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A BIBLIOGRAPHY RELATING TO THE ECOLOGY AND ENERGETICS OF EAST AFRICAN LARGE MAMMALS

J. C. BRIAND PETERSEN and R. L. CASEBEER U.N.D.P./F.A.O. Range Management Project, Nairobi, Kenya

SUMMARY

Many investigations have made contributions to an understanding of energy flow through large mammals in East African ecosystems. This paper lists references to such works and compiles them according to their application to various segments as they appear in an energy-flow model. The first part indicates papers on pasture utilization, value of foodstuffs, animal numbers and distribution, population dynamics and secondary production. The second part assembles references dealing with individual animal species, stratifying them according to the subjects of ecology, food habits and nutrient utilization, population dynamics and growth.

INTRODUCTION

Refined wildlife management can only be achieved by a comprehensive understanding of the structures and functions of the ecosystem. Knowledge of the energy flow through the system will contribute to this understanding.

Lindemann (1942) was the first to develop the classic concept of ecological energetics or community dynamics. In describing the flow of energy through the ecosystem he grouped the organisms with similar feeding habits together in food levels or trophic levels. The energy content of each level was stated in mathematical symbols and the rate and efficiency of the energy transfer from one level to another was expressed in mathematical equations and diagrams.

Since then widespread interest has developed in the research of ecological energetics. In constructing a model with particular reference to large mammals in East African ecosystems, attention was directed to gathering information already available. This paper assembles references to that information.

Only few papers deal directly with energy relationships, but all contribute information which has a place in such a design. As a bibliography, the paper will not only be of interest for the study of energetics but also to a wide range of wildlife disciplines. The paper can be regarded as an up-to-date

sequel to Talbot (1965). See also East African Agricultural and Forestry Research Organisation (1970) for a list of current research projects.

The nomenclature used through the paper follows Stewart and Stewart (1963) who relied on Ellerman, Morrison-Scott and Hayman (1953), and, for species they do not consider, Allen (1939).

1. GENERAL REFERENCES TO EAST AFRICAN MAMMALS

1.1 Classification, description, distribution and habits

These items pertaining to mammals of East Africa can be obtained from numerous standard works and publications. This list is not exhaustive but includes the more accessible publications. Some references may be outdated and/or popular, but nevertheless give introductory data.

The following papers should be noted: Ansell (1960a), Lydekker (1908), Maberly (1966), Meinertzhagen (1957), Percival (1928), Roosevelt (1910), Roosevelt and Heller (1915), Simon (1962) and Stevenson-Hamilton (1947).

Checklists of the mammals of Africa have been published by Allen (1939) and, especially for Tanganyika and Zanzibar, by Swynnerton and Hayman (1951). See also Ellerman

kg for a 13-months male yearling to 182 kg for an adult. Similar weights for females were 100 kg and 170 kg.

2.14 Hippopotamus (*Hippopotamus amphibius* (L.))

Ecology: See Bere (1959).

Food habits and nutrient utilization: Petrides and Swank (1963) calculated quantitative food intake to be 18 kg DM/day and Field (1968a and b, 1969) investigated food preferences of the hippo (a grazer). See also Laws (1968a) and Young (1966).

Population dynamics: Laws (1968b) developed ageing criteria for hippo on the basis of tooth characteristics and body measurements and also presented survivorship curves and life tables. See also Ansell (1960b), Longhurst (1957a, 1958) and Laws and Clough (1965). *Weight and growth:* Ledger (1968) lists the weight of adult males as 1,490 kg (1,178-1,714 kg) and of females as 1,277 kg (1,185-1,400 kg). See also Ansell (1965), Ledger (1963c, 1964), Ledger and Smith (1965) and Maberly (1966).

2.15 Impala (*Aepyceros melanopus* (Lichtenstein))

Ecology: See Schenkel (1966).

Food habits and nutrient utilization: Stewart (1969) found that impala ate predominantly monocotyledons (95%), but that their diet varied widely from place to place. There were strong preferences for specific grass species, changing with seasons. There were large differences between individual animals but significant differences between sex and age classes were not detected. Talbot (1962) found impala to be predominantly a grazer (56% grasses), as did Azavedo and Agnew (1968). Maloiy and Hopcraft (1969) found that heat stress and water shortage both caused a decrease in food intake (2.58 kg with free food-supply and water and at 22°C, decreasing to 1.99 kg/100 kg BW/day with a free food supply, restricted water and under heat stress). See also Dasmann and Mossman (1962d).

Population dynamics: Age-criteria from dental characteristics, horn development and skull size were described by Roetcher and Hofmann (1970). Sex and age ratios were

determined by Dasmann and Mossman (1962d) in Southern Rhodesia by regular counts throughout a year. They found that yearlings averaged about 25% of the population, with few young adults and a high percentage of old individuals. In the older age classes there was a high percentage of females. See also Dasmann and Mossman (1962b) and Mossman and Mossman (1962). Dasmann and Mossman (1962d) stated that the minimum breeding age was 2 y, the gestation period between 180 and 210 days and the time of calving to be near the start of the rainy season, the beginning of December in Rhodesia. See also Dasmann and Mossman (1962a) and Kerr (1965). Pregnancy rates were indicated by Dasmann and Mossman (1962d) to be 97% in adult females and 85% in yearlings. They also gave figures on survival and mortality. See also Ansell (1960b), Child (1964) and Stewart, Grieg and Stewart (1966).

Weight and growth: Ledger (1968) gave 56.7 kg as the average for adult males and 42.0 kg for females. Talbot (1963) indicated a daily liveweight gain of 0.09-0.12 kg. See also Maberly (1966) and Sachs (1967).

2.16 Kob, Uganda (*Adenota kob thomasi* (Sclater))

Ecology: See Buechner (1958b, 1961) and Buechner and Schloeth (1965).

Food habits and nutrient utilization: Field (1968a and b, 1970) determined qualitative food preferences over different seasons.

Population dynamics: The study by Bindernagel (1968) includes a variety of data. Herd structure and sex and age structure were determined for about 20% of a population. Age criteria were developed. The population structure in two counts averaged: adult males 20%, immature males 19%, females 38% and calves 23%. First ovulation for females was stated by Buechner, Morrison and Leuthold (1966) to be at 13-14 months of age and may occur once or twice before conception. Sexual maturity in males occurred at one year of age, but possession of territory was first displayed later, at about 3½ y. The same authors suggested that 240 days may be used as normal gestation period. The calving season had a peak in December-January but the Uganda kob can breed throughout the year. The inter-calving

interval was calculated by Bindernagel (1968) to be 10 months. See also Ulmer (1966). *Weight and growth:* Ledger (1968) gave the weight for adult males as 96.7 kg (93-108 kg) and for females 62 kg (59-66 kg). Bindernagel (1968) provided a table with weights of animals of different ages and Ledger and Smith (1964) investigated body composition of the Uganda kob. The mean dressing-out percentage was 58.5% and the lean meat content as high as 81.3% (Boran steers 54.8%). See also Ledger (1963c) and Ledger and Smith (1965).

2.17 Kudu, lesser (*Strepsiceros imberbis* (Blyth))

Weight and growth: Ledger (1968) gave an average weight of 92.1 kg (56-108 kg) for adult males and Maberly (1966) stated about 104 kg. See also Ledger (1964).

2.18 Kudu, greater (*Tragelaphus strepsiceros* (Pallas))

Food habits and nutrient utilization: Wilson (1965) did stomach analyses and found the greater kudu to be almost entirely a browser.

Population dynamics: Ageing criteria from dental characteristics were developed by Simpson (1966). Dasmann and Mossman (1962a) gave the calving period to be February-March in Southern Rhodesia and stated that maturity was reached at 2 y of age. Brand (1963) indicated that most calves were born between January and March and Wilson (1965) stated between January and April. The latter analysed the population structure for 768 animals and found a sex ratio of 1:2.4 (♂:♀). See also Ansell (1960b), Dasmann and Mossman (1962b) and Simpson (1968).

Weight and growth: Wilson (1965) gave average adult weights as 257 kg for males and 170 kg for females.

2.19 Oribi (*Ourebia ourebi* (Zimmermann))

Population dynamics: Bindernagel (1968) quoted Cade as saying that the gestation period was 217-220 days. Bindernagel (1968) also indicated that the calving season extended throughout the year, that the inter-calving interval was 292 days and pregnancy rates were nearly 100% for mature females. He also presented ageing criteria from horn development and dental characteristics.

Weight and growth: Carcass yield was found to be 58.5% and weights of adult animals to vary between 13.6 and 15.4 kg (Bindernagel, 1968).

2.20 Oryx, fringe-eared (*Oryx beisa callotis* (Thomas)) and Oryx, beisa (*Oryx beisa beisa* (Rüppell))

Food habits and nutrient utilization: Taylor and Maloiy (1969) investigated the influence of dehydration and heat stress on intake and digestibility of food of the beisa oryx. Food intake per 100 kg body weight was given for various environmental conditions. It was 2.33 kg/day at 22°C and with free water. Heat stress did not influence intake but a certain degree of dehydration lowered it considerably. This reflected a decrease in the metabolic rate under such conditions. Taylor (1968) determined the amount of water intake for beisa oryx. See also Taylor (1969a).

Weight and growth: Ledger (1968) gave the average weight for adult males as 176.4 kg (167-209 kg) and adult females as 161.5 kg (116-188 kg). Maberly (1966) stated 195 kg as average. See also Ledger (1963c) and Ledger and Smith (1965).

2.21 Reedbuck (*Redunca* spp.)

Food habits and nutrient utilization: Petrides and Swank (1963) calculated quantitative food intake by weight of rumen content. They found it to be 0.23 kg DM/day. Field (1970) determined the qualitative food preferences in different seasons.

Population dynamics: Dasmann and Mossman (1962b) determined sex structure in a population of *Redunca arundinum* (Boddaert) but on a very small sample.

2.22 Rhinoceros, black (*Diceros bicornis* (L.))

Ecology: See Klingel and Klingel (1966b), Ritchie (1963) and Schenkel and Schenkel-Hullinger (1969).

Food habits and nutrient utilization: Goddard (1968, 1970b) studied food preferences and gave lists of food plants and the relative importance of individual species. Klingel and Klingel (1966b) made observations in Ngorongoro.

Population dynamics: Goddard (1970a) developed age criteria based on dental characteristics. He also presented sex-ratios, a survivorship curve, life-tables and calculated annual recruitment and mortality for a population in Tsavo National Park. Schenkel and Schenkel-Hullinger (1969) determined both sex and age ratios. Sex ratios were 1:1.3 (σ : \varnothing) for adult animals and 1:0.6 for immature. Age of maturity according to Goddard (1967a) was 6 y for males and 7 y for females (quoted from zoo records). See also Goddard (1970c) and Foster (1965). Schenkel and Schenkel-Hullinger (1969) stated 3½-4 y for females. The same authors quoted the gestation period to be 450 days. Ritchie (1963) stated 540 days and Goddard (1967a) quoted from different sources the period to be 450-480 days. The inter-calving interval was found by Schenkel and Schenkel-Hullinger (1969) to be 2½-3½ y, while Goddard (1967a) gave 27 months for a healthy female. In his two study populations the inter-calving interval varied but the recruitment rate appeared to be 0.25 calves/female/y. Schenkel and Schenkel-Hullinger (1969) stated that reproduction ceased at an age of 30-35 y. See also Goddard (1970c). Calving occurred at any time of the year (Ritchie, 1963). See also Anderson (1966), Hamilton and King (1969) and Roth and Child (1968).

Weight and growth: Meinertzhagen (1938) indicated weights of 1,165 kg for adult males and 1,081 kg for females. Bourlière and Verschuren (1960) indicated 1,301 kg as an average. See also Maberly (1966) and Talbot (1963).

2.23 Rhinoceros, white (*Ceratotherium simum simum* (Burchell))

Ecology: See Cave (1963), Foster (1960) and Player and Feeley (1960).

2.24 Roan (*Hippotragus equinus* (Desmarest))

Ecology: See Backhaus (1959b) and Child and Wilson (1964).

2.25 Sable (*Hippotragus niger* (Harris))

Ecology: See Child and Wilson (1964) and Dolan (1964).

2.26 Sitatunga (*Tragelaphus spekei* (Sclater))

Ecology: See Owen (1969, 1970).

2.27 Steinbok (*Raphicerus campestris* (Thunberg))

Population dynamics: Chalmers (1963) gave the gestation period as 210 days and inter-calving interval as 8 months. See also Dasmann and Mossman (1962b).

2.28 Topi (*Damaliscus korrigum* (Ogilby))

Ecology: See Vesey-FitzGerald (1955).

Food habits and nutrient utilization: Talbot (1962) determined food preferences by stomach analysis and found that 97% of the stomach contents were grass. Gwynne and Bell (1968) made investigations on the part of grasses which different animals selected for food. The topi was found to take stem and leaves in equal proportions (wildebeest (*Connochaetes taurinus* (Burchell)) took mostly leaves, zebra (*Equus burchelli* (Gray)) stems).

Weight and growth: Liveweight for adult males was given by Ledger (1968) as 130.8 kg (113-141 kg) and for females as 103.9 kg (91-116 kg). Sachs (1967) indicated 130 kg for adult males and 109 kg for females.

2.29 Warthog (*Phacochoerus aethiopicus* (Pallas))

Ecology: See Bradley (1968) and Clough and Hassam (1970), Frädrieh (1965) and Geigy (1955).

Food habits and nutrient utilization: Field (1968a, 1970) made observations on food habits in Queen Elizabeth Park and Petrides and Swank (1963) calculated the quantitative intake, by the weight of rumen content, to be 0.277 kg DM/day.

Population dynamics: Ageing criteria from dental characteristics and eye-lens weight were developed by Child, Sowsls and Mitchell (1965) and Child, Sowsls and Richardson (1965). Sex and age ratios were found by Child, Sowsls and Mitchell (1965) and Child, Roth and Kerr (1968) to vary but they used the ratio 1:1 as normal. Clough (1969) stated 48:52 (σ : \varnothing) in his study. Dasmann and Mossman (1962b) gave figures from a smaller sample. Bindernagel (1968) analysed age structure. Because of difficulty in ageing immature and adult animals only the percentage for young-of-the-year was reliable and was consistently between 50 and 80 per cent throughout

the year. *Minimum breeding age:* Child, Sowsls and Mitchell (1965) and Child, Roth and Kerr (1968) indicated 1½ y as the age for sexual maturity of females and 2 y for males. Clough (1969) gave 17-19 months for both sexes. Roth (1965) stated 3 y for minimum breeding age and Dasmann and Mossman (1962a) said the first litter was dropped at 2 y of age. The gestation period was found by Child, Sowsls and Mitchell (1965) and Child, Roth and Kerr (1968) to vary between 150 and 170 days. Other authors gave the period to be 170-175 days (Asdell, 1946 and Clough, 1969). *Time of farrowing:* Child, Sowsls and Mitchell (1965) and Child, Roth and Kerr (1968) found it varied from place to place but was generally between September and December in Rhodesia. Dasmann and Mossman (1962) found that farrowing time corresponded with the start of the green season. *Pregnancy rates:* Dasmann and Mossman (1962a) found 66-75% of all females to be pregnant (but a sample of only 7). *Litter size:* Dasmann and Mossman (1962a) stated 3-4, and Clough (1969) 3.4 to be the mean. Bindernagel (1968) quoted Clough as saying that young females only produce 1.6 young but older females produce 3.4 as an average. Maximum longevity was stated by Roth (1965) to be 20 y and average life expectation to be 3½-4 y. *Survival and mortality:* Dasmann and Mossman (1962a) indicated a high survival at 80% from 1 to 2 years and at 10% from 2 to 3 years. See also Ansell (1960b). *Weight and growth:* Weight curves for warthog were given by Roth (1965) and Bindernagel (1968). The latter also supplied figures for daily weight gain (varying from 0.77-0.123 kg) and carcass yield (58.6%). Meinertzhagen (1938) gave the weight for adult males as 70-106 kg and for females as 55-68 kg. Sachs (1967) gave 87 kg as the average for males and 53 kg for females. See also Brand (1963), Grzimek and Grzimek (1960b), Ledger (1964, 1968) and Maberly (1966).

2.30 Waterbuck, defassa (*Kobus defassa* (Rüppell) and Waterbuck, common (*Kobus ellipsiprymnus* (Ogilby))

Ecology: See Spinage (1967b) and Verheyen (1955) on defassa waterbuck.

Food habits and nutrient utilization: Kiley-Worthington (1966) found that waterbuck were predominantly grazers but that in the

dry season they took a high percentage of dicotyledons. Taylor, Spinage and Lyman (1969) investigated the water relationship of the defassa waterbuck and found that it required 25% more water than Hereford steers (*Bos taurus* L.) (at 22°C). It could not tolerate water shortage for any prolonged period. Petrides and Swank (1963) calculated the daily food intake to be 1.59 kg DM.

Population dynamics: Spinage (1967a) developed age criteria for defassa waterbuck on the basis of tooth eruption, replacement and wear. Dasmann and Mossman (1962b) did an analysis on population structure in Southern Rhodesia, but on a small sample. Dasmann and Mossman (1962a) stated that the time of breeding in Southern Rhodesia was February to April. Spinage (1970) calculated sex ratios, mortality rates and lifetables for the defassa waterbuck. See also Ansell (1960b), Kiley-Worthington (1965), Spinage (1968a, 1969) and de Vos and Dowsett (1966).

Weight and growth: Ledger (1968) gave the average weight of adult males to be 238 kg (206-267 kg) and of females 181 kg (162-200 kg). Sachs (1967) gave the figures of 226 kg and 175 kg from Serengeti. See also Ledger (1964), Ledger and Smith (1965), Maberly (1966) and Meinertzhagen (1938).

2.31 Wildebeest (*Connochaetes taurinus* (Burchell))

Ecology: See Estes (1968), Talbot and Talbot (1963) and Watson (1967).

Food habits and nutrient utilization: Talbot (1962) and Talbot and Talbot (1963) found wildebeest to be entirely grazers (98% mono-cotyledons). Gwynne and Bell (1968) found that wildebeest fed primarily on the leaves of grasses and Casebeer and Koss (1970) and Talbot and Talbot (1963) showed that there were preferences for certain grasses. Rogerson (1966, 1968) investigated energy utilization. He found that the fasting metabolism was 104.3 k cal/kg BW^{0.75}/day, about 20% more than cattle. The digestibility coefficient was close to that of cattle and the proportion of food utilized as metabolisable energy was 50.8%, the same as for cattle. Utilization of metabolisable energy for maintenance was also near to that of cattle (82%), but for production it was 59.3%, compared to c. 50% for cattle. He also

diet was quite varied. Of 20 different prey species Thomson's gazelle was the most important followed by impala and reedbuck. See also Mitchell, Shenton and Uys (1965). *Weight and growth*: Maberly (1966) stated an average weight between 45.3 and 54.3 kg with females weighing 9.1-13.6 kg less than males.

2.37 Lion (*Panthera leo* (L.))

Ecology: See Makacha and Schaller (1969) and Rudnai (1970).

Food habits and nutrient utilization: Kruuk and Turner (1967) found that wildebeest and zebra made up 49% and 26% respectively of the number of lion kills encountered on the Serengeti Plains. Buffalo formed 8% and small size prey 10% of the kills. An attempt to calculate the predation pressure of lions showed a consumption of 7,800 prey animals/y by the estimated 700 lions. The yearly ratio was assumed to be 1,800 kg of meat per lion. In Lake Manyara National Park Makacha and Schaller (1969) found that buffalo was the most important prey species (69% of kills) followed by zebra (11%). Rudnai (1970) in Nairobi National Park found the most important prey species to be kongoni, wildebeest, zebra and warthog in that order. Calculated killing rates and daily consumption indicated 30 animals per individual lion per y and an intake of 9.4 kg/day/lion. See also Mitchell, Shenton and Uys (1965) and Wright (1960).

Population dynamics: Rudnai (1970) analysed population composition and group structure in Nairobi National Park. Juveniles comprised 57-62% of the population. She also indicated sex ratios and suggested mortality rates. Age of maturity was reported to be about 24 months for both sexes and a gestation period of 100-113 days. Examples of litter size were given. Makacha and Schaller (1969) stated that juveniles made up 20-25% of the population in Lake Manyara National Park.

Weight and growth: Maberly (1966) indicated the maximum weight of a big male to be 227 kg and about 45 kg less for a female.

2.38 Wild dog (*Lycan pictus* (Temminck))

Ecology: See Estes and Goddard (1967) and Kruuk and Turner (1967).

Food habits and nutrient utilization: Estes and Goddard (1967) found that Thomson's gazelle and wildebeest formed 54% and 36% respectively of the kills in the Ngorongoro Crater. The same authors stated that between 2.0 and 4.1 kg of meat were available per day per dog from kills, varying with the size of the pack. Kruuk and Turner (1967) indicated the following sequence in selection of the more important prey species: Thomson's gazelle (64%), wildebeest adult (12%), Grant's gazelle (10%). See also Kühme (1964), Mitchell, Shenton and Uys (1965) and Wright (1960).

Population dynamics: Estes and Goddard (1967) determined the sex ratios of some packs and found a disproportionately large ♂ : ♀ ratio. Litter size was on one occasion determined to be 9 pups.

Weight and growth: Maberly (1966) indicated 27.2-36.2 kg.

2.39 Banded mongoose (*Mungos mungo* (Gmelin))

See Neal (1970).

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Authors' addresses: J. C. Briand Petersen, P.O. Box 30559, Nairobi;
R. L. Casebeer, P.O. Box 30559 Nairobi, Kenya.

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