**Simulation of tsetse control operations by selective hunting:**

**the Nagupande experiment in Zimbabwe.**

**J. W. Hargrove and D. F. Lovemore**

Harare, Zimbabwe

Summary

**Key words.** *Glossina*, tsetse, control, hunting, modelling more?.

Correspondence: Dr. J .W. Hargrove, 9 Monmouth Rd., Avondale, Harare, Zimbabwe. Phone: 263-4-308042 email: john@zappuz.co.zw

**Short title:** Tsetse control by game elimination

**Introduction**

A communiqué issued by the heads of state of the Organisation of African Unity (OAU) following a summit meeting in OAU Heads of State in Lome, July 2000, “declares the years 2001 as the year of the control of tsetse fly, to mark the beginning of renewed efforts in the campaign for the *eradication* of tsetse flies in Africa”. This statement has led to renewed interest in the issue of tsetse control and has led to discussion in the press regarding the feasibility of continent-wide tsetse eradication (Kabayo, 2002; Rogers *et al*., 2002). An implicit sub-text of the discussion concerns the methods which could be used to eradicate tsetse populations under various circumstances.

Recent papers have provided models of the outcome of tsetse control campaigns using odour-baited targets (Hargrove, 2003; Hargrove & Williams, 1998) and insecticide-treated cattle (Hargrove *et al*., 2003). In the present paper we consider early data resulting from an attempt to use selective eradication of certain game animals to eradicate the tsetse fly *G. m. morsitans* (Westwood) in part of Zimbabwe. Hunting had been used as a major form of tsetse control in Zimbabwe until 1957 when, as a consequence of public pressure, it was stopped after the review of tsetse control operations \*\*\*\*. There followed a rapid increase in numbers of game animals in many parts of the country and a consequent increase in tsetse populations and in cases of trypanosomiasis in domestic livestock.

The Gwaai-Shangani area, Sebungwe Region, north-west Zimbabwe was one farming area affected and the distribution of fly indicated that the headwaters of the Nagupande river was the likely source of the infection. Analysis of tsetse blood-meals collected from the Nagupande drainage and elsewhere in the Sebungwe (Robertson, 1983) showed that warthog, bushpig, kudu and bushbuck were the main hosts of the fly. In 1962- 1967 an experiment was carried out to see whether the selective host elimination could be used to achieve tsetse eradication in the area.

In this paper we apply to the results of the Nagupande experiment the analytical techniques developed in the papers cited above, with a view to predicting the circumstances under which selective game elimination could be used, alone or with other methods, to achieve tsetse eradication. We utilise raw data from an unpublished report by Robertson (1968) which details the changes in tsetse catches during the experiment and data from Robertson (1983), largely relating to the analysis of tsetse blood-meals.

Materials and Methods

*Study area and selective game elimination*

Robertson (1983) describes the vegetation of the 541 km2 study area on the headwaters of the Nagupande River (Fig. 1). Ford (1970, 1971) and Cockbill (1971) also provide synopses of the work but there has been no detailed analysis of the data and some important details are omitted in each of the studies. A synopsis of the study area and methods is accordingly provided below.

Before doing so, however, note that an important omission from all descriptions is the fact that a similar hunting exercise had been carried out in the Nagupande area between June 1958 and October 1960 (Lovemore, 19\*\*). In this operation a game fence was erected, running east-west on the edge of the dense tsetse areas of the headwaters of the Nagupande and Busi Rivers and Sengwa and Lutope Rivers (Fig. 1). A further east-west fence was erected to the south, on the edge of the settled areas around the Kana and Shangani Rivers, to prevent the movement of cattle into the hunting area from the south (Fig. 1). The distance between the fences varied between *c*. 16 – 30 km and the area between them was *c*. 3100 km2. All mammals in the area, with the exception of lion, leopard, cheetah, small nocturnal mammals and vervet monkey were shot.

When the Nagupande experiment started, the northern fence of the previous operation was used as the southern fence of the selective hunting area (Fig. 1). As a consequence of the earlier operation, there was a much-reduced game population, and virtually no tsetse flies, south of this fence (Lovemore, *pers*. *comm*.). Further fences were erected as indicated in Fig. 1 and by October 1962 the entire area, apart from a gap left in the north-east at Chebira Springs for some months was enclosed by a 12 strand game fence. Hunting then started and, “as anticipated, [the gap] enabled considerable numbers of elephant and buffalo to evade destruction by moving out of the area” Robertson (1983).

Between October 1962 and September 1964, 60 hunters, working from 20 camps distributed throughout the study area hunted the four favoured tsetse hosts. They also shot elephant and buffalo in the interests of protecting the game fence, and indeed any animals found in the neighbourhood of the fence. The last category accounted for only 40 out of 1950 (2%) animals shot by January 1964.

In February 1965, 90 head of cattle were introduced into the Nagupande area and kept there in nine separate herds. The intention had been to treat these cattle with insecticide but no suitable chemical was developed. The cattle were gradually withdrawn after June 1966 but for 16 months, at least, provided an additional food source for the tsetse population. As a consequence of the early success of the Nagupande trial selective hunting was extended, from October – November 1964, to all sections of the Sebungwe Operations Area which adjoin the Nagupande area, namely in Kamezu and Kariangwe to the north and west and Tivuli to the east.

At the same time, however, hunting in the Nagupande area itself was reduced to only one third of its former level. In October 1964 it was suspended entirely as a consequence of political upheavals; from then and the end of 1966 hunting took place in the Nagupande area only during March, September and October1966. Hunting was resumed in February 1966 but now, instead of the large number of hunters based at static camps (see above), a single mobile team of 25 hunters hunted only selected parts of the area each month. This procedure was continued until the end of 1967, though there was no hunting in November and December 1966 and September 1967.

#### Tsetse population monitoring

No estimates of the absolute tsetse population are available from this study. The only data available are in the form of catches of male and female *G. m. morsitans* from ox fly-rounds. Six 3000-yd (2743 m) fly-rounds were operated in the Nagupande area and two in the control area, at Lusulu Research Station, 30 km to the north east of the study area (Fig. 1). The catches, corrected to the catch per 10,000, are referred to as “apparent densities”. They provide a rough measure of relative population changes, subject to the error that capture probability will undoubtedly vary with time and, particularly, wild host density (see below).

#### Theoretical development

#### Estimating the host population

The numbers of animals killed each month was taken from an unpublished report of the TTCB. Given the approximately constant hunting effort, and that the area was fenced and hence (largely) closed to emigration and immigration, a removal method of population estimation akin to Zippin’s (1958) method is indicated. Since the study lasted >3 years, however, there were clearly births, and deaths from causes other than hunting.

It is possible to allow for these factors if we assume that the births and deaths occur at constant rates *B* and *D* respectively. If, in addition, animals were killed by the hunters at rate *K* then the number, *N*(*t*), of animals remaining at time *t* is defined by:



with solution

 (1)

where *r* = *B* – *D* is the growth rate and *N*(0) is the population size just before hunting started.

Animals are killed at the rate of *KN*(*t*) so that in any month (*i*) the number killed is:

 (2)

Equation 2 was fitted to the data on numbers of animals killed per month using the non-linear least squares regression programme PAR in the BMDP statistical package (Dixon, 1992). If we assume a value for the growth rate (*r*), then *K* and *N*(0) can be estimated from *k*1 and *k*2 and used to estimate the numbers of animals remaining in the Nagupande area at any time during the experiment. Thus:

 (3)

and  (4)

#### Estimating the increase in tsetse mortality due to host elimination

Bursell (1970) estimated the relationship between host encounter and tsetse longevity but did not study the problem of how host encounter was related to host density; the problem is addressed here as part of a more rigorous quantitative development.

In order that a fly feeds on a given day the following conditions must be met:

i) There must be a host in its vicinity.

ii) The fly must “attempt to feed”; we denote this by saying that the fly is “active”.

iii) Given that there are hosts present, and the fly is active, the fly must succeed in finding a host and feeding off it.

Accordingly, we define:

*A* Total area (km2), assumed closed to host immigration and emigration.

*N* Total hosts, assumed randomly distributed in area *A*.

*Pk* Probability there are *k* hosts resident, on a given day, in a given “neighbourhood”. (Which we define as 1-km2 of country surrounding the fly).

*i* Number of days since the fly last fed.

*ηi* Probability fly is active on day *i*.

*σ* Conditional probability that a fly finds a host and feeds on a given day, given that it is the only host resident in a 1-km2 neighbourhood containing the fly, and given that the fly is active.

*fi* Probability that a fly succeeds in feeding on day *i* after its last blood-meal.

*FNA* Probability that a fly succeeds in feeding at some point in a given hunger cycle, given a host density of *N*/*A*.

The complement of any of the above probabilities is denoted by a “prime” suffix; *e*. *g*. *fi’* = 1 - *fi*.

*S* Maximum number of days fly can survive without feeding.

*I* Inter-larval period

On any particular day, the probability (ρ) that a given animal is present in a given neighbourhood is ρ = 1/*A*. If, as in the Nagupande experiment, the area is large, then ρ is small. Assuming, for the moment, independence between the hosts in their movement the probability (*Pk*) that there are *k* animals present in this neighbourhood can then be defined approximately by a Poisson distribution with parameter λ = ρ*N*. That is:

 (5)

Fig. 2 shows how *Pk* changes with the total number of animals present in the study area.

If there is only one host in the fly’s neighbourhood the probability that the fly fails to feed off it on a given day, given that the fly is active, is σ′. If there are *k* hosts in the neighbourhood and we assume independence among the hosts, then the fly fails to feed off any of them with probability (σ′)*k*. The probability that it *does* feed, given that there are *k* hosts present and given that the fly is active, is thus 1 - (σ′)*k*.

With the above definitions, the probability (*fi*) that a fly succeeds in feeding on day *i* of its hunger cycle is:

 (6)

The probability that, given a host density of *N*/*A*, the fly *fails to feed* on *S* consecutive days, and hence starves, is:

 (7)

The probability that a fly starves is a function of its activity pattern (*ηi*), its search efficiency (σ), the host density (*N*/*A*) and the number (*S*) of days it can survive without feeding. Immediately after taking a blood-meal tsetse show essentially zero feeding activity. Hargrove (1999a, b) estimated that the feeding rate in *G. pallidipes* increases exponentially thereafter and, as a first approximation, one can infer from that work probabilities of activity of 0, 0.05, 0.3, 0.9, 1.0 and 1.0 respectively for the six days following a blood-meal.

With this selected activity pattern and with *S* =6 days, the estimated starvation probability closely follows an exponential decline with host density, with the slope depending on the search efficiency (Fig. 3a). Alternatively, if the search efficiency is fixed, the slope depends on *S* (Fig. 3b). These relationships, not immediately evident from equation (7), become clearer if we use the approximation suggested by Rogers (1984) and divide the hunger cycle into “feeding” and “non-feeding” phases. Thus, if *ηi* = 0 for *i* ≤ *s* and *ηi* = 1 thereafter, equation (3) simplifies to:



so that  (8)

Taking *s* = 3 in (8) results in predicted starvation probabilities that are closely similar to those shown in Fig. 3a.

If, as in the Nagupande area, a constant hunting pressure is applied, the number of animals remaining at time *t* declines approximately exponentially such that:

*N*(*t*) = *N*(0) exp((*r*-*K)t*) (9)

where *r* is the population growth rate and where exp((*r*-*K)t*) is the exponential function e(*r*-*K)t*. Then, putting (9) into (8):

 (10)

For the purposes of modelling we need this expressed in terms of a daily mortality (μ). If Φ is the probability that a fly survives *S* days without starving then, using Φ = exp(-μ*S*),

 (11)

Fig. 4 shows how starvation probability and daily mortality levels increase as host densities decrease.

*Estimating the increase in tsetse abortions due to host elimination*

The previous section provides estimates of the increase in mortality consequent on a reduction in host density – and applies to males and female flies. Host density also affects the reproductive rate; at densities low enough to result in starvation, females will often be unable to feed sufficiently frequently to produce a viable offspring. Indeed, Hargrove (1999) concludes that larval production, and not the avoidance of starvation, decides the pattern and frequency of feeding in female tsetse flies.

Thus, at 250C, the inter-larval period (*I*) is *ca*. 9 days in the field (Hargrove, 1995). If the fly requires three meals to produce a larva in this time (Gaston & Randolph, 1993) then the fly must feed every three days on average. If four meals are required (Langley and Stafford, 1990) the interval is reduced to *ca*. 2.5 days. Both estimates are shorter than the estimated times to starvation for field flies at similar temperatures (Vanderplank, 1947; Jackson, 1954; Glasgow, 1961).

The only estimates for the effect of mean temperature on inter-larval period in the field are for *G. m. morsitans* and *G. pallidipes* in Zimbabwe (Hargrove, 1995). The given function:

*I* = 18.39 – 0.352*T* (12)

predicts that *I* declines linearly from 13.5 to 7 days as *T* increases from 14 to 320C.

No quantitative relationship has been developed for the effect of *T* on *S* but, using the sources quoted above, it will be assumed here as a first approximation that *S* declines by 0.5 days per 0C, from 12 to 3 days, as *T* increases from = 14 to 320C.

In estimating the effect of abortions on population growth one needs to discount those flies which may abort but feed with such low frequency that they die anyway. From the graphs of *I* and *S* against *T* (Fig. \*) this is clearly the case for flies which take zero or one feed in a period of *I* days. Thus, if three meals are sufficient to produce a larva, then abortions will only occur in flies which have taken exactly two meals in *I* days.

# Results

#### Changes in host and tsetse populations in the Nagupande area

#### Host population estimates

Warthogs comprised by far the biggest proportions (75%) of the animals shot during the Nagupande operation (Table 1). The total numbers shot, for all six species, declined approximately exponentially during the experiment (Fig. 5). Preliminary efforts to fit equation (2) to these data, however, showed that a markedly higher proportion of the population was shot in the first two months than in subsequent months (Fig. 5). Potts & Jackson (1952) in a similar experiment in Tanzanian noted that “the game early became very wary and retiring and difficult to approach” and this unsurprising effect probably accounts for the early rapid decline in the numbers shot in the Nagupande area.

When the first two data points were excluded from the fit the *r*2 increased from 0.78 to 0.82 and there was a marked reduction in the estimate of the parameter *k*2 (Table 1). The parameter estimates from the latter fit were used for all subsequent calculations.

In order to use *k*1and *k*2 to estimate the remaining population at any time we need first an estimate for the growth rate (*r*; see methods). Cumming (1975) found a maximum rate of increase of 19% per annum (~1.5% per month) in a population of warthog at Sengwa Research Station \*\*km \*\*\* east of Nagupande. Warthog accounted for 75% of animals killed at Nagupande and their birth rate is at least as high as in any of the other of the species hunted . Cumming (pers. comm.) considers, moreover, that \*\*\*. It therefore seems reasonable to assume that 1.5%/month provides a conservative estimate of the upper bound for the natural rate of increase at Nagupande.

The total host population at the beginning of December 1962 was estimated using equations (3) and (4), for values of *r* varying between 0 and 1.5% per month. Population levels for the first two months were then estimated by controlling for the growth rate and then adding in the actual numbers of animals shot in each of these months. Population estimates decreased as the assumed growth rate increased (Fig. 6) but were not, in fact, particularly sensitive to small changes in this parameter. Thus by September 1965 the estimated populations for *r* = 0 and 1.5%/month were 162 and 134 respectively. The estimated value for *K* was, similarly, little affected by the assumed growth rate, varying only between 7.1 and 8.6% (Table \*). It will become apparent below that the probability of starvation in the tsetse population changes as the log of the host population. Moderate errors in estimates of the host population will not therefore seriously affect the outcome of the study.

#### Tsetse catches

In the three months after the start of hunting in October 1962, catches of male and female *G. m. morsitans* in the Nagupande area actually increased (Fig. 5). Robertson (1968) attributed this to the disturbance of the game population and the greater availability of the flies to men as a consequence of the reduced availability of wild hosts, which had declined in number from estimated values of 2559 to 1786. This explanation is thrown into some doubt by the fact that the relative increase in the Nagupande catches had started three months before the onset of hunting, and only continued for two months thereafter (Fig. 6).

Between November 1962 and March 1964 the catches in the Nagupande area declined exponentially relative to the control catches, from a peak of 132% to <2% (Fig. 6). During this period host numbers had declined to an estimated 583. In the next year this figure declined to 234 but there was no further reduction in tsetse numbers. Since there were tsetse populations, not subject to control operations, to the west, north, east of Nagupande, it seems likely that the population had reached a stable equilibrium where small numbers of immigrant tsetse were able to survive on the remaining hosts.

After March 1965 the relative catches in Nagupande increased over a six-month period (Fig. 6) due, in part, to the introduction of cattle into the area (see Methods). The further decline in tsetse catches in the Nagupande area which started in October 1964 may be attributed to changes outside the study area. As a consequence of the success of the Nagupande experiment the Government had decided to introduce selective hunting as a major method of tsetse control in all operational areas. Accordingly, in October-November 1964 hunting was started in all areas adjoining Nagupande. By February 1966 the estimated number of wild hosts in the study area was \*\*\* and tsetse catches had declined to *ca*. 0.4% of the control levels.

The selective host destruction led, as expected, to a decrease in the proportion of blood-meals taken from these animals. This proportion never fell below 50% (Fig. 7), consistent with the indications from Fig. 4 that there were still appreciable numbers of the favoured hosts in the area.

# Discussion

**Acknowledgements**

We thank the Government of Zimbabwe for the use of their facilities and gratefully acknowledge the careful work of the late A. G. Robertson which made this study possible. We thank the AHP \*\*\*\*

**References**

**Bursell**, **E**. (1970) Theoretical aspects of the control of *Glossina morsitans* by game destruction. *Zoologica Africana* **5**, 135-141.

**Cockbill, G.F.C.** (1971) The control of tsetse and trypanosomiasis in Rhodesia. *Bulletin de l’Office International de Epizooties*, **76**, 347-352.

**Cumming, D.H.M.** (1975) A field study of the ecology and behaviour of warthog. *National Museums and Monuments of Rhodesia. Museum Memoir No. 7*, 179 pp. Salisbury Rhodesia.

**Dixon, W. J.** (Ed.) (1992). BMDP Statistical Software. Los Angeles, University of California Press.

**Ford, J.** (1970). Control of trypanosomiasis by control of wildlife. *Joint WHO/FAO African Trypanosomiasis Information Service*. *Tryp/Inf/70.38*, 16 *pp*.

**Ford, J.** (1971) The Role of the Trypanosomiases in African Ecology. A Study of the Tsetse Fly Problem. Clarendon Press Oxford, UK. 568pp.

**Gaston, K.A. & Randolph, S.E.** (1993) Reproductive under-performance of tsetse flies in the laboratory, related to feeding frequency. *Physiological Entomology*, **18**, 130-136.

**Glasgow, P.A.** (1961) The feeding habits of *Glossina* *swynnertoni* Austen. *Journal* *of* *Animal* *Ecology* **30**, 77-85.

**Hargrove, J. W.** (1999a) Nutritional levels of female tsetse *Glossina pallidipes* from artificial refuges. *Medical and Veterinary Entomology*, **13**, 150-164.

**Hargrove, J. W.** (1999b)Lifetime changes in the nutritional characteristics of female tsetse flies *Glossina pallidipes* caught in odour-baited traps. *Medical and Veterinary Entomology*, **13**, 165-176.

**Hargrove, J. W.** (2002) Optimised simulation of the control of tsetse flies *Glossina pallidipes* and *G*. *m*. *morsitans* using odour-baited targets in Zimbabwe. *Bulletin of Entomological Research* **(*submitted for publication April 2002*)**.

**Hargrove, J.W., Torr, S.J. & Kindness, H.** (2002) Simulation of tsetse control using baits. *Bulletin of Entomological Research*, (***to be submitted; July 2002***)

**Jackson, C. H. N.** (1954) The hunger-cycles of *Glossina morsitans* Westwood and *G. swynnertoni* Austen. *Journal of Animal Ecology*. **23**, 368-372.

**Langley, P. A. & Stafford, K.** (1990) Feeding frequency in relation to reproduction in *Glossina morsitans morsitans* Westwood and *G. pallidipes*. *Physiological Entomology*, **15**, 415-421.

**Lovemore, D.F.L.** (19\*\*) The effects of anti tsetse shooting operations on the game populations as observed in the Sebungwe District, Southern Rhodesia. *In???*: *Proceedings 20th Meeting of the ISCTRC*, Arusha, Tanzania, \*\*-\*\* \*\*\*\*, 19\*\*.

**Potts, W.H. & Jackson, C.H.N. (1952)** The Shinyanga game destruction experiment. *Bulletin of Entomological Research*, **53**, 365-374.

**Robertson, A.G.** (1968) The Nagupande selective hunting experiment 1962 – 67. *Tsetse & Trypanosomiasis Control Branch, Government of Rhodesia. Unpublished report*. 8 *pp*.

**Robertson, A.G.** (1983) The feeding habits of tsetse flies in Zimbabwe (formerly Rhodesia) and their relevance to some tsetse control measure. *Smithersia*, **1**, 1-72.

**Rogers, D. J.** (1984) The estimation of sampling biases for male tsetse flies. *Insect Science and its Application*, **5**, 369-373.

**Vanderplank** (1947) Some observations on the hunger-cycle of the tsetse flies *Glossina swynnertoni* and *G. pallidipes* (Diptera) in the field. *Bulletin of Entomological Research*, **38**, 431-438.

**Zippin, C.** (1958) The removal method of population estimate. *Journal of Wildlife Management*, **22**, 82-90.

Table \*. Calendar of events in the Nagupande selective hunting experiment.

|  |  |  |  |
| --- | --- | --- | --- |
| Year | Month | Day of experiment | Event |
| 1962 | October | 1 | Hunting starts in Nagupande. |
| 1964 | October | 721 | Hunting starts outside Nagupande fences; hunting intensity decreases inside fence. |
| 1965 | February | 841 | Ninety cattle introduced. |
| 1965 | November | 1111 - 1170 | No hunting in November or December. |
| 1966 | January | 1171 - 1230 | No hunting in January or February. |
|  | March | 1231-1260 | Hunting in March. [One mobile hunting team from this time on]. |
|  | April | 1261 - 1410 | No hunting in April - August. |
|  | September | 1411 - 1470 | Hunting in September and October. |
|  | November | 1471 - 1530 | No hunting in November or December. |
| 1967 | January | 1531 | Hunting resumes until end of August. |
|  | September | 1800 | End of experiment. |

Table \*. Animals shot per quarter in the Nagupande selective game elimination experiment 1962/1967. Suffixes in the months column indicate the number of months in which no hunting was carried out.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  |  | Elephant | Buffalo | Kudu | Bushbuck | Warthog | Bushpig | Total |
| 1962 | Oct-Dec | 44 | 3 | 65 | 19 | 610 | 32 | 773 |
| 1963 | Jan-Mar | 0 | 12 | 32 | 0 | 264 | 19 | 327 |
|  | Apr-Jun | 0 | 6 | 35 | 4 | 265 | 20 | 330 |
|  | Jul-Sep | 1 | 0 | 27 | 4 | 150 | 8 | 190 |
|  | Oct-Dec | 0 | 1 | 30 | 12 | 152 | 20 | 215 |
| 1964 | Jan-Mar | 1 | 2 | 17 | 3 | 104 | 14 | 141 |
|  | Apr-Jun | 1 | 0 | 22 | 6 | 82 | 8 | 119 |
|  | Jul-Sep | 0 | 0 | 22 | 10 | 61 | 7 | 100 |
|  | Oct-Dec | 1 | 9 | 5 | 6 | 38 | 11 | 70 |
| 1965 | Jan-Mar | 3 | 14 | 5 | 4 | 28 | 6 | 60 |
|  | Apr-Jun | 2 | 2 | 0 | 1 | 16 | 3 | 24 |
|  | Jul-Sep | 1 | 5 | 3 | 4 | 32 | 3 | 48 |
|  | Oct-Dec2 | 0 | 1 | 0 | 1 | 11 | 1 | 14 |
| 1966 | Jan-Mar2 | 5 | 0 | 3 | 1 | 22 | 5 | 36 |
|  | Apr-Jun3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
|  | Jul-Sep2 | 0 | 0 | 4 | 0 | 5 | 0 | 9 |
|  | Oct-Dec2 | 0 | 0 | 3 | 0 | 4 | 1 | 8 |
| 1967 | Jan-Mar | 0 | 0 | 12 | 0 | 35 | 12 | 59 |
|  | Apr-Jun | 0 | 0 | 4 | 1 | 20 | 5 | 30 |
|  | Oct-Dec | 0 | 0 | 0 | 4 | 23 | 1 | 28 |
| Total | | 59 | 55 | 289 | 80 | 1922 | 176 | 2581 |
| % of GT | | 2.3 | 2.1 | 11.2 | 3.1 | 74.5 | 6.8 |  |

Table \*. \*). Parameter estimates (± standard errors) resulting from fitting the equation:

*NK*(*i*) = *k*1(exp(*k*2(*i*-1) - exp(*k*2(*i*-1)) to data on the total number (*NK*(*i*) of animals shot at Nagupande in each month *i* between October 1962 and September 1965 (see Fig.\*).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | Parameter estimates | |  |  |
| First month | *k*1 | *k*2 | *R*2 | *n* |
| Oct 1962 | 2205.6 ± 119.5 | -0.129 ± 0.017 | 0.78 | 37 |
| Dec 1962 | 2214.4 ± 131.9 | -0.0707 ± 0.0069 | 0.82 | 35 |

Table \*. Monthly killing rates (*K*) and number (*N*(3)) of hosts present at the start of December 1962 estimated for various assumed levels of the growth rate *r*.

|  |  |  |
| --- | --- | --- |
| *r* | *K* = *r*-*k*2 | *N*(3) = -*k*1*k*2*/K* |
| 0.000 | 0.0707 | 2214.1 |
| 0.001 | 0.0717 | 2183.2 |
| 0.002 | 0.0727 | 2153.2 |
| 0.003 | 0.0737 | 2124.0 |
| 0.004 | 0.0747 | 2095.5 |
| 0.005 | 0.0757 | 2067.9 |
| 0.006 | 0.0767 | 2040.9 |
| 0.007 | 0.0777 | 2014.6 |
| 0.008 | 0.0787 | 1989.0 |
| 0.009 | 0.0797 | 1964.1 |
| 0.010 | 0.0807 | 1939.7 |
| 0.011 | 0.0817 | 1916.0 |
| 0.012 | 0.0827 | 1892.8 |
| 0.013 | 0.0837 | 1870.2 |
| 0.014 | 0.0847 | 1848.1 |
| 0.015 | 0.0857 | 1826.6 |

Table \*. Blood-meals from *G. m. morsitans* caught at Nagupande in 1962.

|  |  |  |
| --- | --- | --- |
|  | Blood- |  |
|  | meals | Percent |
| Warthog | 168 | 22.5 |
| Bushpig | 2 | 0.3 |
| Warthog; bushpig | 314 | 42.0 |
| **Total from suids** | **484** | **64.7** |
|  |  |  |
| Kudu | 26 | 3.5 |
| Bushbuck | 42 | 5.6 |
| Bushbuck; kudu | 18 | 2.4 |
| Bushbuck; kudu; eland | 3 | 0.4 |
| Eland | 2 | 0.3 |
| Roan | 1 | 0.1 |
| Impala | 2 | 0.3 |
| Unknown bovid | 97 | 13.0 |
| **Total from bovids** | **191** | **25.5** |
|  |  |  |
| Rhinoceros | 12 | 1.6 |
| Man | 6 | 0.8 |
| Baboon | 1 | 0.1 |
| Unknown primate | 26 | 3.5 |
| Cat | 1 | 0.1 |
| Antbear | 2 | 0.3 |
| Unknown bird | 25 | 3.3 |
|  |  |  |
| **Grand total** | **748** |  |

Table \*. Total kills of the “selected game species” in the Nagupande selective hunting area 1962-67. (Including kills on the Nagupande game fence).

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  |  | Oct | Nov | Dec | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 1962 | Elephant | 35 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| to 1963 | Buffalo | 0 | 2 | 1 | 1 | 6 | 5 | 1 | 2 | 3 | 0 | 0 | 0 |
|  | Kudu | 20 | 29 | 16 | 16 | 10 | 6 | 6 | 16 | 13 | 16 | 6 | 5 |
|  | Bushbuck | 9 | 6 | 4 | 0 | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 3 |
|  | Warthog | 218 | 302 | 90 | 123 | 89 | 52 | 78 | 102 | 85 | 81 | 41 | 28 |
|  | Bushpig | 18 | 13 | 1 | 7 | 5 | 7 | 1 | 9 | 10 | 3 | 2 | 3 |
|  | Totals | 300 | 361 | 112 | 147 | 110 | 70 | 87 | 130 | 113 | 101 | 50 | 39 |
|  | Cumulative | 300 | 661 | 773 | 920 | 1030 | 1100 | 1187 | 1317 | 1430 | 1531 | 1581 | 1620 |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 1963 | Elephant | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| to 1964 | Buffalo | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
|  | Kudu | 10 | 12 | 8 | 9 | 4 | 4 | 8 | 5 | 9 | 9 | 7 | 6 |
|  | Bushbuck | 6 | 5 | 1 | 2 | 0 | 1 | 3 | 0 | 3 | 2 | 4 | 4 |
|  | Warthog | 59 | 54 | 39 | 60 | 22 | 22 | 23 | 31 | 28 | 24 | 14 | 23 |
|  | Bushpig | 6 | 10 | 4 | 3 | 7 | 4 | 2 | 1 | 5 | 2 | 5 | 0 |
|  | Totals | 82 | 81 | 52 | 75 | 34 | 32 | 36 | 38 | 45 | 37 | 30 | 33 |
|  | Cumulative | 1702 | 1783 | 1835 | 1910 | 1944 | 1976 | 2012 | 2050 | 2095 | 2132 | 2162 | 2195 |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 1964 | Elephant | 0 | 1 | 0 | 0 | 3 | 0 | 2 | 0 | 0 | 0 | 1 | 0 |
| to 1965 | Buffalo | 0 | 0 | 9 | 2 | 6 | 6 | 0 | 2 | 0 | 0 | 5 | 0 |
|  | Kudu | 3 | 2 | 0 | 3 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
|  | Bushbuck | 3 | 3 | 0 | 0 | 1 | 3 | 0 | 1 | 0 | 2 | 1 | 1 |
|  | Warthog | 7 | 19 | 12 | 8 | 10 | 10 | 4 | 7 | 5 | 6 | 13 | 13 |
|  | Bushpig | 3 | 4 | 4 | 0 | 4 | 2 | 1 | 1 | 1 | 0 | 2 | 1 |
|  | Totals | 16 | 29 | 25 | 13 | 26 | 21 | 7 | 11 | 6 | 9 | 23 | 16 |
|  | Cumulative | 2211 | 2240 | 2265 | 2278 | 2304 | 2325 | 2332 | 2343 | 2349 | 2358 | 2381 | 2397 |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 1965 | Elephant | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 |
| to 1966 | Buffalo | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
|  | Kudu | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 4 |
|  | Bushbuck | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
|  | Warthog | 11 | 0 | 0 | 0 | 0 | 22 | 0 | 0 | 0 | 0 | 0 | 5 |
|  | Bushpig | 1 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 |
|  | Totals | 13 | 1 | 0 | 0 | 0 | 36 | 0 | 0 | 0 | 0 | 0 | 9 |
|  | Cumulative | 2410 | 2411 | 2411 | 2411 | 2411 | 2447 | 2447 | 2447 | 2447 | 2447 | 2447 | 2456 |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 1966 | Elephant | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| to 1967 | Buffalo | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
|  | Kudu | 3 | 0 | 0 | 0 | 8 | 4 | 0 | 2 | 2 | 0 | 0 | 0 |
|  | Bushbuck | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 4 | 0 |
|  | Warthog | 4 | 0 | 0 | 16 | 12 | 7 | 7 | 3 | 10 | 12 | 11 | 0 |
|  | Bushpig | 1 | 0 | 0 | 8 | 4 | 0 | 3 | 1 | 1 | 0 | 1 | 0 |
|  | Totals | 8 | 0 | 0 | 24 | 24 | 11 | 10 | 6 | 14 | 12 | 16 | 0 |
|  | Cumulative | 2464 | 2464 | 2464 | 2488 | 2512 | 2523 | 2533 | 2539 | 2553 | 2565 | 2581 | 2581 |

Table 2. Animals shot in the Nagupande selective game elimination experiment 1962/1964. Asterisks in the table indicate which were only shot to protect fences.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  |  | 1962 |  |  |  |  |  |  | 1963 |  |  |  |  |  |  | 1964 |  |  |
|  | Oct | Nov | Dec | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec | Jan |  | Total |
| Elephant | 35 | 9 |  |  |  |  |  |  |  |  | 1 |  |  |  |  |  |  | 45 |
| Buffalo |  | 2 | 1 | 1 | 6 | 5 | 1 | 2 | 3 |  |  |  | 1 |  |  | 1 |  | 23 |
| Kudu | 20 | 29 | 16 | 16 | 10 | 6 | 6 | 16 | 13 | 16 | 6 | 5 | 10 | 12 | 8 | 9 |  | 198 |
| Bushbuck | 9 | 6 | 4 |  |  |  | 1 | 1 | 2 | 1 |  | 3 | 6 | 5 | 1 | 2 |  | 41 |
| Warthog | 218 | 302 | 90 | 123 | 89 | 52 | 78 | 102 | 85 | 81 | 41 | 28 | 59 | 54 | 39 | 60 |  | 1501 |
| Bushpig | 18 | 13 | 1 | 7 | 5 | 7 | 1 | 9 | 10 | 3 | 2 | 3 | 6 | 10 | 4 | 3 |  | 102 |
| Eland | 1 | 1 | 1 |  |  |  |  | 1 |  |  |  |  |  |  |  |  |  | 4\* |
| Roan | 1 | 1 |  | 2 | 1 |  |  |  |  |  | 2 |  | 1 |  |  |  |  | 8\* |
| Sable | 3 | 5 |  |  |  |  | 1 |  |  |  |  |  |  |  |  |  |  | 9\* |
| Zebra | 1 | 1 |  | 2 |  |  | 1 |  |  |  |  |  |  |  |  |  |  | 5\* |
| Tsessebe | 1 |  |  |  |  |  |  |  |  |  | 2 |  |  |  | 1 |  |  | 4\* |
| Reedbuck | 4 |  |  |  | 1 |  |  |  |  |  |  |  | 2 | 1 |  | 1 |  | 9\* |

**Figure legends**

Fig. \*. Apparent Densities of *G. morsitans* (males and females) per 10,000 yards. Data derived from catches on six 3,000-yard long bait-ox flyrounds in the Nagupande area and two at Lusulu.