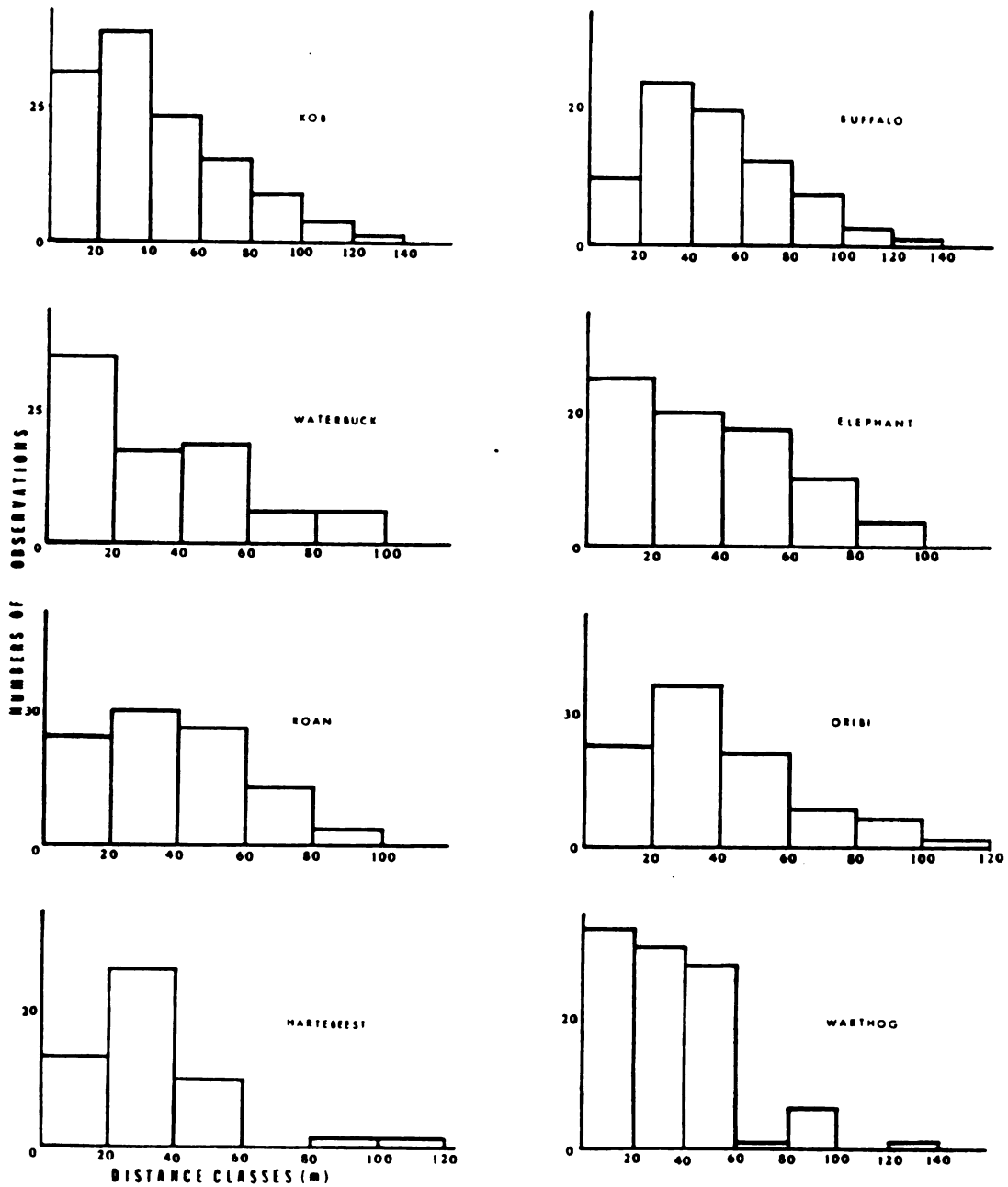


Figure 28. Frequency histograms of observed perpendicular distances for pooled roadside count data in Park W, Niger.

surprisingly low. With buffalo and oribi, for example, good fits are evident for the gamma and half normal distributions, though there were few observations in the first sighting class. But, as is the case for buffalo (Fig. 28), the poor fit at the origin is compensated for by a relatively good fit for the remainder of the frequency distribution.

1976-1978 roadside counts

Results of the 1976-1978 roadside counts in the study area were evaluated in a manner similar to foot transect data. Sample sizes were considerably larger for roadside counts (Table 44), but data were too few to group except in a few cases, and evaluations of grouped data were omitted.

Although angles, sighting and perpendicular distance measures vary considerably between species and between years (Table 45), patterns among density estimates are remarkably constant. These patterns, however, differ from those of the pooled roadside data set, probably because of smaller sample sizes.

The rankings of estimators show that the Hahn estimator is always low, while the Dasmann-Mossman and Webb estimators are always high, as was the case for the pooled data set. The highest estimates, though, are from the Quadratic, Triangular, Polynomial and Exponential (r) estimators. Estimates from the first three are often considerably higher than the Webb and Dasmann-Mossman estimator, and in some cases, completely out-of-line.

Values of the Fourier Series estimator range from very low, below those of the Hahn estimator, to moderate. Among estimators based on perpendicular distances, only the Hemingway-Normal and Generalized

Table 44. Basic measures of roadside counts in the study area in 1976, 1977, and 1978 in Park W, Niger. Distances are in meters.

Species	Number of observations			Mean perpendicular distance			Mean sighting distance			Mean disappearing distance			Mean angle		
	1976	1977	1978	1976	1977	1978	1976	1977	1978	1976	1977	1978	1976	1977	1978
Kob	13	18	21	38.1	44.5	40.1	63.5	68.1	67.4	91.3	86.5	93.5	36.0	39.2	38.1
Waterbuck	15	14	17	30.7	35.8	34.6	62.3	66.8	58.9	100.3	110.4	103.5	30.0	33.9	35.8
Roan	9	28	24	38.3	36.3	38.4	82.4	66.8	80.2	112.5	106.7	98.3	34.2	31.7	31.5
Hartebeest	12	10	8	32.3	46.3	33.0	54.2	72.6	59.6	91.2	106.7	107.1	36.9	44.3	36.0
Buffalo	7	8	5	34.1	45.3	56.0	62.6	71.9	94.0	93.1	102.5	114.0	45.2	41.3	38.2
Elephant	5	8	19	20.1	41.4	43.3	55.0	68.8	84.2	57.0	76.3	94.4	45.2	40.6	36.9
Oribi	14	26	14	31.3	38.1	41.4	50.4	68.5	70.9	80.0	88.5	83.1	35.0	37.7	35.6
Warthog	6	13	22	23.4	30.2	32.8	46.3	51.8	62.8	78.5	71.8	89.6	43.8	39.8	36.0

Table 45. Density estimates from roadside counts in the study area in 1976, 1977 and 1978 in Park W, Niger.

Estimator	Ech			Waterbuck			Reon			Maribeeet			Buffalo			Elephant			Oribi			Verboog		
	1976	1977	1978	1976	1977	1978	1976	1977	1978	1976	1977	1978	1976	1977	1978	1976	1977	1978	1976	1977	1978	1976	1977	1978
(Perpendicular)																								
Exponential	.541	.949	1.535	.440	.120	.561	.014	.016	.014	.130	.011	.046	.067	.019	.002	.016	.058	.025	.215	.084	.116	.054	.060	.012
Hemipray Normal	.783	.781	1.058	.516	.384	.391	.115	.217	.186	.153	.608	.067	.066	.049	.028	.112	.047	.131	.180	.184	.089	.104	.121	.190
Quadratic	3.470	3.577	3.510	1.631	1.564	1.742	.058	.345	.306	.643	.174	.357	.553	.240	.150	.410	.384	.355	.916	.399	.444	.530	.305	.362
Triangular	1.990	1.150	3.238	.989	.823	1.338	.502	.156	.004	.424	.161	.249	.395	.014	.319	.110	.322	.020	.747	.221	.437	.218	.075	.150
Generalized Exp.	.813	1.048	1.430	.537	.505	.622	.094	.110	.133	.150	.039	.063	.086	.036	.026	.093	.062	.066	.264	.151	.096	.072	.094	.160
Polynomial	.060	.986	2.431	1.670	1.256	2.646	.118	.193	.077	.817	.033	.409	.535	.182	.135	.049	.401	.062	1.056	.172	.333	.445	.087	.157
Fourier Series	.620	.526	.691	.379	.348	.252	.094	.169	.148	.112	.059	.041	.053	.036	.026	.093	.025	.107	.124	.131	.054	.072	.096	.153
Daemann & Hozmann	1.210	1.272	1.769	.828	.631	.671	.151	.311	.260	.239	.087	.101	.132	.071	.037	.160	.078	.183	.288	.275	.141	.165	.174	.280
Bebb	1.235	1.315	1.706	.816	.606	.674	.125	.284	.239	.238	.080	.095	.106	.048	.036	.083	.072	.157	.312	.250	.141	.121	.158	.248
(Diagpp. Dist.)																								
Hahn	.505	.654	.759	.253	.205	.224	.052	.106	.102	.086	.037	.031	.049	.032	.018	.057	.042	.084	.113	.137	.070	.049	.073	.102
(Radial Dist.)																								
Geometric	.834	1.006	1.227	.557	.462	.596	.078	.161	.137	.166	.064	.084	.094	.054	.024	.076	.056	.098	.211	.177	.091	.127	.114	.171
Modified Wayne	.867	.973	1.320	.996	.753	.942	.082	.082	.160	.172	.047	.068	.085	.050	.023	.056	.047	.090	.234	.175	.092	.158	.102	.179
Wayne Const. Rad.	.961	1.025	1.572	.922	.781	1.016	.086	.173	.154	.196	.071	.075	.118	.084	.027	.088	.062	.103	.251	.205	.101	.153	.129	.198
Exponential	1.397	1.617	2.056	.789	.652	.765	.133	.293	.244	.274	.106	.105	.134	.067	.040	.105	.088	.183	.346	.300	.159	.236	.195	.285
King	.726	.831	1.053	.408	.338	.290	.070	.149	.125	.143	.056	.056	.072	.045	.022	.059	.047	.094	.179	.153	.082	.084	.101	.146
Aerial count	.49%			.293			.044			.039			.076			.069								

Exponential are consistently moderate (Table 46). Among the radial estimators, only the Geometric estimator is always moderate, though the Modified Hayne nearly always is.

Comparisons of foot transect and roadside count estimates

The patterns of relative values of estimators for all species and censuses are generally consistent between species (Table 47). The Hahn estimator is always low, Geometric always moderate, and the Dasman-Mossman, Webb and Exponential estimators are always high. The Hemingway-Normal and Generalized Exponential are always moderate for roadside counts and usually for foot transects. Both the Fourier Series and King estimators range from low to moderate, while the Modified Hayne and Hayne CR estimators are high to moderate. The remaining estimators, Exponential (x), Triangular, Quadratic and Polynomial, are less predictable, and often give estimates which are extremely high or low.

Comparisons of aerial, roadside and foot transect counts

Comparisons between foot and roadside counts in the study area indicate that for each species, density estimates from roadside counts are nearly always lower than those of foot transects, usually be a factor of two or three. To illustrate these differences, comparisons are shown (Table 48) for three estimators, the Hahn, Geometric and Webb, which represent low, moderate and high estimates. Only in 1977, are density estimates similar for oribi, elephant, buffalo and hartebeest. In all other instances density estimates from roadside counts are lower than those of foot transects. Density estimates from roadside counts of the two riparian species, kob and waterbuck, are surprisingly

Table 46. Rankings of estimators for the 1976, 1977 and 1978 roadside counts in the study area in Park W, Niger.

Estimator	Kob	Waterbuck	Roan	Hartebeest	Buffalo	Elephant	Oribi	Warthog
Exponential	3 5 8	4 1 5	1 1 1	3 1 3	3 1 2	1 7 2	6 1 9	2 1 1
Half-Normal	6 3 3	5 5 4	10 11 11	6 15 7	6 6 9	13 5 11	4 9 4	6 10 10
Quadratic	15 15 15	14 15 14	1 15 15	14 14 14	15 14 15	15 14 15	14 15 15	15 15 15
Triangular	14 12 14	12 9 13	15 5 1	13 13 13	13 1 14	12 13 1	13 11 14	12 3 3
Generalized Exp.	7 9 7	6 7 7	9 3 6	5 4 5	7 4 7	10 9 5	9 4 7	4 5 7
Polynomial	1 1 13	15 14 15	10 13 3	15 13 15	14 13 13	2 15 3	15 6 13	14 4 6
Fourier Series	4 1 1	2 4 2	8 7 8	2 7 2	2 4 6	9 1 10	2 2 1	3 6 5
Dasman & Mossman	11 11 11	10 10 8	14 14 14	11 11 11	11 11 11	14 11 13	10 13 11	11 13 13
Webb	12 13 10	1 8 9	13 12 12	10 10 10	9 10 10	7 10 12	11 12 10	8 12 12
Hahn	2 2 2	1 2 1	2 2 4	1 2 1	1 3 2	2 4 2	1 3 2	1 2 2
Geometric	8 8 5	7 6 6	5 6 7	7 8 6	8 8 5	6 6 8	5 8 5	7 9 8
Modified Hayne	9 6 6	13 12 11	6 9 10	8 5 8	5 7 4	3 4 6	7 7 6	10 8 9
Hayne Const. Rad.	10 10 9	11 13 12	7 8 9	9 9 9	10 12 8	8 8 9	8 10 8	9 11 11
Exponential	13 14 12	8 11 10	12 13 13	12 12 12	12 9 12	11 12 14	12 14 12	13 14 14
King	5 4 4	3 3 3	4 4 5	4 6 4	4 5 3	5 3 7	3 5 3	5 7 4

Table 47. Overall relative values of estimators for foot and roadside counts in Park W, Niger.

Estimator	Foot Transects				Roadside Counts				
	1976	1977	1978	1978*	Pooled	1976	1977	1978	Pooled
Exponential	I	M-H	M-H	I	I	L-M	L	L	I
Half-Normal	M-H	M	M	M	M-H	M	M	M	M
Quadratic	H	H	H	H	M-H	H	H	H	I
Triangular	I	H	I	I	L-M	H	I	I	M
Generalized Exp.	M-H	M	M	M-H	M	M	M	M	M
Polynomial	H	H	I	I	L-M	I	I	I	L-M
Fourier Series	L-M	L	L-M	L-M	M	M	L-M	L-M	L-M
Dassman & Mossman	H	H	H	H	H	H	H	H	H
Webb	H	H	H	H	H	H	H	H	H
Hahn	L	L	L	L	L	L	L	L	L
Geometric	M	M	M	M	M	M	M	M	M
Modified Hayne	L-M	M	I	M-H	I	M-H	M	M	M
Hayne Const. Rad.	M	M	M-H	M-H	M-H	M-H	M-H	M	M-H
Exponential	H	H	H	H	H	H	H	H	H
King	L-M	L-M	L-M	L-M	L-M	L-M	L-M	L-M	M

L = estimates were low in relation to all others
M = estimates were moderate in relation to all others
H = estimates were high in relation to all others

L-M = estimates were low to moderate
M-H = estimates were moderate to high
I = had no definite pattern and values were extreme

Table 48. Comparisons of selected density estimates between foot and roadside counts in the study area from 1976-1978 in the study area in Park W, Niger. Densities are in numbers/km²

Estimator	1976		1977		1978	
	Foot	Road	Foot	Road	Foot	Road
<u>Kob</u>						
Hahn	1.316	0.505	0.877	0.654	1.429	0.759
Geometric	1.986	0.834	1.445	7.000	2.936	1.227
Webb	3.041	1.235	2.416	1.315	3.000	1.706
<u>Waterbuck</u>						
Hahn	0.877	0.253	0.772	0.205	0.124	0.102
Geometric	1.434	0.834	1.004	0.462	1.240	0.596
Webb	1.859	1.235	1.975	0.606	2.105	0.674
<u>Roan</u>						
Hahn	0.138	0.052	0.210	0.106	0.124	0.102
Geometric	0.255	0.078	0.177	0.161	0.414	0.137
Webb	0.362	0.125	0.485	0.284	0.402	0.239
<u>Hartebeest</u>						
Hahn		0.086	0.053	0.037	0.074	0.031
Geometric		0.166	0.068	0.064	0.101	0.064
Webb		0.238	0.071	0.080	0.157	0.095
<u>Buffalo</u>						
Hahn	0.215	0.049	0.062	0.032	0.061	0.018
Geometric	0.303	0.094	0.070	0.054	0.182	0.024
Webb	0.487	0.108	0.189	0.068	0.321	0.036
<u>Elephant</u>						
Hahn		0.057	0.035	0.042	0.112	0.084
Geometric		0.076	0.061	0.056	0.168	0.098
Webb		0.083	0.101	0.072	0.269	0.157
<u>Oribi</u>						
Hahn	0.157	0.113	0.140	0.137	0.238	0.070
Geometric	0.157	0.211	0.181	0.177	0.328	0.091
Webb	0.284	0.312	0.321	0.250	0.526	0.141
<u>Warthog</u>						
Hahn	0.369	0.049	0.211	0.073	0.210	0.102
Geometric	0.741	0.127	0.264	0.114	0.359	0.171
Webb	1.333	0.121	0.321	0.158	0.526	0.248

lower than those of foot transect counts, since roads traverse areas of high kob and waterbuck densities.

A comparison between aerial and roadside counts (see Table 45) shows that for hartebeest, buffalos and elephants density estimates are similar. For kobs, roans, and waterbucks, estimates from roadside counts are generally much lower than aerial counts. The same pattern is evident for foot transect counts, in that estimates for the large buffalos and elephants are comparable.

There are mainly two factors which contribute to the lower density estimates from roadside counts. First, comparisons between the numbers of groups counted per kilometer of transect clearly shows that values from roadside counts are below those of foot transects in nearly every case (Table 49). Because roads poorly sampled the central portion of the study area, comparison counts were made only in the two high-animal-density areas where roads provide better coverage.

Values from roadside counts, however, are still below those of foot transects in most cases, though discrepancies between values are considerably less for several species (Table 50). For roans, buffaloes, elephants and warthogs, numbers-per-linear-kilometer are quite close in at least one of the years. Large differences remain, however, for kobs, waterbucks, oribis, and in one or more years, for roans, hartebeests and warthogs.

Second, the shape of the frequency distribution can contribute to lower density estimates. Burnham et al. (1980) found through simulation tests that density estimates may underestimate actual abundance by as much as 100% when fewer observations are made near the transect line than at longer distances. The frequency distributions in Figure 29

Table 49. Comparisons between numbers of groups recorded per kilometer of foot and roadside counts during the 1976, 1977 and 1978 censuses in the entire central study area in Park W, Niger.

Species	1976		1977		1978	
	Foot	Road	Foot	Road	Foot	Road
Kob	.286	.042	.200	.062	.333	.080
Waterbuck	.200	.016	.167	.051	.278	.080
Roan	.032	.008	.026	.027	.029	.018
Hartebeest	-	.010	.009	.005	.029	.007
Buffalo	.016	.012	.017	.019	.015	.011
Elephant	-	.006	.009	.005	.022	.023
Oribi	.032	.021	.043	.025	.036	.013
Warthog	.064	.006	.017	.016	.015	.020

Table 50. Comparisons of numbers of groups counted per kilometer of transect for foot and roadside counts in high animal-density areas within the central study area in Park W, Niger.

Species	Year					
	1976		1977		1978	
	Foot	Roadside	Foot	Roadside	Foot	Roadside
Kob	.286	.092	.200	.113	.333	1.42
Waterbuck	.200	.051	.167	.045	.278	.147
Roan	.066	.012	.050	.023	.028	.020
Hartebeest		.016	.008	.008	.022	.007
Buffalo	.040	.009	.025	.007	.025	.004
Elephant		.006	.017	.007	.023	.016
Oribi	.026	.018	.050	.021	.039	.012
Warthog	.053	.008	.042	.011	.028	.018

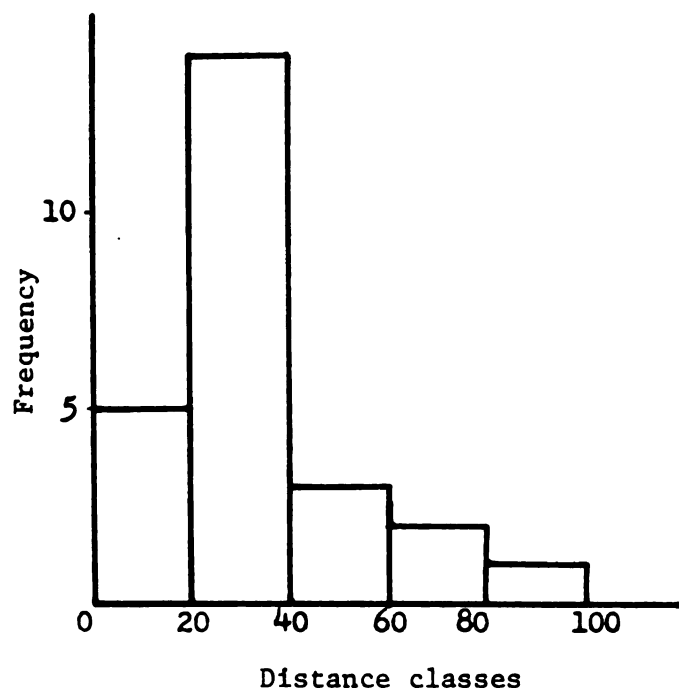
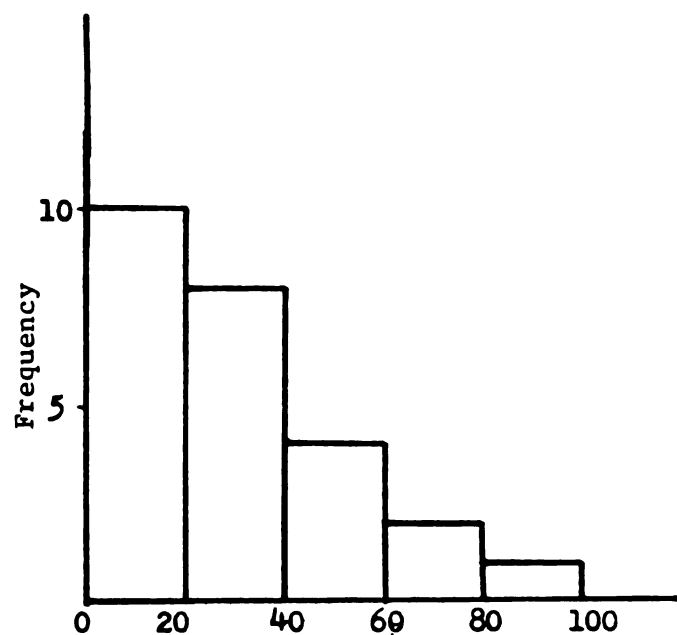


Figure 29. Frequency histograms of foot transects (top) and roadside counts (bottom) of kobs from the 1978 park-wide survey in Park W, Niger. (n=25).

represent observations from foot and roadside counts from the 1978 park-wide survey. The distribution of perpendicular distances from foot transects are approximately half-normal, while those of the roadside count are skewed (fewer observations in the first sighting class). The corresponding density estimates from roadside counts are below those of foot transects for most estimators (Table 51).

Goodness of fit tests

Goodness of fit tests to distributions (Table 52) revealed that the detection functions were rarely triangular, and that good fits could seldom be obtained with the polynomial or quadratic distributions. Despite the skewed detection functions, however, they were seldom significantly different from the exponential or half-normal distributions. The large values for the Generalized Exponential distribution were again believed the cause of program errors.

Tests of assumptions

For pooled data, tests of the validity of radial estimators revealed that for most species, the critical values have been exceeded (Table 53). Fits to the Cosine theta distribution were significantly different from expected distributions for all species except hartebeest. Similarly, Z values are significant for most species. Despite these indications that radial estimators are not appropriate for roadside counts, the patterns and relative values of estimates from radial estimators remained constant, whether or not the tests were significant. Moreover, these patterns were similar to those for pooled foot transect data, most of which were not significant.

Table 51. Density estimates for a distribution which is approximately half normal and one which is skewed (fewer observations in the first sighting class).

Estimator	Half-Normal	Skewed	Difference
Exponential	3.886	3.270	-.616
Hemingway Normal	2.580	2.388	-.192
Quadratic	5.084	5.660	+.576
Triangular	5.317	6.066	+.749
Generalized Exp.	2.580	1.244	-1.366
Polynomial	5.211	3.154	-2.057
Fourier Series	1.250	1.244	-.006
Dasmann-Mossman	4.048	3.406	-.642
Webb	3.834	3.238	-.596
(Grouped data)			
Kelker	2.118	1.442	-.676
Eberhardt-Cox	2.294	.721	-1.573
Splined	2.118	2.163	+.045
Polynomial	2.384	2.232	-.152
Quadratic	2.124	1.754	-.370
Triangular	2.550	2.318	-.232
(Radial distances)			
Geometric	2.186	2.186	.000
Modified Hayne	2.451	2.114	-.337
Hayne Const. Rad.	2.464	2.464	.000
Exponential	3.857	3.869	+.012
King	1.967	1.967	.000

Table 52. Values of goodness of fit tests to specified distributions for the 1976, 1977 and 1978 roadside counts in the Central Study Area in Park W, Niger.

	Kob			Waterbuck			Roan			Hartebeest			Buffalo			Elephant			Oribi			Marthot		
	1976	1977	1978	1976	1977	1978	1976	1977	1978	1976	1977	1978	1976	1977	1978	1976	1977	1978	1976	1977	1978	1976	1977	1978
K-S Criterion:																								
Distribution	.393	.330	.304	.363	.377	.340	.481	.262	.284	.410	.453	.514	.555	.514	.680	.680	.514	.321	.377	.272	.377	.608	.393	.297
Exponential, α var	.158	.105	.118	.092	.117	.203	.187	.085	.081	.144	.245	.144	.246	.165	.207	.339	.297	.154	.096	.088	.093	.252	.109	.096
Exponential, $\alpha = 1.0$	.183	.100	.099	.094	.122	.247	.198	.194	.180	.115	.269	.140	.315	.148	.331	.482	.346	.258	.090	.109	.153	.273	.133	.108
Half normal	.115	.141	.150	.187	.176	.293	.312	.189	.189	.214	.104	.183	.191	.140	.182	.134	.243	.235	.133	.106	.186	.242	.117	.097
Triangular	1.385*	1.616*	.758*	.401*	1.866*	.819*	1.567*	.564	.170	.419*	.864*	.965*	1.315*	.386	3.240*	.546	2.431*	.317	1.151*	.389*	.809*	.317	.174	.473*
Gamma, $\alpha = 1.0$	.356	.179	.114	.262	.651*	.245	1.000*	1.000	1.000*	.306	1.000*	.355	.357	1.000*	1.000*	.000*	.282	1.000*	.200	.490*	.188	.473	1.000*	1.000*
Generalized Exp.	.100	.946*	.081	.178	.929*	.218	.889*	.964*	.958*	.219	.900*	.200	.191	.875*	.800*	.800*	.190	.947*	.857*	.153	.169	.803*	.923*	.955*
Gamma, $\alpha =$ variable	.079	.087	.073	.170	.109	.224	.221	.073	.133	.211	.105	.215	.180	.203	.156	.187	.178	.095	.107	.117	.155	.220	.139	.091
Quadratic	.681*	.522*	.419*	.654*	.820*	.563*	.839*	.570*	.719*	.726*	.923*	.692*	.691*	.942*	1.000*	1.000*	.542*	.814*	.440*	.600*	.452*	.807*	.792*	.685*
Polynomial	.268	.285	.417	.580*	.256	.380*	1.000*	.593*	.719*	.543*	1.000*	.645*	.000	.747*	1.000*	.175	.745*	.038	.573*	.005	.675*	.780*	.666*	

*Significant at the 95% confidence level.

Table 53. Test values from the goodness of fit test to the cosine theta distribution, whether θ is significantly different from 32.7 and $\sin \theta$ is significantly different from 0.5 for the pooled data in Park W, Niger.

Species	Cos theta	Test	
		I_1	I_2
Kob	30.52*	3.32*	5.03*
Waterbuck	17.59*	1.80	3.17*
Roan	18.45*	0.22	1.49
Hartebeest	12.31	1.85	3.06*
Buffalo	32.49*	3.55*	4.64*
Elephant	#	2.41*	3.42*
Oribi	24.13*	1.64	2.99*
Warthog	15.50*	2.56*	3.94*

* Significant at the 95% level.

Observations too few to calculate cos theta distribution

The Z tests for 1976-1978 roadside counts are mostly non-significant, though several values are only slightly below the critical value (Table 54). These results are in direct contrast to those of the pooled roadside count data (Table 53) despite the larger mean angles for several species. The non-significance though, is largely the result of smaller sample sizes. With buffaloes, for example, the mean angle and sample size in 1976 are 42.1 and 7, and the Z tests are both non-significant. If, however, the sample size had been 20, the test values would both be significant.

Assumption i, the random distribution of animals or transects was probably violated for roadside counts. As shown earlier, animal distributions were influenced by water availability, with a gradient of high to low density as distance from water increased. Much of the kilometerage of roads were parallel with rather than perpendicular to streams. An examination of animal sightings along roads revealed that sightings were clumped near water sources. In spite of the extensive road system, roadside counts did not appear to traverse a representative sample of animal populations. As noted for foot transects positioned parallel to streams, roadside counts sampled, a particular density of each riparian species rather than an average density over the study area.

An examination of field records showed that assumption ii, the independence of sightings and assumption iii, no animal counted more than once, was met. During roadside counts, the activities of one animal were not observed to influence the sighting of another except when other members of a group were detected. Movements of animals in response to observers were local, and did not result in duplicate counts on other roads.

Table 54. Test values to determine if θ is significantly different from 32.7° and $\sin \theta = 0.5$ for data from the 1976, 1977 and 1978 roadside counts in Park W, Niger.

Species	1976		1977		1978	
	Z_1	Z_2	$\bar{Z}_1$	Z_2	Z_1	Z_2
Kob	.153	1.096	1.279	1.940	1.148	1.858
Waterbuck	.485	.005	.209	.748	.593	1.213
Roan	.209	.645	.245	.467	.273	.382
Hartebeest	.675	1.205	1.701	2.174*	.433	.860
Buffalo	1.154	1.558	1.128	1.568	.570	.917
Elephant	1.296	1.623	1.036	.1477	.849	1.516
Oribi	.399	.954	1.183	1.970*	.503	1.064
Warthog	1.261	1.630	1.187	1.750	.718	1.426

* Significant at the 95% level.

$$Z_1 = E(0) = 32.7^\circ$$

$$Z_2 = \sin(0) = 0.5$$

Assumption iv, that all animals seen were in the exact position occupied as the observer approached, was violated to some degree for most species. Except for oribis and elephants, the percentages of animals running when first noticed were less for roadside counts than for foot transect counts. Approximately one-half of all oribis and elephants were in motion, either walking or running, when first spotted (Table 55). Many of those oribis, at full gallop when first seen, moved parallel to the road. In those instances, perpendicular distances were not affected by movements. Most animals which were in motion when first seen, especially those which were close to the road, usually angled away from it on being disturbed.

Bias from movement of animals which were walking when first noticed was believed to have been minimal. Nearly all movements of this type were natural movements, not induced by the vehicle. Though not quantified, observations indicated that animal movements toward and away from roads were approximately equal.

One additional assumption is needed for roadside counts: the visibility of animals along roads remain constant during the counting period. An examination of the numbers of groups counted per hour reveals variability between morning and afternoon counts (Fig. 30). A comparison between counts made during the morning, mid-day and afternoon shows that only values for roan, buffalo and hartebeests are relatively constant (Table 56). Values for other species are quite variable, though these differences are significant only at the 90% and 80% levels. For kob and waterbuck, however, the larger values obtained during afternoon counts could translate into considerably higher density estimates.

Table 55. Percentages of animals observed in activity categories when first observed along road transects and percentages of animal response to vehicles from 1976-1978 in Park W, Niger.

Species	Activity				Response		
	Standing	Walking	Running	Lying down	Remained	Walked away	Ran
Kob	69	20	2	8	48	46	6
Waterbuck	57	29	6	9	47	47	6
Roan	53	28	8	11	23	53	24
Hartebeest	45	33	11	11	11	67	22
Buffalo	68	16	0	16	47	47	6
Elephant	45	50	5	0	36	50	9
Oribi	45	10	35	10	30	25	45
Warthog	63	29	8	4	17	39	44

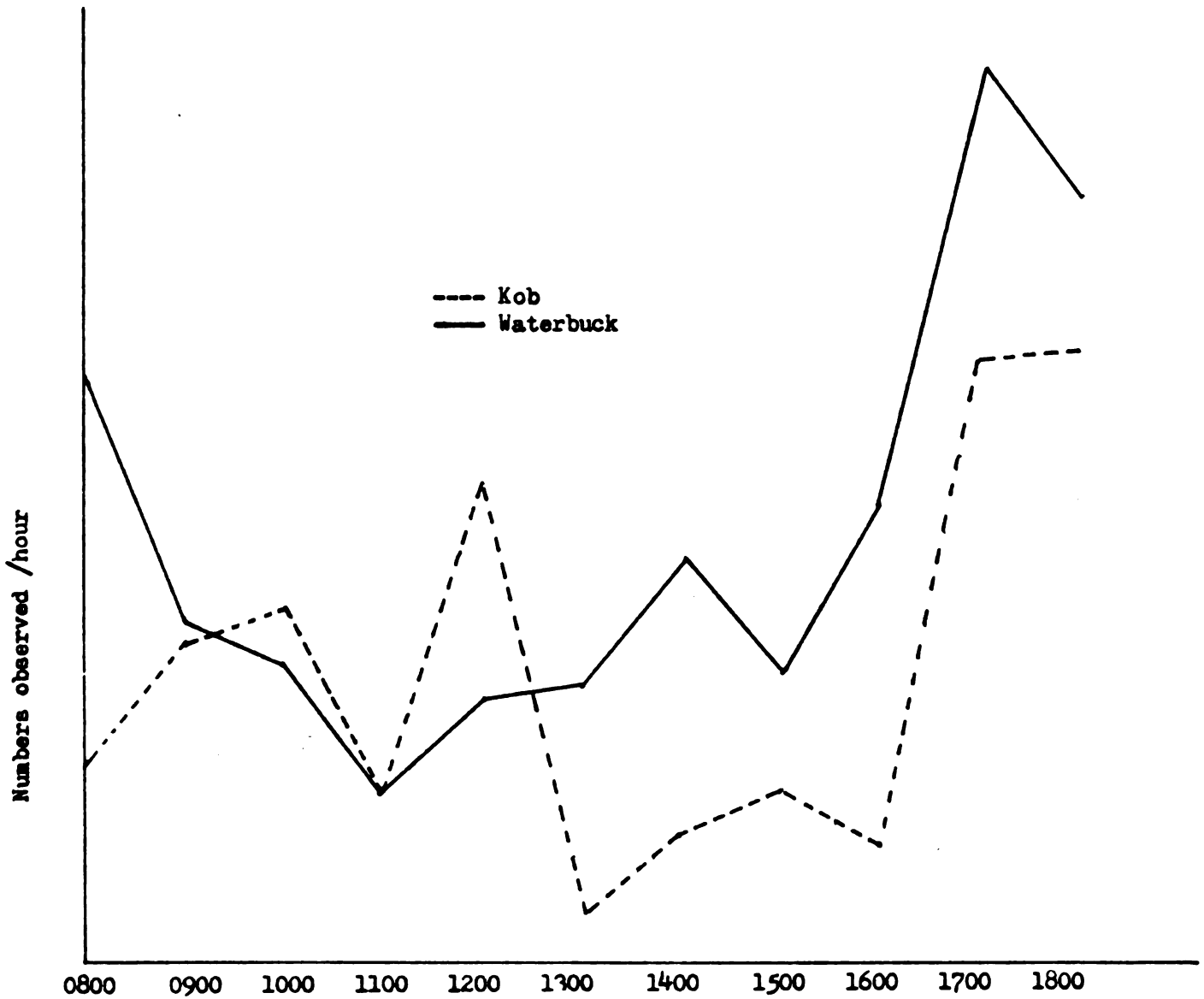


Fig. 30. Numbers of kob and waterbucks observed along roads per hour driving between 0800 and 1800 hours during the 1976-1978 roadside counts in Park W, Niger.

Table 56. Mean numbers of groups counted per hour during the 1976-1978 roadside counts in Park W, Niger.

Species	0800-1100	1100-1500	1500-1800
Kob	.245	.215	.428**
Waterbuck	.148	.105	.378**
Roan	.123	.153	.188
Hartebeest	.058	.040	.088
Buffalo	.072	.060	.100
Elephant	.058	.060	.003**
Oribi	.100	.070	.008**
Warthog	.190	.102*	.102*

* Significant at the 80% level from morning counts.

** Significant at the 90% level from morning counts.

The differences found for kobs and waterbucks were not surprising because those species were most active during mid-to-late afternoon, and actively sought water then. In many locations they had to traverse roads to reach water, and, in doing so, were more likely to be seen.

Estimation of Population Size

The estimation of population size for each species required choosing between density estimates from aerial, roadside or foot transect counts. Because aerial and roadside counts were not useful for some species, estimates from foot transects were adopted as the general basis for the calculating of population sizes.

The transition from estimates of group density to population density and population size required determinations of mean group sizes for each species and the total area surveyed. Both measures were easily obtainable, but may have been biased.

Group means obtained from each survey were compared with group means from all observations made during the counting period. These included those data collected during foot transect counts, roadside counts and other activities. These pooled group means provided larger samples which in all likelihood more accurately reflected true mean group sizes.

Among those species which occurred in small groups such as oribis and bushbucks, sample and pooled means were similar (Table 57). However, for roan, antelope, hartebeest and elephant, which occurred in large groups, there were substantial differences between means in some years. Few of these means were significantly different at the 95% confidence level, mainly because their variances were large. It was

Table 57. Mean group sizes of species measured during the 1976, 1977 and 1978 foot transect surveys in the central study area and total park in Park W, Niger.

Species	1976		1977		1978		Sample: Park-wide
	Sample	Pooled	Sample	Pooled	Sample	Pooled	
Kob	3.00	2.71	2.75	2.69	2.75	2.58	2.75
Waterbuck	3.00	2.87	3.00	3.07	2.33	3.16	3.77
Roan	9.50	3.73	3.67	6.50	3.00	4.60	2.42
Hartebeest		3.50	6.00	5.82	5.00	6.17	6.38
Buffalo	4.33	2.27	2.00	2.41	1.50	2.17	1.90
Elephant		8.00	23.00	7.92	12.00	5.88	8.83
Oribi	2.00	1.55	1.67	1.68	2.17	1.60	1.81
Grimm's duiker	1.00	1.50	1.20	1.08	1.11	1.07	1.08
Bushbuck	1.00	1.29	1.00	1.14	1.50	1.39	1.35
Reedbuck		1.14	1.50	1.33	2.00	1.30	1.50
Warthog	3.20	2.71	3.50	2.92	2.20	2.56	2.44

Table 58. Estimated square kilometers occupied by species during the foot and roadside counts from 1976-1978 in the central study area and total park in Park W, Niger.

	Central Study Area	Total Park
Kob	57	181
Waterbuck	71	198
Roan	600	2100
Hartebeest	600	2100
Buffalo	600	2100
Elephant	600	1500
Oribi	500	1600
Grimm's duiker	600	2100
Bushbuck	47	172
Reedbuck	22	127
Warthog	600	2100

Table 59. Population estimates based on sample and total mean group sizes in the central study area from 1976-1978. Density estimates are based on the Geometric mean estimator.

Species	1976		1977		1978	
	Sample Mean	Total Mean	Sample Mean	Total Mean	Sample Mean	Total Mean
Kob	396	358	327	319	293	275
Waterbuck	378	361	320	327	282	446
Roan	1847	725	813	1439	585	897
Hartebeest	*	*	212	206	363	448
Buffalo	1265	663	211	254	257	372
Elephant	*	*	952	328	986	483
Oribi	276	214	301	302	596	440
Grimm's duiker	515	773	635	572	1418	1428
Bushbuck	57	73	94	107	198	183
Reedbuck	*	*	179	159	142	92
Warthog	2037	1725	859	716	668	777

*None observed during survey.

DISCUSSION

Methods of surveying populations

The best method to estimate animal density in Park W depends largely on the animal species studied and the kind of information desired. Each census method has both advantages and disadvantages.

Aerial counts

If elephants or buffaloes are the primary focus of a survey, aerial counts are perhaps the most useful. Both species occur in large groups, and while accurate counts of group sizes usually are possible from the air they often are difficult to obtain by ground surveys. Furthermore, the amount of information obtained in a few hours of flying could require several weeks on the ground.

The use of aircraft for counting large mammals in Park W, however, had several major disadvantages. The Park's budgets were too small to permit such surveys, even on an occasional basis. If funds were made available, they would mean less money for such basic operations such as patrols and maintenance. Many international agencies and organizations have funded aerial counts, but these funds may not always be available when needed or for comparative follow-up counts. Even if funds were available, suitable aircraft and experienced pilots may not be. During this study, for instance, despite the availability of funds, a suitable aircraft could not be located during January or February, 1978.

Detailed studies have shown that aerial counts are less than 100% efficient (Caughley 1977), often yielding estimates considerably below true population sizes. In this study, too, the densities of most antelope species estimated from aerial surveys were much lower than those derived from foot transect counts. Where estimates of species other than buffaloes and elephants also are desired, the use of combined aerial and ground surveys would increase the total cost.

Roadside Counts

Based on results here and elsewhere in Africa, roadside counts appear to be of limited value for estimating densities of large mammals in wooded areas. Their value even as an index to animal abundance is questionable.

In instances when both foot and roadside surveys have been used to estimate the same population, density values obtained from roadside counts often are either much higher or lower than those based on foot transects (Harris 1970; Sihvonen 1977; Van Lavieren and Bosch 1977; Barber 1980). In this study, most estimates from roadside counts were lower than those derived from foot transects.

Discrepancies between foot and roadside counts seem likely to occur especially because road transects do not traverse a representative sample of the study area. Norton-Griffith (1978) noted that roads tend to be built in good game-viewing areas and along, rather than across contour lines. Much of the road transect followed in Park W was situated on well-drained sites perpendicular to streams and across-contours. The total length of such road transects, moreover, was short in relation to the area sampled. Roads tended to be located on well-drained soils

characterized by low animal densities rather than traverse a representative samples of the study area. In areas of high animal density, mainly along streams and near waterholes, roads followed mostly along contours.

Inaccurate density estimates also resulted because animals tended to avoid roads. Even though some individuals seemed unafraid of vehicles, disturbance by tourist traffic was seen to cause others to move away. This was especially true when tourists exited their vehicles for a better view or to take photographs.

Using roadside counts also was less desirable because estimates could be obtained for only 8 of the 11 species. Bushbucks, reedbucks and Grimm's duikers mostly were inactive during the day. Often they rested in dense vegetation and were unlikely to flush or be seen unless the vehicle stopped. The effects of tourist traffic and of small samples often prevented valid population estimates.

Foot transect counts

Foot transect counts are considered to have been the most useful in Park W. They were at least as accurate as aerial counts for buffaloes and elephants and could be used for all 11 common species.

Their main disadvantage was that they were time-consuming. The number of skilled personnel in the park was too few to have carried out such a census without the outside assistance of several trained biologists. The 1978 park-wide survey, for example, required a full month to complete even though three and sometimes four walking teams were available. It would have required a party of two individuals nearly three months to

complete the same survey, and would have required time be spent away from other duties. As noted by Rogers (1975, unpublished paper), the near-universal shortage of trained personnel results in few ground counts undertaken in African parks and reserves.

Recommendations on selecting estimators for foot transect counts

Although foot transect counts can provide useful samples of large mammals, accurate estimates of population density are dependent on the selection of an estimator for each species which yields unbiased estimates.

Estimators differ in that they are based on radial, perpendicular or disappearing distances. And, for each of these categories, there are choices regarding the collection and recording of data in the fields. It is desirable to identify those estimators which have been demonstrated consistently to be accurate.

The selection process for the best or best set of estimators has been simplified somewhat in recent reviews of line transect methods (Eberhardt 1978; Gates 1979; Burnham et al. 1980). Burnham et al. (1979, 1980) have provided guidelines for assessing the usefulness of density estimators on the basis of five desirable properties:

1. Model robustness.
2. Pooling robustness.
3. Shape criterion.
4. High efficiency.
5. Theoretical development.

An estimator is said to be model robust if it can be applied to a wide variety of habitats, observers and conditions under which counts

are made. Nonparametric estimators require no assumption about the pdf and generally meet the requirement of model robustness. These are in contrast to parametric estimators which involve assumptions about some known probability density function (pdf).

An estimator is pooling robust if it satisfies the condition that

$$\bar{n} f(0) = \sum n_i f(0)$$

Data from strata or replicate samples involving several detection functions can be combined without causing bias. A robust estimator, for example, would give the same estimate of density whether an overall or weighted estimate was used.

The shape criterion refers to the general shape of the detection function. The true detection curve $g(x)$ should have a "shoulder" near $x = 0$ since, near the origin, the probability of detection should be 1.0 or nearly so.

Estimator efficiency is also a desirable property. Not all estimators are equally efficient, and it is desirable that the sampling variance be as small as possible. Small sampling variance, of course, does not insure that an estimator is unbiased.

Finally, the estimator should be theoretically sound, based on both logical and mathematical considerations.

In the context of these desirable properties, the number of prospective estimators can be reduced. Burnham et al. (1980), in fact, recommended only four estimators for general use in line transect studies (Table 69). Those were all nonparametric estimators and generally met the five qualifications outlined above. The authors noted, however, that no single estimator is best for all data sets.

Gates (1979) followed a somewhat different approach in endorsing estimators for general use. For use with perpendicular distances, he advocated seven estimators (Table 59). His approach was to fit the estimator to the data. This was based on the premise that a parametric estimator whose assumed distribution was met provides the least biased estimate. For radial distances, he advocated the Hayne and Exponential estimators, and gave a blanket endorsement of nonparametric estimators. Gates also recognized that there is not necessarily any single best estimator for a given data set.

Evidence from this study indicated that both approaches have merit. With the exception of the Polynomial, those estimators recommended by Burnham et al. (1980) appeared promising in this study. Their recommended use of only two estimators for perpendicular distances, however, was found to be too restrictive, especially when sample sizes were small. Though several estimators he recommended did not perform well in this study Gates' more flexible approach has more appeal.

Present recommendations on the use of estimators

The Webb and Dasmann-Mossman, were included in the calculations mainly as a basis of comparison because they have been shown to be biased (Robinette et al. 1974; Evans 1975). Neither has been proven to have sufficient mathematical development yet were of value in this study, because they proved to be consistently biased in a positive direction.

Methods based on Radial distances

The King estimator has since been modified by Gates (1969), but it is believed that the original King estimator still has merit. It usually yielded estimates which were low in relation to others. The actual numerical differences, however, were small, and it was among the most consistent estimators. In field studies by Robinette et al. (1974), estimates from the King model were consistently below true values, but only by small amounts.

In certain cases, the King estimator may be the least biased radial estimator. Gates (1979) noted that radial estimators based on reciprocals of r are sensitive to short radial distances. Small r values have a disproportionate effect on the harmonic mean, and can result in over-estimates. In a simulation test (Table 61), estimates were obtained for the King, Hayne and Geometric estimators where mean radial distances were constant but the number of short r values increased. When two or three short sighting distances were included, estimates from the King estimator remained constant whereas those of the other two were considerably higher. The Hayne estimator was the most seriously affected while the Geometric mean was affected to an intermediate degree.

The Hayne and Modified Hayne estimators performed reasonably well in this study (Table 15) when there were few small r values. Modified Hayne estimates were usually slightly lower than those of the original Hayne estimator because of the correction factor. Burnham et al. (1980) recommended the modified estimator as a replacement for the Hayne. Gates (1979) advocated the original Hayne estimator though he noted several drawbacks to this method. It is restrictive in that θ is required to be

Table 61. Simulated effects of short sighting distances on radial distance estimators, where $L = 10$ km and $n = 10$. The number of small r values increases from test 1 to 4.

Observation	Test number			
	1	2	3	4
1	5	16	26	15
2	11	3	4	2
3	36	15	39	19
4	14	23	25	35
5	28	22	29	28
6	8	40	14	1
7	21	4	1	15
8	18	25	7	1
9	10	1	12	36
10	7	7	1	3
Arithmetic mean:	15.8	15.6	15.8	15.5
Geometric mean:	13.23	10.0	9.0	5.1
Harmonic mean:	11.14	9.35	3.7	3.2
Density per square kilometer				
<u>Estimator</u>				
King	.032	.032	.032	.032
Geometric	.049	.056	.067	.098
Hayne	.045	.102	.134	.156

about equal to 32.7° . In practice, θ is often larger than this, especially when detection depends on the observer.

The Geometric estimator was proposed by Gates (1969) to fill the void between the harmonic and arithmetic means of radial distances. It has not, however, been regarded as useful by most investigators. Later, Gates (1981) stated that it has no basis in reality because there is no evidence that logarithms of radial distances yield unbiased estimates. In a series of simulations, he found this estimator always to be negatively biased, yet the bias was small when the underlying distributions were triangular or half-normal rather than exponential. In contrast, Robinette et al. (1974) found this estimator to be biased in a positive direction. The amount of bias, though, was relatively small, and they found it to be among the best estimators evaluated. When applied in connection with stratified data, they determined the amount of bias was quite small.

In this study, the Geometric estimator yielded one of the most consistent set of results. Its estimates were always moderate in relation to those of other estimators, even when sample sizes were quite small. Its performance in this study indicated that perhaps its potential usefulness has not been fully explored. Its theoretical development seems sound, though its properties relative to robustness have not been investigated. Where sample sizes were too small for estimation by many other methods, this estimator always yielded moderate estimates, though of unknown accuracy.

The Exponential estimator did not perform well in this study. Derived estimates were consistently high in relation to other estimators,

whether or not the distribution of radial distances was exponential. It yielded estimates as high or higher than the Webb and Dasmann-Mossman estimators, which have been shown (Robinette et al. 1974) to yield overestimates of density by more than 100% in several cases, and always to be at least 20% high.

Under the assumption of a negative exponential distribution, Gates (1969) showed that the Exponential estimator performed well in simulation studies. Gates also showed, however, that when the underlying distribution was half normal or triangular, this estimator overestimated densities by significant amounts. Kovner and Patil (1974) also examined its properties and found it to be an efficient estimator, but examined it only under the exponential distribution.

The reason for the high estimates from the Exponential estimator in this study was not clear in view of Gates' simulation studies. Possibly, it is extremely sensitive even to small departures from the assumed exponential distribution. Overall, this estimator was judged to have little use for estimating densities in Park W.

Methods based on perpendicular distances

The Polynomial, Quadratic and Triangular methods all yielded values close to those of more moderate estimators when sample sizes exceeded 40. As sample sizes decreased from 40, however, these estimators gave increasingly variable results for ungrouped data. Estimates were sometimes completely out-of-line with those of other estimators. For sample sizes between 20 and 40, these estimators gave reasonable estimates only when operating on grouped, truncated data. Thus, it appeared that those

methods were only useful for relatively large sample sizes, and for grouped, truncated data sets.

Burnham et al. (1980) recommended the Polynomial because it meets the 5 criteria outlined earlier. Robinette et al. (1974) found that the Polynomial estimator had relatively small bias and also recommended it as one of the better estimators. Gates (1974) recommended the Triangular estimator for use when the detection function is approximately linear. It appears that when data sets include over 40 observations each of these estimators may yield useful density estimates. Of the three, the Polynomial best meets the properties outlined earlier.

Several other estimators, the Kelker, Eberhardt-Cox and Spline operate only with grouped data. When sample sizes are adequate (40 or more) their estimates were similar and appeared to be reasonable. An important drawback to the Kelker and Eberhardt-Cox estimators, however, was the subjective selection of w , the maximum distance at which all animals are presumed to be observed.

In areas of open vegetation, these models are likely to be useful for large mammal counts because few individuals are likely to be missed. If sample sizes are large enough (eg. 50 or more), too, reliable decisions regarding w are more likely. In the wooded savannas of Park W, however, gradual declines in observations and relatively small sample sizes commonly encountered increases the subjectivity in selecting w .

Gates' (1979) Spline method is a probable improvement on Kelker's method since subjectivity in selecting w is reduced. In Park W, estimates from the Spline and Kelker formulas yielded either the same density or the Spline showed only modest increases over the Kelker.

The performance of these estimators with respect to bias has been examined only for Kelker's method. It yielded good results in field tests on inanimate objects (Robinette et al. 1974) and on white-tailed deer (Evans 1975). Yet Hirst (1969) found that it yielded underestimates of large ungulate densities in southern Africa. Gates (1979) considered the Kelker estimator to be generally useful for perpendicular distances, but suggested that the Spline method was a better alternative. Gates also considered the Eberhardt-Cox estimator to be useful, but with the same reservations. He noted that estimates with both the Kelker and Eberhardt-Cox estimators can be quite variable, depending on which w is used. Eberhardt (1978) too, felt that the Eberhardt-Cox estimator should be employed only as a last resort. Burnham et al. (1980) recommended its use only as a rough guide to density because of the subjectivity factor discussed earlier.

It appears that when data sets are large enough to group the data, the Kelker and Spline estimators give moderate estimates comparable to those of other estimators proven to have performed well in simulation and field tests. The Eberhardt-Cox estimator is more variable and is believed less useful than the Kelker or Spline, especially for sample sizes smaller than 40.

The Exponential estimator has been found by most investigators to be too restrictive for general use. It is sensitive to departures from the negative exponential distribution, and has been found to give badly-biased estimates when the detection function is not exponential (Robinette 1974; Eberhardt 1978; Gates 1979). In this study too, values from the Exponential estimator were often very high or very low in relation to other estimators and not believed to be useful.

Among the parametric estimators, the Hemingway Normal yielded estimates which were consistent for a wide variety of species, detection functions and sample sizes. In some instances, estimates tended to be higher than others, but the method may be more generally useful than sometimes viewed. Burnham et al. (1980) for instance, felt that this estimator was more desirable than the Exponential, but nevertheless was too restrictive for general use. The underlying detection function, of course, must be half-normal for estimates to be unbiased. Gates advocated its application only when the assumed distribution has been tested.

In this study, detection functions were seldom significantly different from the half-normal except when sample sizes were small. Though estimator is neither model robust nor pooling robust, it almost always provided a moderate estimate which was close in value to other estimators which were robust in those ways.

The Generalized Exponential estimator, also a parametric estimator, was in performance similar to the Hemingway Normal. The Generalized Exponential should be more robust than other parametric estimators because it is based on a generalized exponential distribution which includes the negative exponential, half-normal and uniform distributions (Pollock 1978).

This estimator has not been studied in simulation tests, and its properties are largely unknown. In this study, its performance relative to robust estimators was relatively good for sample sizes above 30. Below that level, the variability of estimates increased, but even with very small samples, it often yielded moderate estimates. Because of its involved computations, neither Gates (1979) nor Burnham et al. (1980) recommended this method.

The Fourier Series estimator was developed for line transect data by Burnham and Anderson (1976) and Crain et al. (1978). This estimator represents a most-significant advance in line transect theory. Its use over other estimators has been strongly recommended by Burnham et al. (1980) since this estimator meets all the desirable properties outlined earlier. They determined through simulation tests that it is often more accurate than parametric estimators even when the underlying parametric distributions have been met. It was especially useful in application to Park W data. It had the flexibility and robust properties for the variety of detection functions typically encountered when tallying multiple species. In consequence, it proved to be the single most useful estimator.

For pooled data sets, estimates from the Fourier Series were reasonable and well within the range of moderate values. Its reliability for data sets smaller than 40, however, appeared to be questionable. Under those conditions it yielded estimates which were equal to or below those of the Hahn estimator and completely out-of-line with those of other estimators. One plausible explanation is that frequently, the pdf declined rapidly from the transect line in the manner of an exponential distribution.

In simulation studies (Burnham et al. 1980), where the pdf was negative exponential, the Fourier Series estimator yielded negatively biased results which were as much as 20% low. In other simulation tests in which there were fewer observations near the transect line than at succeeding distances, this estimator underestimated densities by 20 to 90%. In Park W, the rapid falloff and skewed distributions often were due at least partly to movements of animals away from the transect line

and the detection of animals only after they were in motion. Though movements were not always directly away from the transect line, a relatively small number of such movements could bias the estimates.

Another reason for low density estimates relates to sample sizes. It was found that sample sizes under 40 yielded estimates which were ranked much lower than those above 40. For sample sizes less than 30, estimates were sometimes lower even than those of the Hahn estimator, regardless of the shape of the pdf.

From this study, the Fourier Series estimator appeared to be reliable when sample sizes exceeded 40 and when movements of animals prior to detection were minimal. In instances when the pdf was a approximately negative exponential or when observations nearest the transect line were fewer than longer distances, this estimator yielded lower estimates than the Hahn estimator. The present findings seemed to confirm Burnham's et al. (1980) observation that few if any estimators perform well when the pdf is skewed.

Though widely used in Africa, the accuracy of the Hahn estimator could not be duplicated in this study with respect to bias has been examined in only one study. Hirst (1969) found success with this method in South Africa but there was strong evidence in Park W that this estimator yielded underestimates. Possibly it is in more open habitat where visibility declines over longer distances that the Hahn method is most useful.

The results of this study do not necessarily invalidate other methods of determining visibility profiles such as those employed by Lamprey (1964), Harris (1970) or Hahn (1949). From the experience gained in Park W, however, it appears unlikely that even where profiles have been

carefully determined by measuring disappearing distances of assistants at frequent intervals along the transect, this does not accurately represent the area in which all individuals of a broad spectrum of animal species can be counted. Correction factors for very large and very small animals would appear to provide only crude estimates of density for species of extreme sizes. In the studies of Kranz (1973) and Evans (1975), the profile method underestimated the effective area, whereas in Park W, it was overestimated. Their conclusions were based on both simulation and field tests.

The main differences between their studies and the present one apparently involves the interpretation and application of disappearing distances. In their approach, they measured the area visible at any one point along the center line and assumed that animals which were obscured by vegetation at that point could not be detected further along the line. Possibly, in the vegetation encountered in their study area this was the case. In Park W, however, an animal might temporarily be obscured from view but as the observer continued along the transect, the animal came into view again from a second vantage point. Also in Park W, there was usually a gradual decline in visibility and the animals became increasingly more difficult to see as distances increased. In Evan's study the disappearance of animals was apparently more abrupt, as a shrub or hill caused them to disappear.

One possible method of bringing the Hahn method as applied in this study into accord with estimates of other estimators would be to truncate observations at some distance beyond which most animals would not likely be detected. An examination of the Park W observations, however, revealed that a large number would have to be deleted for density estimates

to be reduced to the level moderate ones such as the Fourier Series. This truncation introduces an additional subjective variable into the formula and often would drastically reduce the sample size. Examining frequency histograms of disappearing distances for a fall-off point where the data could be truncated was not helpful in most cases. No truncation points were obvious. The Hahn method is considered to be of limited usefulness. It can serve, perhaps, only as a rough index to animal abundance and as a minimum estimate for comparing the relative values of other estimators.

Selection process for estimators

Although several radial and perpendicular distance estimators have been recommended, further guidelines are desirable to narrow the array of choices. It is suggested that r and θ routinely be measured in the field in addition to x , to enable a flexibility of choices should sample sizes be less than 40.

The approach of examining the pdf, testing it against parametric distributions such as the negative exponential, and then selecting the parametric estimator whose assumed distribution has been most closely matched, is not recommended here. This is mainly because for any given pdf there are usually several distributions which are not significantly different from the observed distribution. Density estimates based on these parametric estimators are often quite variable and it is not clear which would likely be the most accurate. It has been noted (Gates 1979; Burnham et al. 1980), too, that these parametric estimators can yield badly-biased estimates even when there are small departures from the assumed distributions.

A selection key (Figure 32) has been prepared in which the Fourier Series is recommended for data sets greater than 40 and where the pdf is not skewed. The Polynomial is recommended as a second choice. These estimators are believed to be the most applicable to a wide range of detection functions. Nevertheless, under certain circumstances, other estimators may be more appropriate.

For sample sizes smaller than 40, the Generalized Exponential estimator is recommended where observations are based on perpendicular distances (Figure 32). This parametric estimator has been advocated because it proved to be more flexible than other such estimators, and gave consistent results even when sample sizes were quite small.

Estimators based on radial distances were believed to be more reliable for smaller sample sizes. They can be applied to larger data sets as well. For sample sizes smaller than 20, only the King, Geometric and Generalized Exponential estimators are recommended. As noted earlier, the King estimator is generally considered to be an inaccurate and out-of-data method. Based on field tests by Robinette et al. (1974) and results of this study, however, the King estimator proved to have merit, especially with small sample sizes. When small r values (flushing distances less than 5 m) were encountered, as with Grimm's duiker and bushbuck, and King estimator may be the most reliable radial estimator.

Usefulness of density estimates

As noted by Gates (1979), one of the most disturbing problems facing biologists in the application of line transect methods is the movement of animals prior to detection. The assumption that all animals are first seen in the position originally occupied is commonly violated to varying

<u>Measurements</u>	<u>Recommended estimators</u>		
<u>x only</u>	<u>n > 40</u>	<u>pdf. not skewed</u>	<u>Fourier Series, Modified Hayne</u> <u>Generalized Exponential</u>
<u>x and r</u>	<u>n > 40</u>	<u>pdf. skewed</u>	<u>Splined, Generalized Exp.</u>
	<u>n < 40</u>	<u>n > 20</u>	<u>Generalized Exp., Modified</u> <u>Hayne, Geometric, Polynomial, Kelker</u>
		<u>n < 20</u>	<u>Generalized Exponential</u>
	<u>n < 20</u>	<u>>10% r values are small</u>	<u>King</u>
<u>r only</u>		<u>10% r values are small</u>	<u>Geometric</u>
	<u>n > 20</u>		<u>Geometric, Modified Hayne</u>

Figure 31. Key to the selection of an estimator(s) for estimating densities of large mammals in Park W, Niger.

degrees with most species. The effect of this failure can be expected to cause underestimates, both due to missed animals and to depressed estimates caused by skewed distributions. There have been no field studies undertaken to measure this effect.

For each species, too, there is potentially a unique pdf. The distribution of perpendicular distances is influenced by activity patterns, response behavior, habitat preferences, animal size, protective coloration and herding and other behaviors. The effects of all these factors, often coupled with small sample sizes, results in a wide range of sighting and perpendicular distance distributions for a given census. These change both by season and year and may be strongly influenced by the occurrence of burned vegetation.

The search for a single best estimator for each animal species may lead to several radial and several perpendicular distance estimators for each census. Such a situation is less than desirable, especially in the absence of computers and with personnel untrained in quantitative methods. In consequence of the increased complexity of estimators, the broad array of choices and the questionable accuracy of many estimators, there may be a decrease in censusing efforts.

Value of information from Line transect methods

Despite the modest sample sizes and sampling design problems encountered in Park W, the line transect method appears to be a useful management and research tool. Density estimates that are carefully chosen and carefully computed may, in fact, be reasonably accurate.

Density estimates of line transect surveys, nevertheless, must be interpreted with caution, especially when small sample sizes are involved. As noted by Gates (1979) and Burnham et al. (1980), there may be no estimate which is accurate for small sample sizes.

While sampling design can compensate for the clustered distributions of most species including kob and waterbuck, the usefulness of estimates of bushbuck and reedbuck is questionable. Because of their patchy distributions and close association of these two species with riparian habitats, neither the perpendicular or riparian transects are believed accurately to sample their densities. Also, because of their unknown distributions in the park, population estimates would seem especially unreliable. It is thought, therefore, that line transect methods are not well suited for estimating bushbuck or reedbuck densities. Sample counts along streams may, however, serve as indices of population trends.

The results of this study also indicate that small-scale line transect surveys are of little use for estimating densities or detecting population trends. Because of time limitations, replicate samples over the same area are impracticable. Furthermore, it is not physically possible to saturate small areas with enough transects to achieve adequate sample sizes without risking duplicate counting of animals. Surveys therefore, should cover at least 50% of the park in order to obtain reasonably-large sample sizes.

The future use of line transect methods in Park W, Niger is encouraged with the precaution that the survey is carefully designed, accurate measurements are made and a large enough area is sampled to achieve meaningful sample sizes. Though variances may be too large to

detect small changes in population abundance, large scale changes and trends may be discernable.

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