THE INTRODUCTION OF LOVEBIRDS (AGAPORNIS) TO LAKE NAIVASHA, KENYA, AND THEIR EFFECT ON THE LAKE'S AGRICULTURE AND INDIGENOUS AVIFAUNA

By

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A THESIS SUBMITTED IN COMPLETE FULFILMENT FOR THE DEGREE OF MASTER OF SCIENCE IN THE UNIVERSITY OF NAIROBI

1987

D E C L A R A T I O N

This thesis is my original work and has not been presented for a degree in any other University

JEREMY JOHN THOMPSON

This thesis has been submitted for examination with our approval as University Supervisors.

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and

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ACKNOWLEDGEMENTS

I am indebted to my supervisors Dr. W. Karanja and Dr. J. Hebrard for their guidance throughout the course of my research and for reviewing earlier drafts of this thesis. I am grateful to Mr. T. Ahutah for his help in the computer analysis of the hybridisation data and to Dr. A.R.D. Taylor for providing and running the cluster analysis package. Thanks also to Mr. C. Van-Someren, Mrs. J. Hayes and Dr. L. Malaret for their helpful advice. I would also like to thank the East African Wildlife Society who provided financial support for this research.

Finally, I appreciate the help of Mr. Yusuf Sulemain for assisting in the construction of the lovebird trap, the farmers and residents of Lake Naivasha for their cooperation during my fieldwork and to Miss Doreen Munene for the diligent typing of this thesis.

ABSTRACT

Fieldwork was conducted between August 1985 and June 1986 in the forest surrounding Lake Naivasha. The number of lovebirds was estimated by both the fixed-width line-transect and mark-recapture methods. There was good agreement between the various estimates and the final population estimate for 95 per cent confidence was 5942 ± 612 lovebirds. The strengths and limitations of the methods are discussed in relation to over-or-underestimation of population size and in relation to the results of previous workers. The present work provided a comparison of some bird census methodologies over a medium-sized area.

Lovebirds were observed to initiate most of the avian damage to maize at Naivasha. Their strong bill and efficient technique of exposing kernels not only make them an important maize pest but also allows faster depredation by other species. At present, lovebirds have a relatively minor impact on commercial maize production since most maize grown at Naivasha is intended for consumption by cattle and harvested before being vulnerable. Worst damage to maize grown for human consumption was measured in small plots farmed on a part-time basis. Large commercial fields were either adequately protected or too large for lovebirds to have a significant impact.

Lovebirds were aggressed upon by many other species and their behaviour is one of retreat rather than aggression. Lovebirds may out-compete other hole-nesting species by more indirect methods

however. For example their modification and permanent inhabitation of nesting cavities.

Primary moult was examined and no regular annual moulting periodicity could be detected. Since primary moult is linked with breeding, this could indicate their ability to breed at any time of the year at Naivasha.

All lovebirds captured had intermediate hybrid characters although biased towards the fischeri phenotype. This bias is probably the result of an unbalanced genetic expression in plumage colouration rather than a difference in fitness of the fischeri genotype or the result of assortative mating.

CHAPTER ONE

INTRODUCTION

The genus *Agapornis* is a group of nine closely related and allopatric forms readily able to hybridise in captivity. Confined to Africa and Madagascar, their closest living relatives are the Hanging Parakeets (*Loriculus* spp.) of Asia, from which they are thought to have recently evolved (Moreau 1948), perhaps in the Miocene. While there are nine types, the number of species recognised depends on the treatment of the four east and south-central African (*A. fischeri*, *personata*, *lilianae* and *nigrigenis*) or white-eye-ringed forms. Dilger (1960) treats them as conspecific and therefore recognises only six species of lovebird. Dilger has concluded from behavioural studies that the white-eye-ringed forms are the most recently evolved of all the lovebirds and hence the most evolutionarily advanced.

Feral Agapornids within Kenya were first reported in the literature in 1967 when Zimmerman (1967) noted a specimen of *A. fischeri* collected near Isiolo. He claimed this to be a legitimate addition to Kenya's avifauna. Van Someren (1975) disputed the matter and reiterated *A. fischeri* and *A. personata's* distributions as in Moreau (1948), pointing out that many reports had been received of lovebird escapes from aviaries elsewhere in Kenya. Up to date, they have been reported from Nairobi, Lake Naivasha, Nakuru, Molo, Kisumu, Meru, Embu and the Kenyan Coast.

It is impossible to pin-point when the first breeding pair of feral lovebirds (A. fischeri X A. personata) became successfully established at Lake Naivasha. Certainly lakeside residents kept caged lovebirds during the 1930's and 1940's but apparently none were released. According to the man generally credited (or blamed) with releasing them, lovebirds did not establish themselves until following the extremely good long rains in 1962. 1960 would therefore seem to be a convenient benchmark to work from for their introduction to Naivasha.

Since their introduction, the hybrid lovebirds have spread to encircle the lake, inhabiting the surrounding forest. Being a hole-nesting species, they threaten to compete with other hole-nesters for cavities and are generally considered to be the most serious avian pest of maize (Zea mays) around the lake. The impetus for this research therefore was to determine

(a) their numbers and distribution around Lake Naivasha

(b) any competitive interaction and effect upon other hole-nesting birds and

(c) the extent to which they depredate crops in the area.

CHAPTER TWO

STUDY AREA

2.1 General Location and Description

Lake Naivasha is one of a series of lakes in the Rift Valley of South Western Kenya (Figure 1). It is approximately circular with (in 1969) a surface area of 170.9 square kilometres (Parker and Watson 1969) and a circumference of approximately 75 kilometres. The lake lies between latitudes 0° 50'S and 0° 40'S and longitudes 36° 15'E and 36° 25'E. Its level varies considerably and has fluctuated between approximately 1883 and 1897 metres above sea level in the past century (see Hartley 1985).

Lake Naivasha shares a common depression with two saline lakes, Elementaita and Nakuru, but unlike these and other nearby Rift Valley alkaline lakes, Naivasha's water is fresh. The Nakuru-Naivasha basin is bounded to the East by the Aberdare Range and the Kinangop Plateau, and by the Mau Escarpment to the West. To the North, the Naivasha basin is partially separated from the Elementaita-Nakuru basin by the Eburru mountains and to the South, Longonot and several smaller volcanoes form a barrier breached by the Njorowa Gorge (Figure 2), a former outlet of the lake (Litterick *et al*. 1979).

Figure 1. Map of Kenya showing position of Lake Naivasha in relation to some other Rift Valley lakes

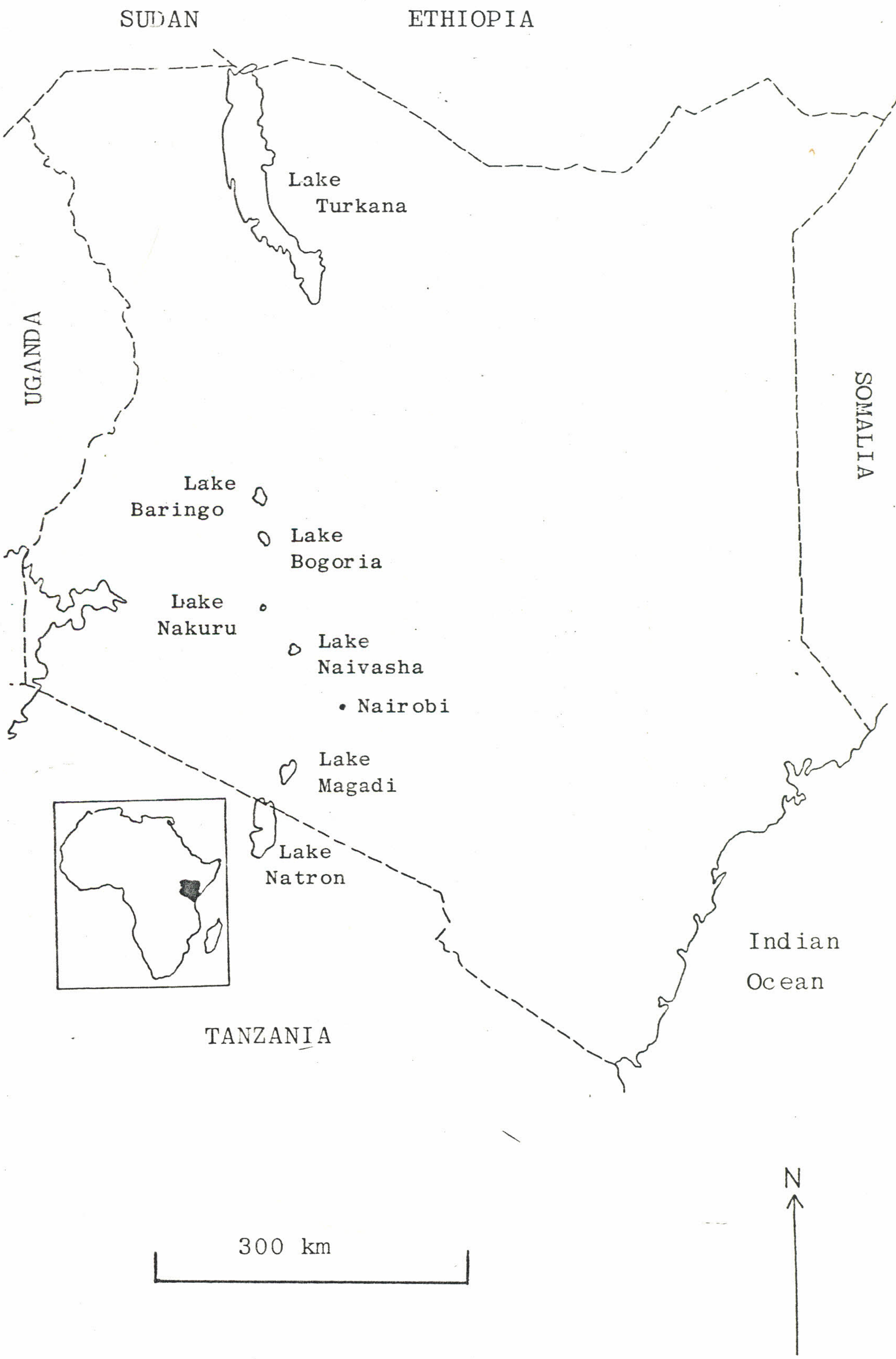
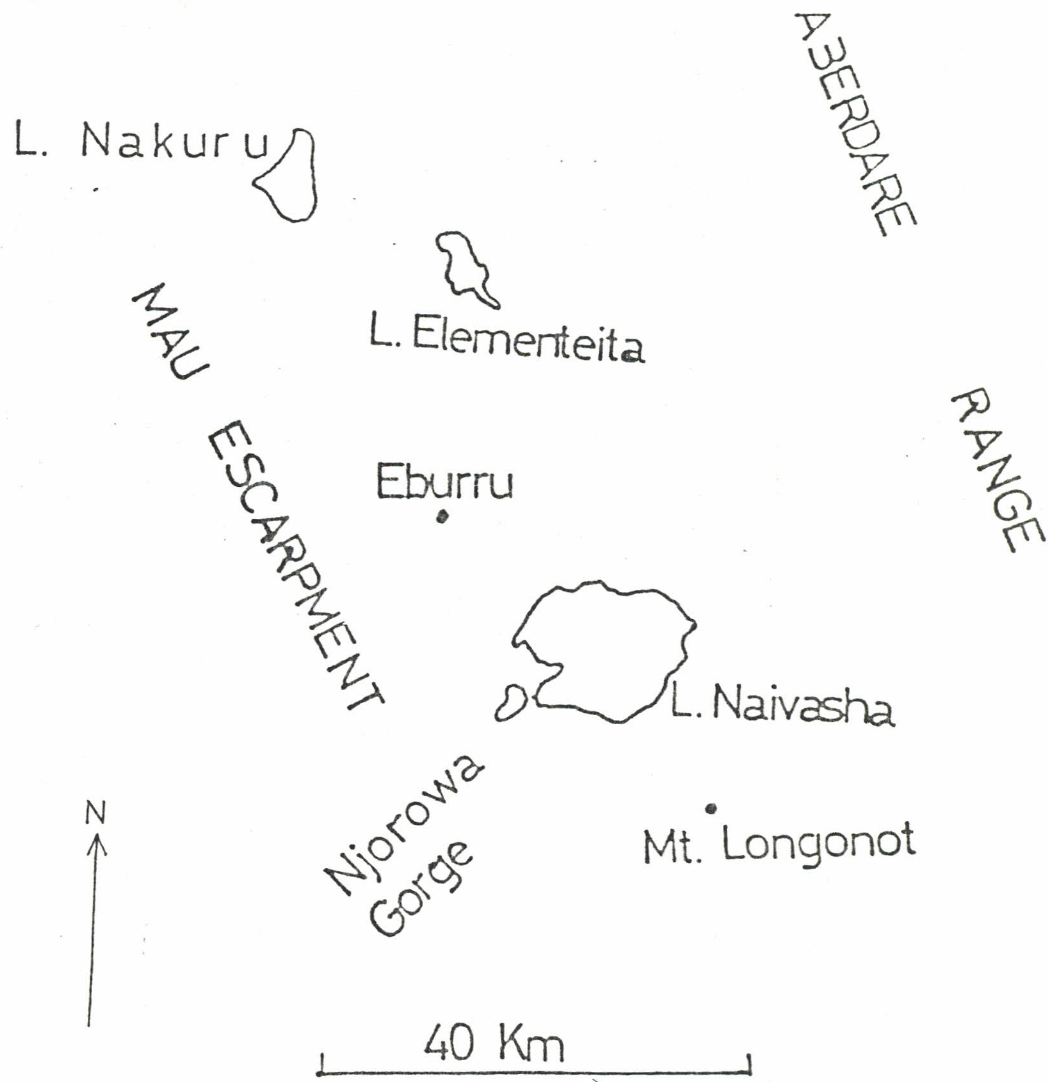


Figure 2. The Naivasha-Nakuru basin



The lake shores are, for the most part, composed of gently sloping alkaline volcanic soils. In the South-West however, there are areas of steeply sloping volcanic rocks.

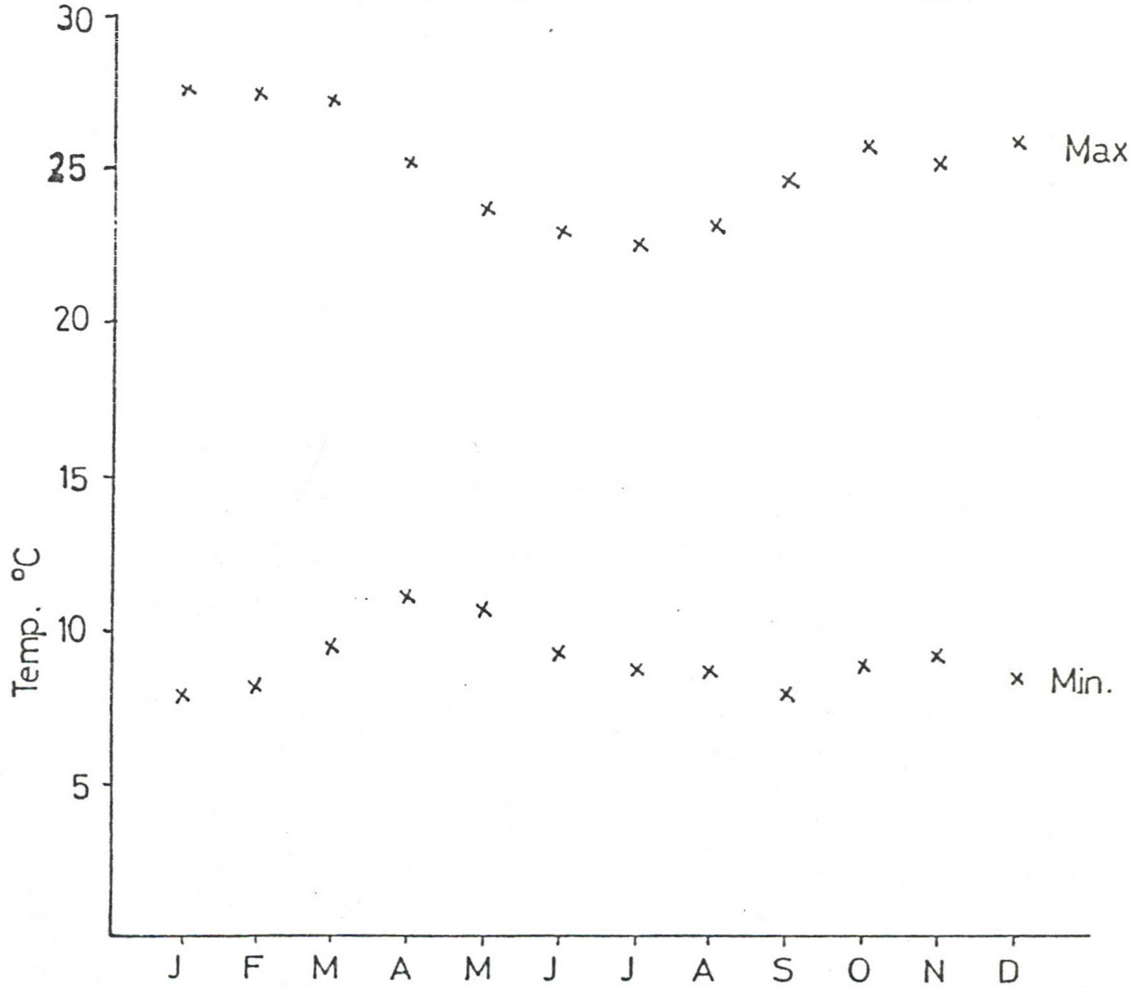
2.2 Climate

The climate of the area is warm and semi-arid with an average annual rainfall of 627 millimetres. Rainfall sometimes occurs in a bimodal pattern but is highly unpredictable in both timing and quantity (Zack and Ligon 1985). The general pattern is of relatively heavy rains in April-May with lighter rains in other months. Mean temperature and rainfall data are presented in Figures 3(a) and 3(b).

2.3 Vegetation

Surrounding the lake is a belt of forest, comprised of a virtually monotypic stand of *Acacia xanthophloea* woodland combined or interspersed with areas of irrigated cultivation or grassland for intensive livestock management (Plate 1). Within the natural forest openings are thickets of *Euphorbia* spp., *Aloe* spp. or *Opuntia* spp. and common shrubs include *Achyranthes aspera*, *Hypoestes verticillaris* and *Solanum incanum*. Three grasses predominate, their distribution dependent on height above lake level (Hayes pers. comm.) ranging from *Pennisetum clandestinum* at the lake edge to *Cynodon nlemfuensis* and *C. plectostachyus* in the higher areas.

Figure 3a/ Average temperature and rainfall data for lake Naivasha (Kenya Department of Meteorology)



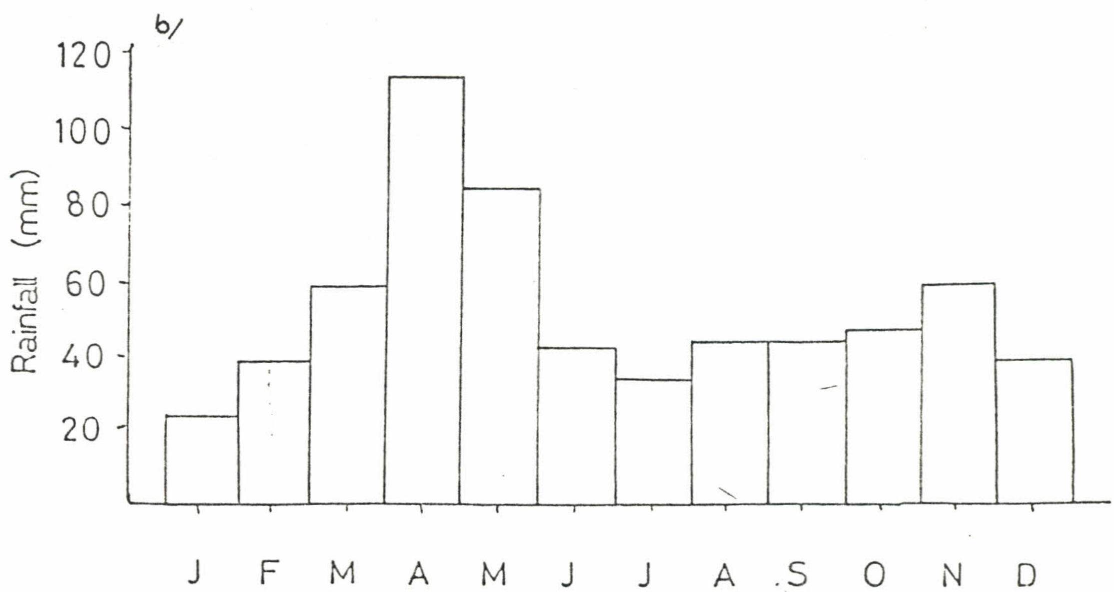


Plate 1. Lovebird colonies at Naivasha are found in mature Fever tree forests such as this one. This particular paddock is part of a racehorse stud and training farm

Outside the forested area the land abruptly gives way to semi-arid <u>Tarchonanthus camphoratus</u> bushland, typical of the Rift Valley floor. Because of this sharp demarcation of vegetation types and because lovebirds depend on the Fever trees (<u>A. xanthophloea</u>) not only for nesting cavities, but also as a food source, the study area only includes the belt of forest surrounding the lake's edge.

2.4 Delimitation of Study Area

Because Fever trees grow where their roots can easily find water (Lind and Morrison 1974) their distribution around the lake is restricted to a certain height above lake level (Plate 2). There are exceptions to this rule, for instance in areas of better drainage from surrounding hills or irrigated land where the forest spreads beyond its normal distribution. On aerial photographs there is a close correlation between the forest edge and the 1900 metre above sea level contour line. I have therefore defined the study area as that region between this contour line and the lake's edge, an area of approximately 1788 hectares (Figure 4). Lovebirds will occasionally leave this area on foraging trips but at any one time, the defined study area probably contains at least 95 per cent of the lovebird population.

2.5 General Ecology of Study Area

<u>Acacia xanthophloea</u> (Plate 3) is a flat-topped species growing up to 24 metres in height (Government Printer 1936),

Plate 2. This small crater lake illustrates how Fever tree distribution is confined to a certain height above water level. On the far side to the left can be seen the abrupt change from forest to bushland with increasing height above water level

Figure 4. The study area defined by the lake shore (inner limit) and 1900 metre above sea level contour line (outer limit)

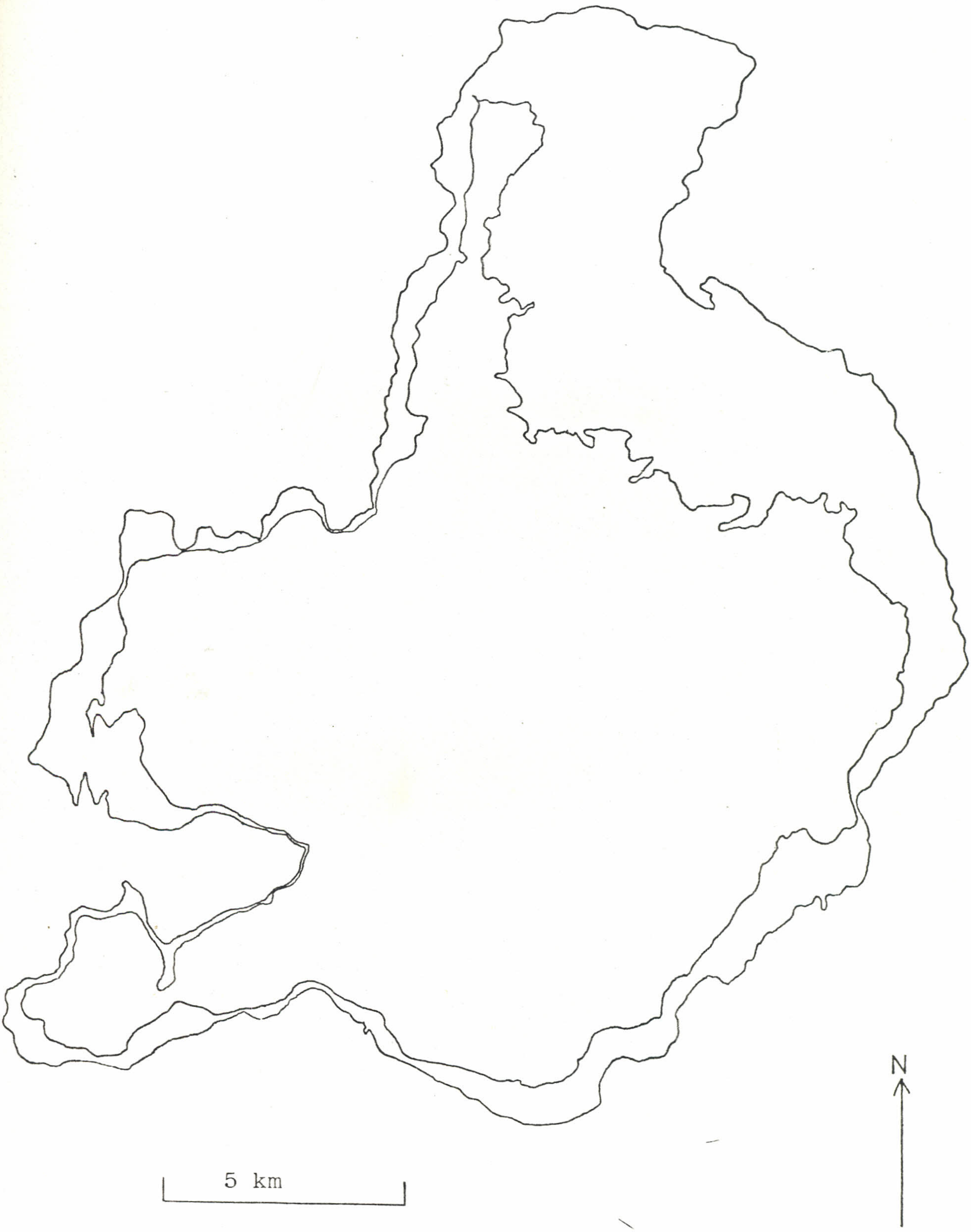


Plate 3. An isolated Fever tree (*Acacia xanthophloea*) growing to more than 20 metres in height. Note the abundance of dead and broken branches suitable for cavity excavation by hole-nesting birds.

fast growing and with a short life expectancy of about 40 years (Hayes pers. comm.). A comparison of aerial photographs from 1969 and 1984 showed that, in general, the extent of Fever tree distribution and overall maturity of the forest is increasing, probably due to a Government ban on tree-felling. Therefore, hectarage of suitable hole-nesting habitat has been increasing in recent years.

Included in the study area are areas used for agricultural production. These can be broadly grouped into two categories, according to the degree of habitat modification, and the compatibility of Fever trees with the particular land use. They are:

1. Fever trees and land use largely incompatible
   (a) vegetable production - maize, beans, cabbages etc.
   (b) flower production
   (c) fruit production - strawberries, citrus fruits, grapes etc.

2. Fever trees beneficial to land use
   (a) dairy production
   (b) beef production
   (c) lucerne production
   (d) horse training/breeding
   (e) recreational/tourism

Fever trees are beneficial for either the encouragement of vegetative growth of grass and lucerne by the provision of shade to slow evaporation, or simply for aesthetic reasons.

2.6 Avian and Mammalian Fauna

According to Hartley (1985), some 55 species of large mammals (including one introduced species) have been recorded in the Naivasha area. However, since the lake's forest is now heavily cultivated and largely fenced off, the mammalian fauna is very poor. The lake is renowned for its birdlife though and, according to Hartley, over 400 species have been recorded in the area. Because the regional limits for this list are indistinct I have prepared a list of the 107 species I have seen within the defined study (appendix 1). This is by no means a definitive list but should be added to by future workers with particular interests and expertise in various fields. Of these 107 species, 20 are partially or completely cavity-nesting species, and 16 the type of cavity nester likely to be competing with lovebirds for nest sites. These were the Pearl-spotted Owlet (Glaucidium perlatum), Woodland Kingfisher (Halcyon senegalensis), Lilac-breasted Roller (Coracias caudata), African Hoopoe (Upupa epops), Green Wood Hoopoe (Phoeniculus purpureus), Grey Hornbill (Tockus nasutus), Red-fronted Barbet (Lybius diadematus), Red-throated Wryneck (Jynx fuficollis), Nubian Woodpecker (Campethera nubica), Cardinal Woodpecker (Dendropicos fuscescens), Grey Woodpecker (Mesopicos goertae), Bearded Woodpecker (Thripias namaquus), White-bellied Tit (Parus albiventris), Blue-eared Glossy Starling (Lamprotornis chalybaeus), Ruppell's Long-tailed Glossy Starling (L. purpuropterus), Superb Starling (Spreo superbus).

CHAPTER THREE

POPULATION ESTIMATES

3.1 INTRODUCTION

Knowledge of the number in a population is essential for effective wildlife resource management since changes in population levels over time can be determined and effects of management effort assessed (Bull 1981). There is, however, no single universally applicable method for censusing avian communities (Nichols *et al.* 1981) and the methodology chosen should be appropriate for the particular situation under study. Since each census technique has its own weaknesses and limitations, the use of several independent methods is important as checks of each other (Southwood 1978). The census of lovebirds also provides a useful comparison of counting methodologies because of their conspicuousness.

3.1.1 Line-Transect Counts

One of the methods commonly used to estimate avian community size, is the fixed-width line-transect (see Jarvinen and Väisänen 1975, Franzreb 1981a, Emlen 1971, 1977). This method requires the observer to sample belts of given widths on either side of the established transect. This can then be converted to a density estimate ($\hat{D}$) by the equation

$$\hat{D} = \frac{n}{2LW} \quad \text{(Tilghman and Rusch 1981)}$$

where n is the number of observations within the strip width W (on either side of the transect) and transect length L.

The fixed-width transect method was appropriate for counting lovebirds at Naivasha for seveal reasons. Firstly, distance estimation is less critical than if using variable width transect methods (Franzreb 1981a) thus forgoing the need to use distracting range finders or tape measures (Scott 1981). Secondly, it is more suitable for narrow habitat strips or patchy environments (Franzreb 1981a). The method is efficient at censusing large areas (Jarvinen and Väisänen 1975, Emlen 1977) and lastly, recording observations and data analysis is relatively simple (Franzreb 1981a).

3.1.2 Mark-recapture Estimates

As an alternative check to the line-transect counts, Lincoln Index and Frequency of Capture methods were used to estimate Naivasha's lovebird population size. These methods have the advantage of including all lovebirds resident around the lake and not only those lovebirds within the study area at any one time. This is because line-transect counts were performed only within the study area so that any lovebirds temporarily foraging outside its boundaries during the day would have been missed. The mark-recapture methods, however, include in the sampling all individuals since lovebirds were captured at each location over a period of several days. Therefore, even if they would occasionally leave the study area, they would be exposed to trapping pressure at some time at each site.

3.1.3 Avian Habitat Selection

As an adjunct to measurements of lovebird density in different habitat types, a series of "Timed Species-counts" (Pomeroy and Tengecho 1986) were performed to detect differences in species' abundance in two different habitat types. Not only does this yield data on habitat selection for a wide variety of species but also gives a simple index of their relative abundance at Lake Naivasha. If lovebirds are out-competing other hole-nesters, it will be important to have some baseline data with which future workers can refer, to detect changes in the relative abundance of hole-nesting birds.

3.2 METHODS

3.2.1 Line-Transect Counts

Because of the extremely patchy nature of the study area and the variable age of each forest patch, the habitat was stratified into various types in which separate density estimates were made. The defined habitat types were mutually exclusive and exhaustive within the study area and were sampled in approximate proportion to their occurrence. Two censuses were performed, the first between 22/7/85 to 28/7/85 and the second between 19/1/86 to 3/2/86. A different method of stratification was used for each and habitat strata are defined below.

Method 1

Ia - Within 100 metres of human habitation with acacia trees present; cultivation within 200 metres.

Ib - Within 100 metres of human habitation with acacia trees present; no cultivation within 200 metres.

IIa - Cultivated land. Trees greater than one metre in height more than 50 metres apart.

IIb - Cultivated land. Trees greater than one metre in height between 10 and 50 metres apart.

IIc - Cultivated land. Trees greater than one metre in height less than 10 metres apart.

IIIa - No cultivation within 200 metres. Trees greater than one metre in height more than 50 metres apart.

IIIb - No cultivation within 200 metres. Trees greater than one metre in height between 10 and 50 metres apart.

IIIc - No cultivation within 200 metres. Trees greater than one metre in height less than 10 metres apart.

Note: Cultivation refers to any modification of the ground surface for growing vegetables, lucerne or other agricultural purposes.

Method 2

Ia - Within 100 metres of human habitation with acacia trees at least 15 metres in height; vulnerable crops (maize or sorghum) within 200 metres.

Ib - Within 100 metres of human habitation with acacia trees at least 15 metres in height; no vulnerable crops within 200 metres.

IIIa - Acacia trees at least 15 metres in height greater than 100 metres apart.

IIIb - No acacia trees of any height present.

IIIc - Acacia trees at least 15 metres in height between 50 and 100 metres apart.

IIId - Acacia trees at least 15 metres in height between 10 and 50 metres apart.

IIIe - Acacia trees at least 15 metres in height less than 10 metres apart.

IV - In, or adjacent to, vulnerable crops.

Note: Any trees less than 15 metres in height were ignored.

The assignment of the appropriate stratum to each forest type in the field is somewhat subjective due to the visual estimation of tree height and density and may be a source of disagreement between different census takers. An attempt has been made to keep the habitat categories as simple as possible and therefore some compromises have been made. The critical tree height of 15 metres, above which the acacia trees are maximally suitable for hole-nesters due to the appearance of dead and broken branches, is an approximate figure. With some practice, good hole-nesting habitat can be recognised instantly and it is this which was really stratified against although it usually correlates well with tree height. It is important therefore, that census takers decide before they begin, what each habitat category represents in relation to both tree height and density in the field.

Lovebirds are extremely vocally active. For instance, over a three hour period (0700hr - 1000hr) individual call frequency was measured at an average of one call every six seconds. Also, they do not exhibit the usual vocal peaks at dawn and dusk, typical of many other birds, but were vocally active throughout the day. This allowed counts to be performed at any time of day providing weather was suitable (cloud cover less than 50 per cent, no rain and wind speed less than three metres per second) although all counting was done between 0730 - 1100 hours and 1400 - 1700 hours.

Lovebirds were counted 50 metres to each side and 30 metres forward or behind the observer. Perching and flying birds were counted and recorded separately. Transect lengths and distance to lovebirds were paced and visually estimated, respectively. Before each census, pacing was calibrated and visual estimation practiced against known distances. Progress speed varied between five kilometres per hour and 0.25 kilometres per hour depending on the habitat type being transected and the density of lovebirds. In optimal lovebird habitat progress was slow in order not to miss lovebirds whereas in open treeless areas walking speed was rapid. Occasionally it was necessary to walk off the transect line in order to count a group of lovebirds at the edge of the transect strip.

Transect lines were chosen randomly but their length and direction usually depended on the size of the farm and nature of the habitat. On large farms, straight transects were several kilometres long while footpaths, fence-lines and other convenient guides were used on smaller farms. While progressing along each transect, note was taken of the habitat type being passed through, the transect length in each habitat type and the number of perching and flying lovebirds present. Densities for each habitat type were calculated by summing the total number of birds flying or perching within a particular habitat stratum and dividing by the total area of that stratum transected.

In the second census, lovebirds feeding in vulnerable maize or sorghum fields or perching in adjacent trees were counted by walking once quickly around the field in order to approximate an instantaneous count. This count was omitted in the first census.

With the aid of 1:50 000 topographical maps, a visual estimate was made of the proportion (in hectares) of each habitat type present within each kilometre square covering the study area. Total numbers of lovebirds were then calculated by multiplying bird density of each stratum by that stratum's total area. Totals for each stratum were then summed and added to counts made in crops (for the second census only).

3.2.2 Mark-Recapture Estimates

A Modified Australian Crow Trap (MAC Trap) or mist-nets were used to capture lovebirds. The trap is shown in Plates 4 and 5 and Figure 5. It was especially designed and built to be collapsible to enable transportation in a Volkswagon Combi car. It is operated by placing two to four lovebirds inside as bait which were previously obtained by mist net. Due to the lovebird's habit of giving constant contact calls, any flying overhead are attracted down to the trap where they land on the top. From this point they can look down and see other lovebirds feeding on the rich food supply and water placed on the feeding table inside. With some exploration, they pass through the entry slots which are just wide enough for their body to pass through. When trying to escape, they tend to fly up into the blind corners at the top of the cage. They are prevented from grasping the lower edge of the entry slots by the smooth sheet metal nailed around their edges.

Figure 6 shows capture and recapture locations where lovebirds were captured, ringed or recaptured. Between two and seven days were spent at each location catching either with the lovebird trap and/or mist-nets in maize fields. The trap was not placed in lovebird colonies but under commonly used flight lines to ensure as even a mixture of birds exposed to the trap as possible. The trap was moved up to 50 metres every one or two days. Two capture circuits of the lake were completed, the

Plate 4. The trap used to capture lovebirds at Lake Naivasha

Plate 5. The lovebird trap

Figure 5. Plan of lovebird trap (x $\frac{1}{30}$)

Notes

1. Frame made 4.5 x 4.5 cm timber

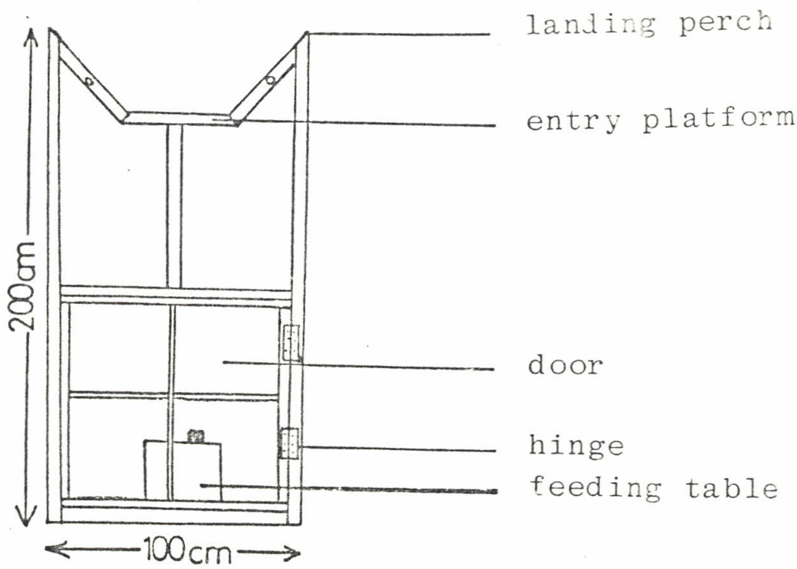
2. Covered with 10 mm wire mesh

3. Collapsible into five pieces (two ends, two sides, one top)

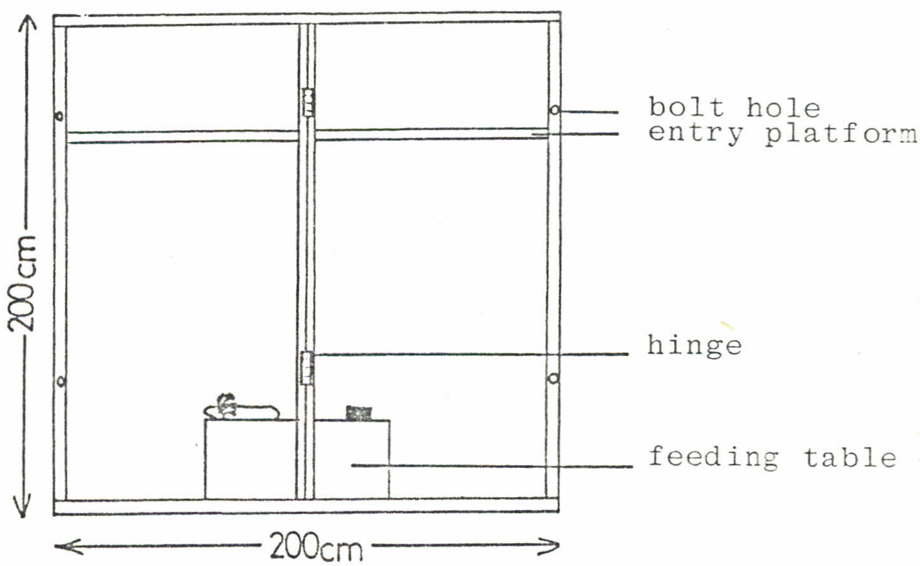
4. Pieces held together by 50 mm bolts

5. Mixed seed and whole maize ears used as food bait

End Elevation



Side Elevation



Overhead Elevation

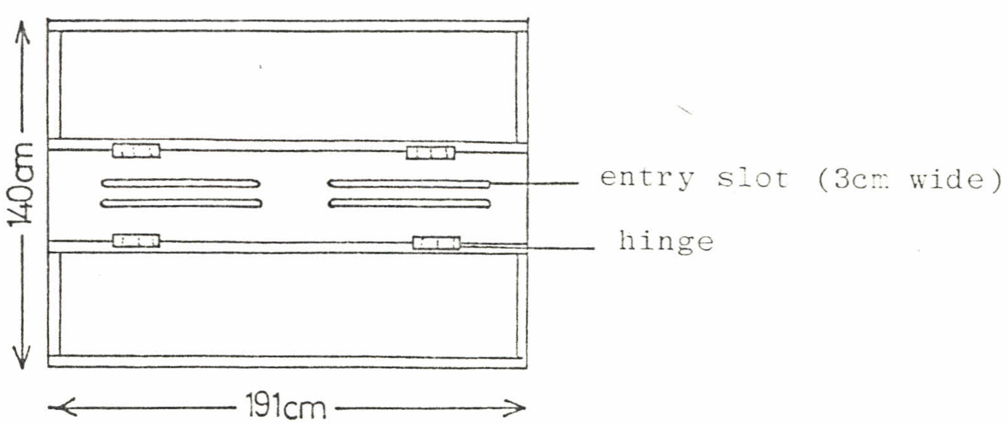
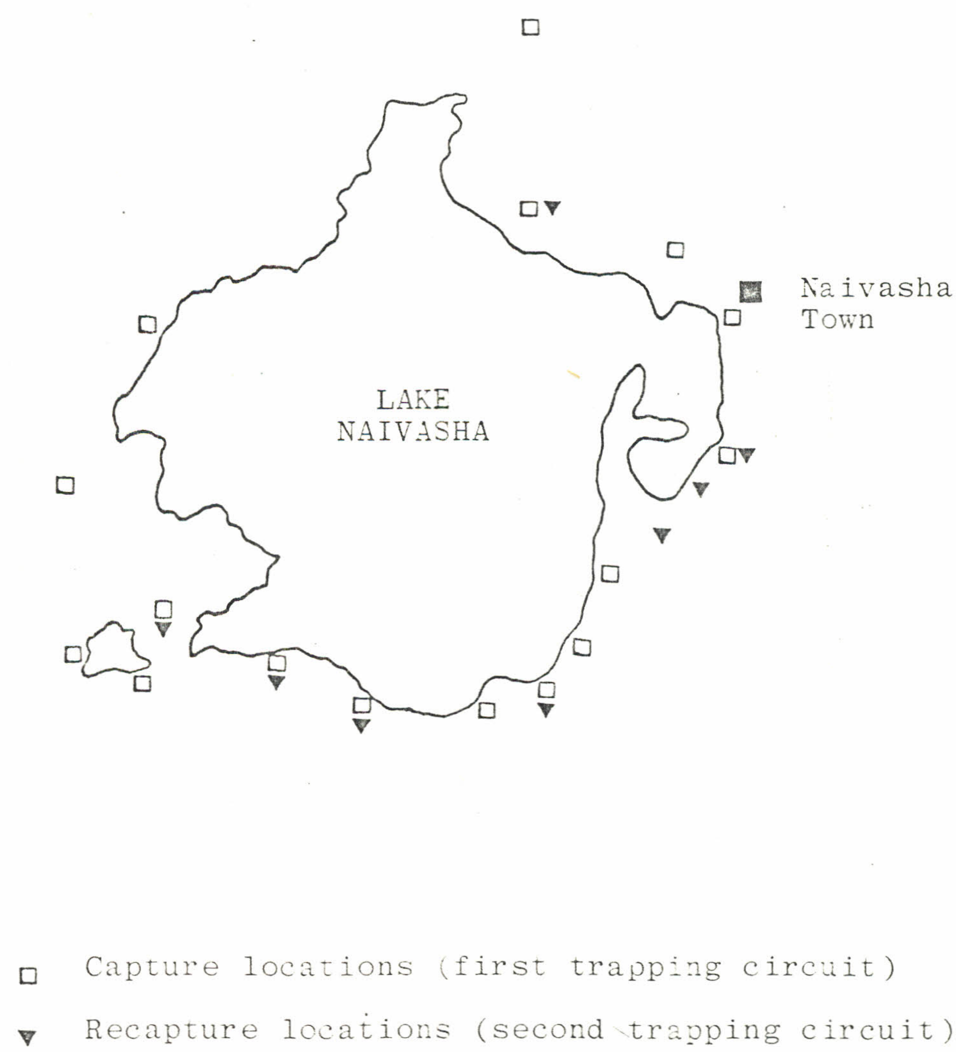


Figure 6. Locations of capture sites on first and second trapping circuits around Lake Naivasha



first between 14/8/85 - 13/12/85 and the second between 5/2/86 - 30/6/86. Therefore, approximately six months passed between marking and retrapping in the same location. It was assumed that a ringed bird once released would not mix evenly with the population but would remain in the general vicinity of the trapping site, hence the need for multiple capture locations for an even distribution of ringed birds. Each circuit of the lake, while in reality spread over several months, will be treated as a single discrete event for Lincoln Index calculations.

Trapped lovebirds were removed and ringed at night, and released the following morning, three to five being retained as bait for further trapping. Mist-netted lovebirds were ringed and released within two hours of their capture. They were fitted with stainless steel "B" size split-rings with an internal diameter of 4.2 millimitres fitted around their tarsus. A record of each bird's capture history was kept.

For the Lincoln Index analysis, only birds ringed on the first capture circuit were considered, and subsequently ringed birds were considered as unmarked if recaptured. Also, if a ringed bird from the first capture circuit was recaptured more than once on consecutive days, it was still only considered as being recaptured once. This is because some lovebirds were obviously trap "happy" and repeatedly re-entered the trap thus biasing the results. All captures were considered for the Frequency of Capture analysis.

3.2.2.1.1 Lincoln Index

Bailey (1952) gives a modified Lincoln Index formula for small samples (where the number of recaptures, r, is less than 20) which gives a less biased population estimate than the usual Lincoln Index formula. Bailey's equation is given by

$$\hat{N} = \frac{a(n+1)}{r+1}$$

where a is the number marked on the first marking occasion, n is the number caught on the second capture effort and $\hat{N}$ is the population estimate. The number of recaptures by mist-net and trap were analysed separately and the corresponding formulae using Bailey's method are given by

$$\hat{N} = \frac{a(n_m+1)}{r_m+1} \quad \text{and} \quad \hat{N} = \frac{a(n_t+1)}{r_t+1}$$

where n_m and n_t are the number of lovebirds caught on the second trapping circuit by mist-net or trap respectively, and r_m and r_t the number of recaptures by mist-net or trap on the second circuit.

The corresponding variance is given by Bailey as

$$\text{Var } \hat{N} = \frac{a^2 (n+1) (n-r)}{(r+1)^2 (r+2)}$$

and therefore the variances for mist-netted and trapped samples respectively will be

$$\text{Var } \hat{N} = \frac{a^2(n_m+1)\ (n_m-r_m)}{(r_m+1)^2\ (r_m+2)} \quad \text{and Var } \hat{N} = \frac{a^2(n_t+1)\ (n_t-r_t)}{(r_t+1)^2\ (r_t+2)}$$

3.2.2.1.2 Gaskell and George Method

Gaskell and George (1972) give an important formula for population estimation because it incorporates an estimation devived from a previously calculated independent method and is given by

$$\hat{N} = \frac{an + 2N^1}{r+2}$$

where N^1 is the independently derived estimate. Two sets of estimates were derived by substituting for N^1, the two Lincoln estimates (from mist-net and trap figures) and the second estimate from line-transect counting. The first set includes in the calculation all lovebirds captured and recaptured on the second circuit. The second data set considers only mist-netted captures and recaptures on the second circuit. Formulae are given by

$$\text{Set 1:} \quad \hat{N} = \frac{an+2N^1}{r+2} \qquad \text{Set 2:} \quad \hat{N} = \frac{an_m+2N^1}{r_m+2}$$

3.2.2.2.1 Frequency of Capture

For techniques using Frequency of Capture data, records are kept of f(x), the frequency of cases in which the same bird (or animal) is caught x times x = 1,2,....., until a total of S captures of R different birds have been made.

3.2.2.2.2 Geometric Distribution

An estimation equation for the Geometric distribution is given by Eberhardt (1969) as

$$\hat{N} = \frac{R(S-1)}{S-R}$$

which, in effect, relates the total number of captures to the total number of recaptures.

3.2.2.2.3 Poisson Distribution

Craig (1953) gives six methods for calculating $\hat{N}$ (all of which he found to give similar results) of which two have been used here. The first is given by

$$\frac{R}{S} = \frac{1-e^{-\lambda}}{\lambda}$$

where λ is the mean of the Poisson distribution or in other words the "mean capture rate" (Eberhardt 1969), and which must be solved for iteratively. Total population size ($\hat{N}$) is then given by

$$\hat{N} = \frac{S}{\lambda}$$

Craig's second method is given by the formula

$$\hat{N} = \frac{S^2}{S_2 - S}$$

where

$$S_2 = \Sigma x^2 f(x)$$

3.2.2.2.4 <u>Regression</u>

The number of birds not caught at all is unknown but is an essential piece of information for population estimation. By fitting a curve to capture frequency data though and extending it to the y axis, or the zero capture frequency class, an estimate is obtained of the number of unmarked animals. Regression curves have been fitted to both raw and transformed data.

3.2.3 <u>Avian Habitat Selection</u>

Timed Species-counts are used to count the number of species present within a particular habitat type within a particular time period. During the count period the observer can move anywhere within the habitat type and record, visually and aurally, the species present.

Two broad habitat types were chosen for comparison and correspond to habitat types IIIc and IIId/e from the second line-transect method. This was good hole nesting habitat, with tall trees and many broken or dead branches. The major difference was tree density so that open woodland characterised the first habitat type whereas dense woodland with a closed canopy typified the second.

Within each habitat type, observation periods were kept to 15 minutes and 20 bird species recorded for their presence. All counts were performed between 0700-01100 and 1500-1800 hours. Care was taken to ensure that the area of each habitat type was large enough to reduce edge effects and the area was at least 200 metres square. Walking direction and speed were adjusted randomly, according to where birds were sighted and observation sites chosen from representative areas all around the lake.

3.3 RESULTS

3.3.1 Line - Transect Counts

Details of habitat areas, lovebirds densities and total numbers derived from both censuses are given in Tables 1, 2 and 3. Highest lovebird densities were measured in areas of human habitation particularly nearby vulnerable crops or cultivation. Densities increased with increasing tree density but dropped sharply in extremely thick forest. The final estimates for total lovebird population size (Table 3) differed by 1024 birds. This difference would have been smaller had lovebirds in

Table 1

Summary of areas, densities and total number of lovebirds in each habitat type for the first method of habitat classification

		Habitat				Types			
		Ia	Ib	IIa	IIb	IIc	IIIa	IIIb	IIIc
Total Area (Hectares)		345.5	105.5	1714.0	716.0	103.0	1823.5	1807.0	1062.0
Total distance of transects (kilometres)		5.0	2.5	22.9	7.6	2.2	13.4	28.7	7.5
Average density (Birds/Hectare)	(Perching)	1.56	0.88	0.13	0.79	0.36	0.16	0.68	0.24
	(Flying)	0.28	0.04	0.17	0.28	0.09	0.13	0.14	0.05
Total Numbers	(Perching)	539	93	223	566	37	292	1229	255
	(Flying)	97	4	291	201	9	237	253	53

Table 2

Summary of areas, densities and total numbers of lovebirds
in each habitat type for the second method of habitat classification

		Habitat				Types		
		Ia	Ib	IIIa	IIIb	IIIc	IIId	IIIe
Total Area (Hectares)		43.0	211.0	3754.5	1787.5	829.0	500.0	552.0
Total distance of transects (kilometres)		1.3	10.8	64.1	9.9	19.6	18.2	9.9
Average density (Birds/Hectare)	Perching	4.54	2.50	0.24	0.16	0.78	1.90	0.43
	Flying	0.23	0.24	0.18	0.09	0.16	0.21	0.11
Total Numbers	Perching	195	528	901	286	647	950	237
	Flying	10	51	676	161	133	105	61

Table 3

Total number of lovebirds calculated for each method of habitat classification

	Method 1	Method 2
Number of Perching birds	3234	3744
Number of Flying birds	1145	1197
Number of birds in vulnerable crops	-	462
TOTAL	4379	5403

vulnerable crops been counted during the first line-transect census. If this had been done, and assuming 462 lovebirds had been counted in crops as was the case in the second census, the variation between the two estimates would have been less than 11 per cent.

3.3.2 Mark - Recapture Estimates

Greater difficulty was experienced in trapping lovebirds during the second trapping circuit. Due to this and time constraints, 157 fewer lovebirds were caught on the recapture circuit (Table 4). A total of 15 ringed lovebirds were recaptured, ten by mist-net but only five by trap. Even though a greater number of lovebirds were mist-netted than trapped on the second circuit, a smaller percentage of trapped birds had rings (4.8%) than mist-netted birds (6.6%). This implies the development of an aversion to the trap and/or their reduced ability to avoid being mist-netted as opposed to being trapped.

Table 5 summarises population estimations from Lincoln Index type calculations. Of particular interest are the estimates derived from Bailey's formula and set 2 of Gaskell and George's method. This is because Bailey's formula gives a less biased population estimate using small numbers of recaptured individuals, while set 2 of Gaskell and George's method only uses mist-net data from the second circuit which has already been shown to be less influenced by any effects of trap aversion.

Table 4

Values of variables needed for Lincoln Index and multiple capture formulae

Variable	Value
a	412
n	255
r	15
r_m	10
r_t	5
n_m	151
n_t	104
R	632
S	706

Table 5

Summary of population estimations and statistics derived from Lincoln Index Type Calculations

	Lincoln unbiased	Bailey (1952)	Variance	Gaskell and George (1972) set 1	Gaskell and George (1972) set 2
Total grouped	7004	6592	2,396,386	-	-
Mist-net	6221	5693	2,505,478	6850	6133
Trap	8570	7210	7,001,940	7028	6386
Line-Transect	-	-	-	6816	6084

A total of 706 captures of 632 lovebirds were made so that 74 ringed birds were recaptured one or more times (Table 4). Table 6 gives raw and transformed Frequency of Capture data to which regression curves have been fitted in Figures 7(a), (b) and (c). Final values for $\hat{N}$, estimated from Frequency of Capture data, are given in Table 7. Estimates derived by the regression method were obtained by adding the value calculated for the zero capture frequency class to the number of lovebirds caught once, twice and up to five times. Only the Geometric distribution produced a population estimate close to that obtained by the line-transect and Lincoln Index methods.

3.3.3 Avian Habitat Selection

The number of times a species was detected in each habitat type was compared using a chi-squared test (d.f.=1). Results are given in Table 8 and show that species detected significantly more often in dense woodland included the Black-headed Oriole (Oriolus larvatus), Tropical Boubou (Laniarius ferrugineus) and the Arrow-marked Babbler (Turdoides jardineii). Species detected significantly more often in open woodland included the Grey Woodpecker (Mesopicos goertae), African Hoopoe (Upupa epops), Lilac-breasted Roller (Coracias caudata) and lovebirds (Agapornis spp.). No significant differences were detected for the remaining species.

Table 6

Frequency of capture data and transformations

Number of times each bird caught (x)	Frequency of capture f(x)	Log f(x)	ln f(x)
1	574	2.76	6.35
2	47	1.67	3.85
3	7	0.85	1.95
4	3	0.48	1.10
5	1	0	0

Figure 7. Regression curves for raw and transformed Multiple Capture data

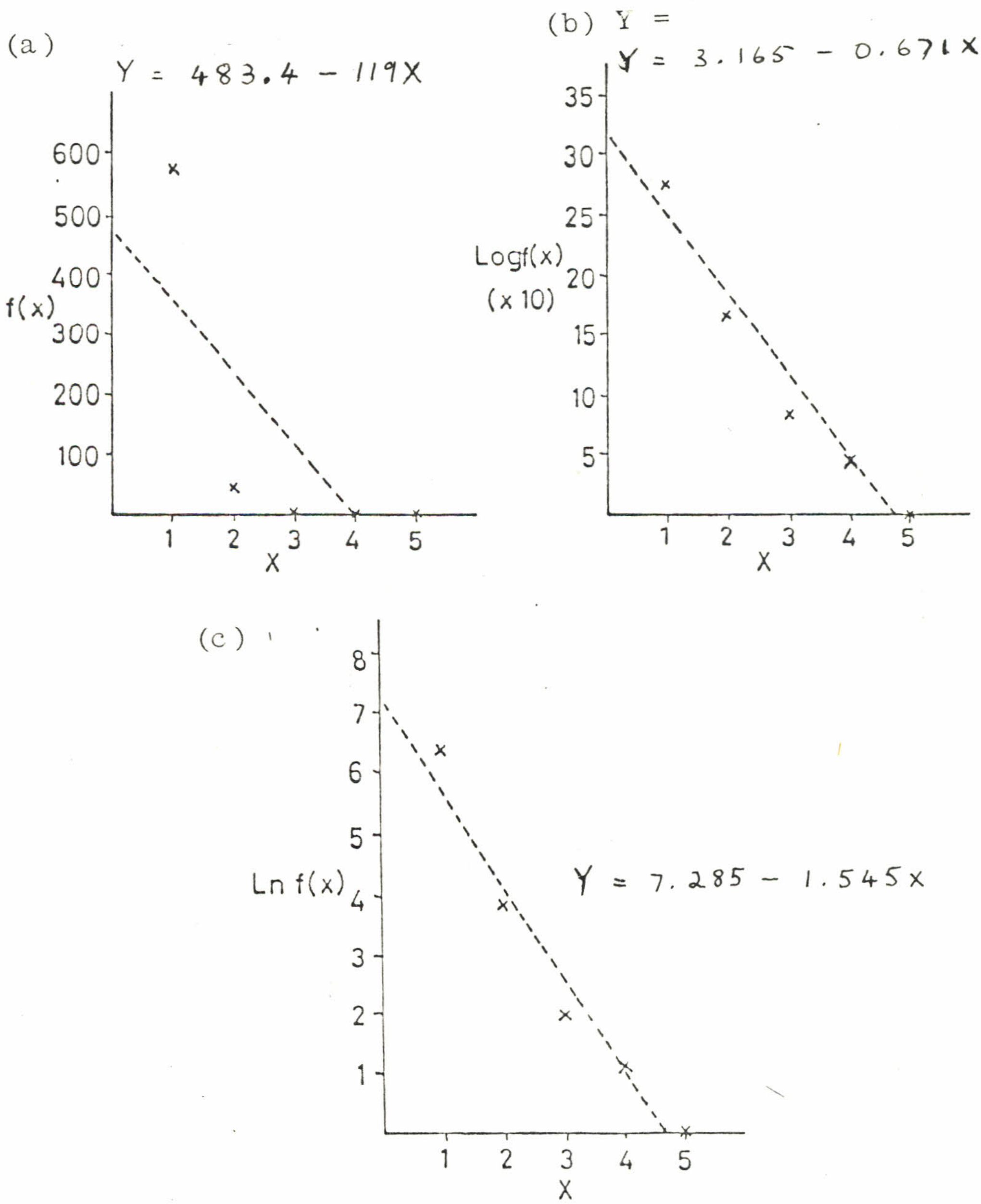


Table 7

Population estimations from frequency of capture data

Geometric	Craig(1)	Craig(2)	Regression Raw	Regression Log	ln.
6021	3138	2596	1115	2094	2090

Table 8

The number of 15 minute intervals each species was observed out of a total of 47 intervals in each habitat type and whether the difference was significant*

Habitat Type / Species Name	III(c)	III(d) and (e)	P≤0.05
Drongo	30	36	No
Black-headed Oriole	11	35	Yes
Superb starling	44	31	No
Tropical Boubou	1	24	Yes
Black-lored Babbler	11	12	No
Arrow-marked Babbler	1	7	Yes
Grey-backed Fiscal	21	29	No
Pied Flycatcher	0	3	No
Grey Woodpecker	32	18	Yes
Nubian Woodpecker	10	10	No
Bearded Woodpecker	7	3	No
Cardinal Woodpecker	3	1	No
African Hoopoe	13	3	Yes
Green Wood Hoopoe	8	15	No
Blue-eared Glossy Starling	32	20	No
Pearl-Spotted Owlet	0	2	No
White-bellied Tit	7	9	No
Lilac-breasted Roller	28	4	Yes
Grey Hornbill	3	1	No
Lovebirds	45	26	Yes

*P≤0.05 level of significance

3.4 DISCUSSION

3.4.1 Line-Transect Counts

3.4.1.1 Habitat Preferences

As shown in Tables 1 and 2, the highest lovebird densities were measured in areas of human habitation with suitable tall trees for hole-nesting. Such areas usually contain vegetable gardens, often with maize, and open lawned areas used by lovebirds for feeding. Their preference for certain habitats may be affected by food availability since lovebird densities were nearly twice as high in areas with maize growing nearby although the difference is not statistically significant. Other food types are provided near human habitation. For example horse food and water is often given in bird baths or available from garden irrigation systems.

The trees surrounding human housing are often among the oldest since they have never been cut to provide areas for cultivation and therefore have many holes suitable for lovebirds. Hole-nesting opportunities are further increased when branches overhanging houses are cut, providing stumps and dead wood used by woodpeckers, lovebirds and other hole-nesters. Nesting in areas of human occupation may also be an anti-predator adaptation and this has been suggested for other hole-nesting birds (Short 1979).

As Tables 1 and 2 show, the density of perching lovebirds increased with tree density up to a point, and then declined in very thick forest. Obviously, the more trees in a given area with suitable holes the greater the number of lovebirds likely to be present. This results from the lovebird's tendency to remain in their nesting/roosting site and make many short foraging trips (see chapter 4 for home range calculation). They also spend much of their time in optimal habitat inspecting prospective holes. The sharp decline in lovebird density with high tree densities reflects the lack of suitable holes and abundance of thick understorey bush in thick forest. Acacia trees in the thickest forest are well protected from wind by their neighbours and consequently do not shed large branches easily. Dead wood and therefore hole-nesting opportunities are not as common as in slightly more open forest. Furthermore, the extremely thick forest and dense undergrowth harbour numerous predators including snakes and small mammals, further discouraging hole-nesters.

3.4.1.2 Assumptions

Before a discussion of the method's accuracy is given, it is appropriate to list the assumptions implicit in the transect methodology. These will be discussed separately and in relation to a possible over-or-underestimate of the Naivasha lovebird population.

1. Birds (animals) should be uniformly and randomly distributed. This assumption is usually unrealistic (Franzreb 1981a) but it should approach reality more

closely within each habitat stratum and thus reduce sampling error (McDonald 1981). Ideally it would be desirable to stratify on bird density itself, but here, variables have been stratified (tree density and height) which are highly correlated with lovebird density. Eberhardt (1978) also suggests that randomly placed transect lines help to remove bias due to clumping of birds.

2. The probability of observing a bird decreases with distance from the transect or remains constant to a given distance and then declines rapidly. The latter situation applied in this case because the primary method of detection was auditory. That is, detection probabilities remained high until the lovebirds were out of auditory range. Since this distance was much greater than the strip width, there was only a relatively small chance of missing a lovebird within the transect strip. Franzreb (1981a) further states that this assumption is generally no problem.

3. The behaviour of birds in one portion of the band width does not influence those in another. Occasionally this became a problem where large numbers of lovebirds were present. If they became agitated due to the observer's presence and gave alarm calls, lovebirds from outside the sampling strip were sometimes attracted inside. It was important to move as quickly as possible through such areas to reduce disturbance but this is a likely source of minor population overestimation.

4. Birds directly on the transect line will never be overlooked. This assumption is difficult to test but since a bird on the transect line is usually closer to the observer than any other, any sound or movement it makes should be maximally detectable. The observer's presence usually stimulated lovebird activity and vocal behaviour, especially lovebirds directly overhead. However, birds remaining within their nesting/roosting holes will go undetected regardless of proximity to the transect line and cause population underestimation.

5. The bird does not move in response to the observer's presence prior to being detected. This was not a problem as lovebirds can usually be heard long before they are approached (up to 200 metres away). They also have the habit of giving a brief contact call when flying from a perch so that even if they had been undetected, their flight usually was.

6. No bird is counted more than once. The lovebird's easy detectability allowed a fast walking pace which alleviates this problem (Franzreb 1981a). Granholm (1983) believes that by shortening the count period (the length of time a motionless bird is within the counting rectangle) less time is allowed for birds to move into the censused area and thus can reduce bias due to movement.

7. There are no measurement errors. Sources of likely error were the measurement of distance by pacing or visual estimation in determining strip width. The areas of each habitat type were also visually estimated and therefore subject to error. While accurate area and distance measurement is desirable, it involves cumbersome, tiring and distracting methods which can affect bird detections with little improvement in measurement precision (Emlen 1977; Jarvinen and Väisäinen 1975). Furthermore, the lakeside terrain was generally flat and pacing was thought to be reasonably accurate. To some extent, such measurement errors should be self-compensating.

8. The response behaviour of the bird does not change appreciably thoughout the sampling period. This is difficult to assess but there appeared to be no overt change. This should generally not be as critical in the tropics as for censuses conducted in temperate areas with short breeding seasons and abrupt changes in advertisement behaviour. It is also more important for censuses of passerines with their complicated vocal behaviour associated with breeding.

9. The response behaviour of individuals of a species is similar regardless of sex or age. Again this is difficult to assess, due to the lack of sexual dimorphism or distinctive juvenile plumage in these lovebirds.

A number of other factors influence the success of transect census methods including the observer's competence, weather conditions, habitat type and environmental noise. Nevertheless, assuming a competent observer counting in suitable weather conditions, the primary determining factor affecting the method's accuracy is the inherent behaviour of the birds being counted (Franzreb 1981b). The accuracy of the census therefore, is largely proportional to the conspicuousness of the species and values for less detectable species, in general, are less reliable than those for conspicuous ones (Franzreb 1981a and b).

3.4.1.3 The Method's Accuracy

While lovebirds are a very conspicuous species, several factors combine to suggest that the derived population estimates are low. Firstly, the degree to which their hole-nesting habit causes density underestimation is unknown. Certainly other workers have found discrepancies in count data when comparing line-transect and nest-box inspection methods (Van Riper 1981). Secondly, at any one time a certain small percentage of the total lovebird population is outside the study area in the surrounding bushland and so not counted. Also, occasionally, individuals or roosting pairs may remain quiet for several minutes, especially if they are at the extremity of the transect strip and undisturbed by the observer's presence. Finally, Bell and Ferier (1985) have suggested that all transect counts, particularly fixed-width transects, tend to underestimate bird density. Factors in the method causing density overestimation are (a) lovebirds being attracted into the census strip by alarm calls of lovebirds within, and (b) the same birds being counted more than once. However, I believe both to be insignificant in comparison with factors causing underestimation.

It is encouraging that population estimates from the two censuses using different habitat classification procedures are in comparatively close agreement. Perhaps reasonable estimates can be achieved regardless of the stratification technique so long as each group of strata are mutually exclusive and exhaustive of all habitat types. I believe the second estimate to be more accurate, not only because it is closer to estimates obtained by the Lincoln Index, but because the habitat stratification system used more closely reflects lovebird habitat preferences and therefore lovebird density itself. This is important for the method's final resolution in cases where bird density is not uniformly distributed.

3.4.2 Mark-recapture Estimates

3.4.2.1 Assumptions

As with other census methods the accuracy of mark-recapture methods is dependent upon the degree to which certain requisite assumptions are fulfilled in the field procedure. Lincoln Index and Multiple Capture methods are usually modelled assuming a closed population, that is, it remains unchanged over the period of study and is therefore not influenced by mortality, recruitment, immigration or emigration. This assumption is particularly difficult to fulfill and is often relaxed (Nichols *et al.* 1981). Obviously during the 12 months of data collection at Naivasha, these processes would have been occurring but I have assumed that their influence is insignificant compared with the method's accuracy. Furthermore, while mortality and recruitment would, to some extent, have balanced each other, bias from immigration and emigration was minimised because of the "island" nature of Naivasha's forest and irrigated agricultural land surrounded by semi-arid bushland.

Two further assumptions of the method are that all animals have equal probabilities of capture in the first sample and that marking does not affect subsequent catchability. Differences in catchability according to sex and/or age have been reported by Petrides (1944), Dunnet and Ollason (1978) and Sulzbach and Cooke (1979). However, the lack of sexual dimorphism and means of age determination in live lovebirds make it difficult to deduce sex or age differences in catchabilities. Capture probability is probably affected more by the individual lovebird's capture history. During the second trapping circuit, half as many ringed birds were recaptured by trap than by mist-net suggesting the development of trap aversion or "shyness". Such behaviour has been described before (Nichols *et al.* 1981, Edwards and Eberhardt 1967) and is perhaps a result of the bird being handled resulting in heightened wariness and avoidance of the trap's vicinity. Conversely some individuals appeared to be trap "happy" (also previously reported by Nichols *et al*. 1981) and may have been recaptured on two or three consecutive days. It is possible they welcomed the plentiful food source in the trap or were attracted to the other trapped birds if a mate or relative was inside.

Two final assumptions are that animals do not lose their marks and all animals in the second sample are reported. This did not present any problem in the present study. More important was the loss of marked birds through mortality or illicit capture by local people for sale as cage pets. This reduced the number of possible recaptures and therefore increases the likelihood of population overestimation.

3.4.2.2 Lincoln Index Estimations

A critical factor determining the effectiveness of mark-recapture methods is the percentage of the population originally marked and the number of subsequent captures. Poole (1974) stated that for the estimation of population size to be effective, the product of the two samples a x n should be greater than four times the true population size. This product (412 x 255) is equal to 105060 and assuming the population to be approximately 6000 birds, this condition is fulfilled giving added confidence to derived population estimates. However, Bergerud and Mercer (1966) found the accuracy of the Lincoln Index to vary according to the ratio of tagged versus untagged birds. The method was unreliable for a ratio of 1:13 but was successful for ratios of 1:5.1 and 1:2.2. Finally Southwood

(1978) quotes Bishop and Sheppard (1973) and claims that for the Jolly-Seber method (an approach closely allied to the Lincoln Index), reliable estimates are usually achieved if nine per cent or more of the population is sampled. Assuming a lovebird population of 6000, after the completion of the first trapping circuit 6.8 per cent had been ringed. Therefore the number of birds marked was the absolute minimum as recommended by earlier workers in order to achieve a reliable population estimate. As a result, a slight difference in the number of recaptures could have changed the population estimate greatly. For example one less recaptured lovebird would have resulted in a total grouped estimate of 439 birds higher than the original (a change of 6.7%).

In the present experiment, sampling for marked birds on the second capture circuit was less biased when using mist-nets because of the trap aversion developed by the lovebirds. Seber (1973) has argued that unbiased population estimates will be achieved if two independent methods of sampling are used in the marking and retrapping procedures. This applies in cases where the animal develops an aversion for one trapping method during marking so that another method should be used for retrapping. This was generally the case here since the majority of lovebirds during marking were trapped while most were mist-netted during retrapping. Therefore, population estimates derived from mist-netted rather than trapped samples should approximate true population size more closely.

Due to the likelihood of some marked birds dying or being caught in the six months between marking and recapture in the same area, the derived figure for mist-netted samples (5693) is likely to be an overestimate. Estimates derived from Gaskell and George's formula are higher but still fall between maximum and minimum values obtained by Lincoln Index estimations from mist-netted and trapped samples. The standard error for $\hat{N}$ is equal to the standard deviation derived from Bailey's formula since there is only one estimate of population size. Unfortunately it is of little use since the derived 95 per cent confidence limits are so wide (5693 $\pm$ 20,112 birds) when using the appropriate t statistic for only one degree of freedom. This emphasises the need for alternative methods of population estimation to support Lincoln Index estimates.

The Lincoln Index has been useful here despite the wide statistical limits of confidence since it has come close to estimates derived from the line transect censuses. It has also given confidence to estimates from the line-transect method and, in reality, has probably given a closer approximation to $\hat{N}$ due to that method's tendency to underestimate population size. While some of the method's requisite assumptions were not fulfilled, this is usually the case in field situations, and other workers (for example Boyd, 1956; Robel _et_ _al_. 1972) while admitting methodological weaknesses, have found the method useful for estimating avian community size.

3.4.2.3 Frequency of Capture (Schnabel Census)

The field methodology used here did not strictly adhere to that usually employed in Frequency of Capture studies. Ideally, with each trapping occasion all individuals in the population should have equal probabilities of capture. But because of the limited movements of lovebirds, only those within a few kilometres of the trapping site were exposed to being caught. I have assumed that this should not significantly affect the analysis since two circuits of the lake were completed and there was considerable overlap of movement between trapping sites.

Population estimates modelled on the Poisson distribution and regression have seriously underestimated population size. Originally designed for use on highly mobile animals such as butterflies (Craig 1953) the Poisson distribution has been found to underestimate population densities or less faithfully represent data in the past (Nixon et al. 1967, Eberhardt 1969, Edwards and Eberhardt 1967). Multiple Capture techniques rely heavily on the assumption that each animal has a constant and equal probability of capture (Marten 1970) which is seldom the case (Eberhardt 1969) and Pollock (1981) has cast doubts on the method's usefulness if there is a change in trap response. The estimate from the Geometric distribution however, closely fits estimates derived from the line-transect and Lincoln Index methods and has given more accurate estimates in previous census work (Nixon et al. 1967, Eberhardt 1969, Edwards and Eberhardt 1967). Given that the mist-net Lincoln Index is accurate though, the Geometric distribution has slightly overestimated population size, also a previously observed tendency of the method (Edwards and Eberhardt 1967, Nixon et al. 1967).

The underlying cause for population underestimation by the Poisson and regression methods may be more easily visualised by examination of Figure 7. Even when the data is transformed into logarithms, regression lines still do not approximate a straight line. It is obvious that some lovebirds were recaptured more often than they should had their probabilities of capture remained constant. This was, more than likely, a methodological fault because of the trap "happy" nature of some lovebirds. Better data may have been arrived at by placing lovebirds in the trap as bait only after the previous days captures had been released and left the area. Unfortunately a record was not initially kept of the capture method for each bird so that a separate analysis of only mist-netted birds is not possible.

3.4.3 Methodological Overview

When all population estimates derived from the two line transect censuses, the Lincoln Index by Bailey's method, Gaskell and George's method but only using mist net values (set 2) and the Geometric distribution are combined, the mean value for $\hat{N}$ and its 95 per cent confidence limits are 5989 $\pm$ 612 birds. But before any conclusions are arrived at too quickly some salient reminders are in order. One author has compared bird census techniques with the medieval theological topic of attempting to estimate the number of angels able to stand on the head of a pin (David 1981). The various techniques rely on assumptions all of which to some extent are broken or, alternatively, it is impossible or very difficult to assess whether they have been violated or not. Verner and Ritter (1985) state that they are "unconvinced that either transects or point counts estimate densities of most or all species accurately enough to satisfy objectives of most studies". In their condemnation of the methodology however, they touch on the heart of the matter, that is, the objectives of the study. It was the aim of this study to estimate population size by at least putting the estimate into the correct order of magnitude. In this case, while an exact statement of population size is not possible, the primary objective has been achieved of having a good base estimate with relatively narrow limits of confidence from which population change with time can be assessed. Although mark-recapture methods are extremely time consuming, here they have at least helped to calibrate the line-transect method so that future population monitoring need only use this census technique.

3.4.4 Avian Habitat Selection

While the majority of species showed no preference for either tree density, their distribution may be dependent on other factors such as grass species and height or locally abundant food patches. Species seeking thick cover may do so as an anti-predator adaptation. The Tropical Boubou, for example, has been noted as a bird which normally inhabits thick cover

(Mackworth-Praed and Grant 1962) although the reasons for this may be complex. Subtle differences in habitat selection may even help to spatially separate closely related species to reduce feeding competition or niche overlap, for example the two species of Babbler.

It is significant that all species preferring the more open habitat type are cavity-nesters. This reflects the greater dangers of predation in areas of thicker forest and undergrowth which may have a greater affect on a bird permanently resident in a particular hole easily located by predators. It may also reflect the greater number of holes available in more open forest types at Naivasha. This explanation has been used previously to account for the higher density of lovebirds found in more open woodland.

CHAPTER FOUR

CROP DAMAGE

4.1 INTRODUCTION

Since their introduction to Lake Naivasha some 25 years ago, lovebirds have established themselves as the most serious avian pest of maize (*Zea mays*) in the area. They have also been noted as agricultural pests elsewhere in Africa. For example *Agapornis nigrigenis* depredating millet (*Eleusine coracana*) in Northern Rhodesia (Moreau 1948), *A. pullaria* on durra (*Sorghum vulgare*) and millet (Mackworth-Praed and Grant 1952, Jackson 1938, Forshaw 1981), *A. fischeri* on maize in Tanzania (Friedmann and Loveridge 1937), *A. swinderniana* on millet in Central Africa (Forshaw 1981), *A. roseicollis* on grain crops in South West Africa (Mackworth-Praed and Grant 1962) and *A. lilianae* on ripening millet in South Eastern Africa (Forshaw 1981).

It may often be the case with crop damage by parrots, that because of their conspicuousness, damage accorded to them is exaggerated and damage by other birds ignored (Forshaw 1981). A survey of selected vulnerable maize fields at Naivasha was necessary therefore, to determine the extent of bird damage to maize, the importance of lovebird damage relative to damage from other species and the total damage attributable to lovebirds.

Maize is grown around Lake Naivasha for both human and domestic animal consumption. It is usually irrigated from the lake which allows growing seasons to be flexible but generally two crops per year are grown, planting coinciding with the bimodal pattern of rainfall. Maize fields varied in size and quality a great deal but were generally small (the largest field no more than a few hectares while the smallest a few square meters) and cut before mature for use as cattle fodder. Poorest quality maize and smallest plots were cultivated by farm-workers, growing maize for personal consumption on a part-time basis. Such maize was usually not irrigated and little attention paid to weeding and often not planted in rows.

4.2 METHODS

In order to determine the accuracy of direct visual estimation of damage to maize, a total of 111 ears of maize were measured to the nearest millimetre for both total length and length of damage after a visual estimation of the percentage damage was made. If an ear was damaged more on one side than the other, the average length of damage between the two extremes was measured (after De Grazio et al. 1969). Total length was measured from base to tip of kernel growth.

Total average damage by the measurement method was calculated by dividing the total length of the damaged portion of all ears by the total length of all ears. The two average values came to 22% damage by visual estimation and 24% by measurement of length of damage. Due to the good match between the two methods, the visual estimation method was chosen to estimate damage due to the speed with which damage could be estimated, as has been found by other workers (Granett et al.1974). Woronecki et al. (1980) found that damage estimates based on surface area of kernels destroyed were correlated with actual loss of biomass.

Several sampling methods were employed to measure bird damage. Since sampling requirements are affected by several factors including plant density, degree of damage and desired reliability of the estimate (Granett et al. 1974) sampling intensity was tailored to suit each particular situation. In order to determine if particular sections of each field had been damaged more extensively than others, parallel lines were walked perpendicular to the planted rows and a sample of between one and five ears measured for damage every three to four rows. Granett et al. (1974) found that sampling perpendicular to rows is more efficient because it covers a greater distance than a sample of the same number of ears taken along a row. Also, growing conditions and bird damage tend to be more uniform along rows than across rows so that perpendicular sampling covers more growth conditions and levels of damage resulting in a more random sample. Granett et al. (1974) conclude by stating that for a half acre field and perpendicular sampling, a sample of 100 ears yields maximum reliability for least time expended. An effort was made to at least equal this sampling intensity, if not exceed it.

To gauge the importance of maize in the diet of lovebirds, the crop contents of ten killed birds (used as study skins)were examined. These were mist-netted in acacia forest more than 300 metres from the nearest vulnerable maize. Crop contents were removed and kept separately in 70 per cent alcohol until ready for drying and weighing.

Lovebird home range was estimated by analysing intercatch distances of ringed and recaptured birds. Ferry et al. (1981) concluded that the quadratic mean of intercatch distances (x) is the best estimation of the home range radius (R) by the formula

$$R = \sqrt{\frac{\sum x^2}{N}}$$

where N equals the number of recaptures.

4.3 RESULTS

Damage estimates are presented in Table 9. Damage tended to be lowest in the largest fields grown commercially. In one such case (the last field in Table 9) people were employed full-time as bird scarers to discourage bird damage. The occurrence of suitable trees for roosting near vulnerable maize tended to increase the extent of damage and damage levels tended to be higher in areas of near trees. For example, two identical fields had been planted, differing only in their proximity to acacia trees. The field closer to the trees (the first field in Table 9) was more heavily visited by lovebirds and other avian

Table 9

Estimates of damage to maize fields

Grid number of plot location	Area (ha)	Number ears examined	% ears damaged	Average damage per damaged ear	Total % damage	Intended use of maize
13-11	0.80	231	4.4	2.75	0.1	Human consumption
09-08	0.03	78	67.0	47.2	31.6	Human consumption
09-08	0.01	93	5.4	13.3	0.7	Human consumption
07-06	0.90	420	34.0	46.9	16.0	Cattle
08-03	0.10	52	33.0	44.0	14.4	Cattle
08-03	0.09	61	33.3	50.0	16.7	Cattle
16-14	0.01	65	78.5	48.5	38.1	Cattle
08-03	0.12	205	19.5	12.1	2.4	Human consumption

maize pests and resultant damage heavier than in the identical field closer to the lake's edge and away from the tree-line.

Highest damage levels were measured in the very small non-commercial plots grown by farm labourers. These areas provided a wide variety of food types from maize and green vegetables to weed seeds all of which lovebirds consume. Trees or bushes often surrounded these areas providing convenient roosting perches. Birds usually had free access as people did not remain to scare them away.

While estimates have been made of the amount of maize consumed, secondary loss through fungal infection and insect invasion has not been taken into account. Woronecki et al. (1980) found that the extent of secondary loss increased when damage by Red-winged Blackbirds (Agelaius phoeniceus) was inflicted at the milk stage of plant maturity, precisely the time lovebirds begin to attack maize. Measured damage levels may therefore be treated as underestimates. Loss may also occur in the market due to the inability to sell unsightly damaged ears.

An analysis of lovebird's crop contents is presented in Table 10. While they varied in their composition, their principle components were maize and acacia seeds. Other food items were impossible to identify due to their small size but may have been flower fragments from acacia trees, grass and other seed types.

Table 10

Lovebird crop contents

Sample number	Dry weight of crop contents (g)	Total dry weight of maize (g)	% maize in crop by weight
1	1.5	0.4	27
2	0.8	0.8	100
3	0.4	0.3	75
4	0.7	0	0
5	0.5	0.1	20
6	2.1	1.9	90
7	2.2	2.2	100
8	Empty	–	–
9	Empty	–	–
10	Empty	–	–

Frequencies of intercatch distances are presented in Table 11. Recapture distances varied between zero and 14.25 kilometres and home range radius estimated as 2.6 kilometres. The average distance between trapping locations was 3.6 kilometres (see Figure 6) which may explain the large number of recaptures at four kilometres from the ringing site.

4.4 DISCUSSION

4.4.1 Home Range

It is surprising that the home range for this bird with such strong powers of flight should be so restricted, especially when one considers the narrowness of much of the forest strip that surrounds the lake. Being so narrow one would expect any lateral movements by the birds to be exaggerated in order for them to cover the same area in search of food. A possible reason may be Naivasha's highly agricultural nature, providing a mosaic of natural and cultivated food types so that lovebirds need not move far in order to secure adequate and suitably varied foodstuffs.

Alternatively, it is possible that the calculated home range estimate is low. Stoddart (1979) claims that live-trapping will usually underestimate home range because a trapped animal cannot move further until it has been released. The result does however emphasise the importance of the nest/roost site to lovebirds. Although they are strong fliers, they appear to make many short foraging trips rather than a few long ones. The

Table 11

Frequencies of intercatch distances

Intercatch distance (Km)	Number of recaptures
0	48
1	1
2	2
2.25	1
2.50	1
3.00	1
3.25	1
4.00	14
4.50	1
14.25	1

breeding status of each bird probably affects the length of feeding trips and lovebirds free from the constraints of rearing young may be expected to travel further in search of food or other essential requirements.

4.4.2 Damage attributable to lovebirds

While many other species contribute to maize damage, it is principally the lovebirds which initiate and encourage further damage. The reason is their perfectly designed bill which they use extremely efficiently to peel back the covering husk of each ear. They do this in two ways. Their first method uses vertical scissor-like cuts made down the length of the husk. They then position themselves in a normal or inverted position, grasp the top of the strip to be torn away with their beaks and swivel their heads either up or down peeling away the strip. By using their beak as a fulcrum they achieve considerable leverage similar to how a can-opener operates. Alternatively, by biting horizontally across the husk, they gradually break up its outer structure in a small patch which is then quickly exposed as the husk dries (Plates 6 and 7). Weavers (*Ploceus* spp.), the other principle avian pest of maize, do not possess the curved bill or the added leverage provided by the lovebird's greater ability to move their upper mandible in relation to the skull (kinesis) which gives their bite increased strength (Forshaw 1981). To expose maize kernels, weavers must peck away at individual strips of husk-leaves, a much slower process.

Plate 6. Lovebirds removing the outer husks of maize ears

Plate 7. Lovebird biting horizontally across the husk to expose kernels

Once exposed by the lovebirds, the kernels are attacked by a host of species. They either feed directly on exposed kernels or force their beak between the husk and ear to reach the still covered kernels. The longer the beak therefore, the further their reach and the greater their ability to penetrate under the husk. Lovebirds and Mousebirds (Colius striatus) have quite a short bill of about 15 millimetres while weavers have longer bills (20 millimetres) so they consume that which cannot be reached by the lovebirds (Plate 8).

The maize resource therefore, is shared by a variety of consumers even though they do not directly participate in exposing the maize for consumption. The lovebirds are responsible for the majority of the damage since they open the maize for feeding by the other birds. Without lovebirds, damage to maize would probably still occur but at a very much reduced rate due to the relatively slow method other birds use to expose kernels.

4.4.3 Compensatory Growth

It has been shown that compensatory growth of kernels can occur in response to bird damage (Woronecki et al. 1980; Dyer, 1975). This occurs by translocation of dry matter, that would have been incorporated into the damaged kernels, into the remaining undamaged kernels. Dyer (1975) suggested that at low damage levels compensatory growth may balance out loss due to birds and that total protein yield of simulated-damaged corn ears

Plate 8. A weaver using it's longer bill to penetrate deeply between the husk and ear

Plate 9. A lovebird making a vertical cut in a maize ear

is actually higher than that for undamaged ears. However, Woronecki et al. (1980) found that any compensatory growth can be just as important as secondary losses due to insects and fungal infection. They conclude that the extent to which the effect of compensatory growth is negated by secondary loss depends on environmental factors (for example fungal infection will be more severe if rain falls on damaged ears) but that any such compensation in their study was comparatively insignificant. In this study therefore, measured damage levels probably represent real damage and compensatory growth was unimportant.

4.4.4 Conclusions

The inclusion of maize in the diet of lovebirds (as shown in Table 10) has been a major reason for their success at Lake Naivasha. Lovebirds have established themselves in the Nakuru area 50 kilometres to the north-west, but not in Lake Nakuru National Park itself. Although this park contains suitable acacia trees for hole-nesting birds and many of the species in common with Lake Naivasha,lovebirds (so far) are apparently absent. I believe the principle reason for this is the lack of maize or cultivation in general in the park. As already mentioned, lovebirds have been noted as a pest of maize in their natural range in Tanzania and their association with agricultural areas noted for other lovebird species. This choice of cultivated areas by the introduced Lovebirds may be a transitory state of affairs and they may move into and live in less agricultural lands as other Agapornids do elsewhere in Africa.

Nevertheless, their preference for cultivated crops appears to be a major reason for their success in Kenya.

Overall, damage to maize by lovebirds at Lake Naivasha does not represent a serious national threat and probably never will be. Much of the maize grown is intended for cattle fodder and the rest adequately protected. The obvious adaptability of hybrid lovebirds to new habitats and their capacity to enlarge their range within Kenya though, make them a species which may in the future cause problems in important maize growing areas.

CHAPTER FIVE

INTERSPECIFIC AGGRESSION AND CONSEQUENCES OF LOVEBIRD INTRODUCTION

5.1 INTRODUCTION

Lake Naivasha is one of the areas in Kenya famous for its varied birdlife. Consequently, some concern was expressed about the effect of the newly established lovebirds on the Lake's hole-nesting avifauna. Since there are only a finite number of cavities which can be used by birds unable to excavate their own hole, the arrival of a new hole-nesting species may cause others to suffer through competitive forces. Lovebirds have been noted previously as occupying and probably breeding in other species' nests (Moreau 1948) including the Rufous-tailed Weaver (Histurgops ruficauda) and old swifts' nests (Forshaw 1981), and a barbet's nesting hole (Mackworth-Praed and Grant 1952). Whether their occupation involved the usurpation of the former species was not mentioned.

Competition for nesting cavities among hole-nesting birds has been recorded both in natural avian communities and between introduced and native species. The introduction into North America of European Starlings (Sturnus vulgaris) and House Sparrows (Passer domesticus) has forced Eastern Bluebirds (Sialia sialis) to nest almost exclusively in artificially provided nest-boxes (Gowaty 1985). Woodpeckers such as the Northern Flicker (Colaptes auratus) and the Red-headed Woodpecker (Melanerpes erythrocephalus) have also probably been affected adversely (Short 1979). Von Haartman (1957) was among the first to suggest that hole-nesting birds (his study only covered passerines in temperate regions) are limited by the availability of nest sites and he placed more importance on these than on food availability as an ecological limiting factor determining the maximum number of nesting pairs. Short (1982) further points out that competitive and aggressive interactions occur for roosting and nesting holes among not only birds but mammals as well, many such interactions being directed interspecifically.

To determine the extent to which the introduced lovebirds have interfered with the success of resident hole-nesting birds, an attempt was made to answer four questions.

1. What is the overlap between lovebirds and other hole-nesters in the preferred nest/roost-hole type?

2. How aggressive are lovebirds toward other species?

3. Are lovebirds capable of usurping other hole-nesters from their hole?

4. Are some hole-nesting species absent from the Lake area where they have commonly been recorded in the past?

5.2 METHODS

In order to identify occupied roost/nest holes, daily watches were kept on likely cavities during the last hour of daylight. Information was recorded on the occupying species, height above ground level (estimated visually) and cavity type.

A list of interspecific encounters between all bird species was compiled to determine any dominance hierarchy. The contestants in each encounter were judged as "winners" or "losers", the "winner" always being the aggressor while the "loser" being the bird driven away or forced to retreat. Observations were recorded from all times of the day.

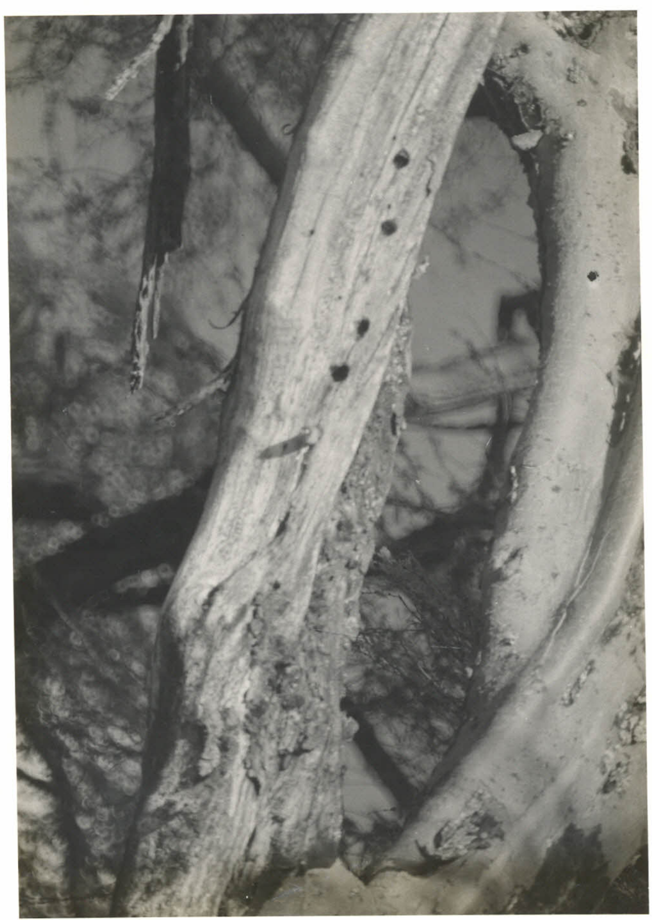
5.3 RESULTS

Cavity types fell into three well defined categories. Firstly, many hole-nesters used the end of a broken branch or a crevice along its length to nest in, excavating the central rotten wood to form a cavity. Secondly, a tree-knot or small lateral outgrowth sometimes forms (Plate 10) allowing entry by birds into the main trunk. Lastly, holes excavated and occupied by woodpeckers (almost always in dead wood) or taken by other hole-nesting species (Plate 11).

A total of 94 cavities occupied by birds were positively identified, 57 of which were used by lovebirds. Of these 57, 58% were of the broken branch type, 14% of the tree-knot type and 28% old woodpecker holes. Average height above ground level was 6.2

Plate 10. A "tree-knot" type of cavity

Plate 11. Woodpecker holes taken over and used by lovebirds



metres, 7.3 metres, and 6.2 metres for the three cavity types, respectively. Many other holes that were watched were either unoccupied or used by Tree mice (Apodemus spp.)

The remaining species for which cavities were located are listed below with the number of cavities observed, cavity type and average height above ground level.

Grey Woodpecker (Mesopicos goertae) - 13 holes located, all conventional woodpecker holes, average height five metres.
Nubian Woodpecker (Campethera nubica) - one hole, conventional woodpecker type, two metres above ground level.

Bearded Woodpecker (Thripias namaquus) - four holes, conventional woodpecker type, average height 10.3 metres.

Cardinal Woodpecker (Dendropicos fuscescens) - two holes, one conventional the other in a cavity at the junction of a dead branch and tree trunk. Average height, five metres.

Red-fronted Barbet (Lybius diadematus) - one cavity in an old woodpecker hole four metres high.

Green Wood Hoopoe (Phoeniculus purpureus) - three cavities, one in a broken branch, one in a tree knot and one in an old woodpecker hole. Average height, 6.6 metres.

African Hoopoe (Upupa epops) - one cavity in a tree knot eight metres above ground level. These hoopoes were seen twice roosting in the tree tops.

Blue-eared Glossy Starling (Lamprotornis chalybaeus) - three cavities, one in each cavity type. Average height, four metres.

Pearl-spotted Owlet (Glaucidium perlatum) - One cavity in an old woodpecker hole, five metres high.

Superb Starling (Spreo superbus) - two cavities, one in a broken branch and one in a tree knot. Average height, 8.5 metres.

Woodland Kingfisher (Halcyon senegalensis) - two cavities, both in old woodpecker holes. Average height, seven metres.

Lilac-breasted Roller (Coracias caudata) - two cavities, both in old woodpecker holes. Average height, 15.5 metres.

Except in maize fields, lovebirds were seen to aggress on another bird species only once. This occurred between a Grey Woodpecker (Mesopicos goertae) and a group of lovebirds using holes 20 centimetres apart on the same branch. Individual lovebirds were seen twice to approach the woodpecker's hole and peer into it while the woodpecker retreated inside. Another Grey

Woodpecker was perched on a branch near the hole but with the arrival of a lovebird there, it flew to an adjacent tree trunk two metres away. At one time nine lovebirds were perched on a branch one metre above the woodpecker hole. Although perhaps not a clear case of aggression, the woodpecker appeared to be intimidated by the lovebird's presence and certainly did not retaliate by attacking.

Lovebirds were observed as clear "losers" in encounters with Lilac-breasted Rollers (Coracias caudata) (three times), Green Wood Hoopoe (Phoeniculus purpureus) (once), Drongo (Dicrurus adsimilis) (once), Red-fronted Barbet (Lybius diadematus) (once, defending its roost hole), Fiscal Shrike (Lanius collaris) (once), Grey Woodpecker (Mesopicos goertae) (once), Blue-eared Glossy Starling (Lamprotornis chalybaeus) (once), Superb Starling (Spreo superbus) (once), Grey-backed Fiscal (Lanius excubitorius) (once).

Other incidences of interspecific aggression or dominance are given below with the arrow pointing to the sub-ordinate species followed by the number of times such an encounter was observed.

Lilac-breasted Roller

(Coracias caudata) ——→ Drongo (Dicrurus adsimilis) (1)

——→ Crowned Plover (Vanellus coronatus) (1)

——→ Blue-eared Glossy Starling (Lamprotornis chalybaeus) (1)

——→ Fiscal shrike (Lanius excubitorius) (5)

——→ Unidentified Doves (2)

Green Wood Hoopoe (Phoeniculus purpureus ——→ African Hoopoe (Upupa epops) (2)

——→ Drongo (Dicrurus adsimilis) (1)

——→ Bearded Woodpecker (Thripias namaquus) (1)

African Hoopoe (Upupa epops) ——→ Grey-backed Fiscal (Lanius excubitorius) (1)

Drongo (*Dicrurus adsimilis*) → Superb Starling (*Spreo superbus*) (1)

→ Northern Olive thrush (*Turdus abyssinicus*) (1)

→ African Hoopoe (*Upupa epops*) (1)

→ Grey-backed Fiscal (*Lanius excubitorius*) (1)

→ Bearded Woodpecker (*Thripias namaquus*) (1)

→ Unidentified Dove (1)

Grey-backed Fiscal (*Lanius excubitorius*) → Black-headed Oriole (*Oriolus auratus*) (1)

→ Black-lored Babbler (*Turdoides jardineii*) (1)

→ Superb Starling (*Spreo superbus*) (1)

→ Unidentified Dove (2)

Superb Starling (*Spreo superbus*) → Lilac-breasted Roller (*Coracias caudata*) (1)

→ Grey Woodpecker (*Mesopicos goertae* (1)

Black-headed Oriole (<u>Oriolus auratus</u>) → Pearl-spotted Owlet (<u>Glaucidium perlatum</u>) (1)

→ Unidentified Dove (1)

Woodland Kingfisher (<u>Halcyon senegalensis</u>) → Superb Starling (<u>Spreo superbus</u>) (1)

Fiscal Shrike (<u>Lanius collaris</u>) → Drongo (<u>Dicrurus adsimilis</u>) (1)

→ Lilac-breasted Roller (<u>Coracias caudata</u>) (1)

Grey Woodpecker (Mesopicos goertae) → Bearded Woodpecker (<u>Thripias namaquus</u>) (2)

Blue-eared Glossy Starling (<u>Lamprotornis chalybareus</u>) → Green Wood Hoopoe (<u>Phoeniculus purpureus</u>) (1)

→ Grey Woodpecker (<u>Mesopicos goertae</u>) (1)

→ Superb Starling (<u>Spreo superbus</u>) (1)

Tropical Boubou (<u>Laniarius ferrugineus</u>) ⟶ Northern Brubru (<u>Nilaus afer</u>) (1)

Crowned Plover (<u>Vanellus coronatus</u>) ⟶ Unidentified Dove (1)

All hole-nesting species previously recorded at Lake Naivasha were seen but some were less common than expected (Van Someren pers. comm.). These were the Cardinal Woodpecker (<u>Dendropicos fuscescens</u>) seen four times, and the Red-fronted Barbet (<u>Lybius diadematus</u>), seen three times.

5.4 DISCUSSION

Evidence of competition for nest holes among other species comes from both behavioural and experimental data. Interspecifically directed aggression among hole-nesting birds has been commonly noted (Von Hartman 1957, Orians and Willson 1964, Welty 1964, Armstrong 1965, Short 1979, 1982) as being caused by competition for a limited supply of suitable holes or cavities. The Wryneck (<u>Jynx torquilla</u>), for example, will even empty out the nesting material and eggs of another bird. Evidence also includes the densities of hole-nesting birds increasing with the provision of nest boxes (Welty 1964, Von Haartman 1957) and nesting pairs, when removed from their hole, immediately being replaced by, up until then, non-breeding individuals.

Recently however, the role of competition as a force controlling a species' numbers and distribution has been questioned (Connor and Simberloff 1979, 1986, Jackson 1981). Brush (1983) found competition between hole-nesters to be unimportant since cavities were not fully utilised and did not limit breeding despite extensive habitat and nesting season over-lap. He did conclude though that interference competition may be more crucial in situations where nest sites are in short supply.

Interspecific aggression is a conspicuous event in an avian community and one which may easily lead to false conclusions relating to direct competition. Various authors have suggested many alternative reasons for such behaviour including anti-predator behaviour (Welty 1964, Wittenberger 1981), the release of fighting behaviour to a subnormal stimulus (Hinde 1952), aggression between two species that have only recently come into contact (Hamilton 1962, Murray 1981), aggression between potentially hybridizing species (Post and Greenlaw 1975, Payne 1980), cases of mistaken identity (Murray 1971) and the display of belligerency and fighting abilities to mates (Neuchterlein and Storer 1985).

The importance of competition for nest sites may therefore be situation specific and although its role has been established, its significance may have been occasionally overemphasised in the past.

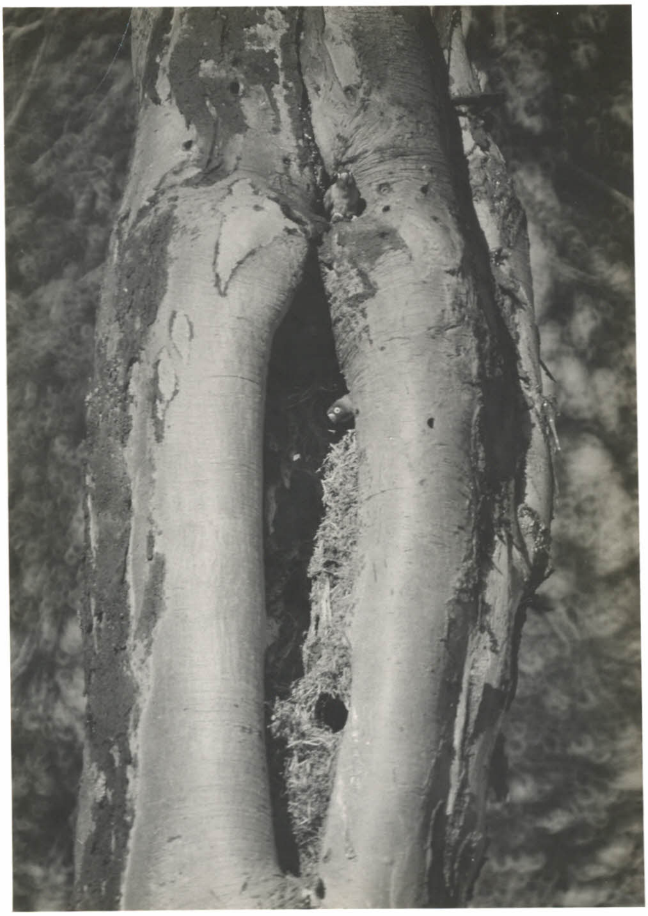
Lovebirds are often aggressed upon by other hole-nesting species, and their general behaviour is one of retreat rather than aggression. They may exert a competitive threat for hole possession by more indirect methods however. During the day, lovebirds will investigate and modify the cavities of other hole-nesters. For example, lovebirds were observed bringing to a Green Wood Hoopoe's (Phoeniculus purpureus) nest acacia twigs (which lovebirds use in the construction of their own nests) which the hoopoes would remove on their return to roost. Similar behaviour has been observed in the Tityras (Tityra semifasciata and T. inquisitor) by Skutch (1969). They are successful in usurping woodpeckers by filling their holes with leaves and debris so that the woodpeckers eventually tire of removing it and abandon the nest. Lovebirds were also seen to peck away at the entrance of a Pearl-spotted Owlet (Glaucidium perlatum) hole. On the owlets return, it was swooped upon by a Black-headed Oriole (Oriolus larvatus) (this owlet is often mobbed by other birds (Williams 1980)) thus preventing the defence of it's hole. Alteration of the entrance hole by usurping species has also been noted before (Short 1979, Lanning and Shiflett 1983).

Lovebirds are persistent in their efforts at nest usurpation. Three lovebirds were seen investigating a Red-fronted Barbet's hole (Lybius diadematus) one actually entering for some minutes. On the return of the barbet they were forced to leave by its aggressive behaviour but four months later, lovebirds were still seen investigating the hole. Such persistence may eventually cause a harassed bird to give up it's hole. Lanning and Shiflett (1983) have concluded in their study on Thick-billed Parrots (Rhynchopsitta pachyrhyncha) however, that investigation of cavities may occur for reasons other than their usurpation. This possibly explains the long time period over which the lovebird had been investigating the barbet's hole without usurping it. Nevertheless, it is probably this tendency towards investigation which attracts aggression from other hole-nesters. Woodpeckers, for example, are able to "recognise" potential nest competitors and will readily attack them even when there is no direct threat to the nesting hole (Short 1979).

Lovebirds may indirectly prevent woodpeckers from excavating new holes due to the lovebird's habit of burrowing down and nesting in the central core of dead branches. By taking up much of the branches length as an entrance tunnel and nest cavity (Plate 12) woodpeckers are prevented from excavating a hole, especially when confronted with a family of noisy lovebirds. Old woodpecker holes are used by many other species of hole-nesters so that the lovebirds are also preventing the excavation of potential homes for a variety of species.

It is the flocking behaviour of lovebirds which, at least in part, compensates for their lack of aggressiveness. Dilger (1960) concluded that although nest cavity defence is apparently non-existent in A. fisheri and A. personata, it may be adequately

Plate 12. A lovebird nest cavity showing it's several entrances and delicately weaved entrance tunnel



compensated for by increased mobbing activity in these birds. By giving alarm calls they quickly muster the support of other lovebirds, a more intimidating prospect for a potential nest competitor. For example, according to a local resident, a pair of Lilac-breasted Rollers (Coracias caudata) which had regularly nested on their land, was forced to leave due to the sheer numbers of lovebirds. While a very aggressive species, Lilac-breasted Rollers are shy at the nest and desert easily (Mackworth-Praed and Grant 1962). High lovebird densities may also cause desertion by increased aggressive activity of the defending species and the consequent attraction of predators (Short 1982).

Lovebirds permanently occupy their various cavities throughout the year unlike some other hole-nesters. This and the substantial modification of the nesting cavity prevents sequential use of the hole by several hole-nesters in the same season, an adaptation suggested to be important for the reduction of aggression and nest interference (Brush 1983). Woodpeckers are particularly vulnerable because of their use of several alternate holes which are vulnerable to usurpation by lovebirds (Short pers. comm.). Alternate holes are especially important for fledging woodpeckers and the risk of predation is increased without them. Furthermore, the majority of woodpecker holes at Naivasha are excavated in dead wood increasing the risk of usurpation since the entrance hole can be enlarged more easily than if excavated in live wood (Short 1979).

The only situation where lovebirds were consistently overtly aggressive towards other species was in maize fields. For example, if a Grey Woodpecker (Mesopicos goertae) landed on a maize ear where a lovebird was feeding, the lovebird would often lunge at the woodpecker driving it away. Weavers (Ploceus spp.) were treated similarly. This apparent reversal in aggressiveness may be due more to a reduction in aggression of other species usually dominant over lovebirds. It would be maladaptive for other species not as proficient as lovebirds at opening maize ears (see chapter 4) to force lovebirds off maize. By waiting until the maize is opened, species such as mousebirds and weavers may have to spend less time exposing maize and more time consuming. Orians and Willson (1964) reported a similar behavioral reversal between Red-winged (Agelaius phoeniceus) and Yellow-headed Blackbirds (Xanthocephalus xanthocephalus) in North America between feeding grounds and breeding territories. They argued that selection should favour heightened aggression in habitats where each respective species is better adapted since the more suitable the habitat, the greater the benefits of fighting for it. Whatever the explanation, the behavioural change at Naivasha was marked allowing all species to benefit maximally.

There was no obvious preference by lovebirds for any particular cavity type or height above ground level used. They have been described as indiscriminate cavity-nesters (Moreau 1948) and therefore all hole-nesting species may be likely to compete with lovebirds for nest sites. The occurrence of many apparently unoccupied holes does not necessarily imply an overabundance of them. They may be occupied by a variety of organisms from Tree Mice (Apodemus sp.) to insects or be unsuitable for occupation due to accumulated microfauna including parasites and other vermin after continuous habitation by birds (Short 1979).

An amateur bird-watcher reported to me that near Nakuru he had observed lovebirds systematically dismantle several Red-headed Weaver (Anaplectes rubriceps) nests so that they eventually fell to the ground. This is an interesting observation on its own but what was the cause of this directly aggressive behaviour? Possibly it could be directed towards the convenient procurement of nesting material (Karanja pers. comm.). Alternatively, were the weavers feeding in competition with the lovebirds in nearby maize fields and the latter reacted by destroying the weaver's nests? Such an explanation for the observed behaviour presumes a remarkable intelligence on the lovebird's part and not only their ability to recognise and remember other species but also to react at another time and place to prevent the successful breeding of a competitor. Parrots however, do have a relatively large brain (Forshaw 1981) and are among the more intelligent of birds.

It has been difficult to positively identify lovebirds as a species which has caused the reduction in numbers of other hole-nesting species at Naivasha due to their lack of aggressiveness. Unfortunately no data are available on the densities of vulnerable species before the introduction of lovebirds, but two species which warrant particular attention are the Cardinal Woodpecker (Dendropicos fuscescens) and the Red-fronted Barbet (Lybius diadematus) both of which were rarely sighted. Both are similar in size to lovebirds and hence most likely to draw the greatest degree of competition (Short 1979). Furthermore, the Cardinal Woodpecker was the only woodpecker to be seen not to always roost in a conventional woodpecker hole but sometimes to roost in holes similar to that which lovebirds use.

Lovebirds have successfully established themselves at Naivasha and it is hard to believe that other hole-nesters have not suffered as a result. Slobodkin (1961) has argued that for an invading species to establish itself, its ecological niche must have been previously unoccupied or inefficiently exploited and that either condition is less likely in a complex community. Since lovebirds have indeed established themselves in a complex community where every niche is likely to have been utilised, an element of competition at the expense of other species is implied.

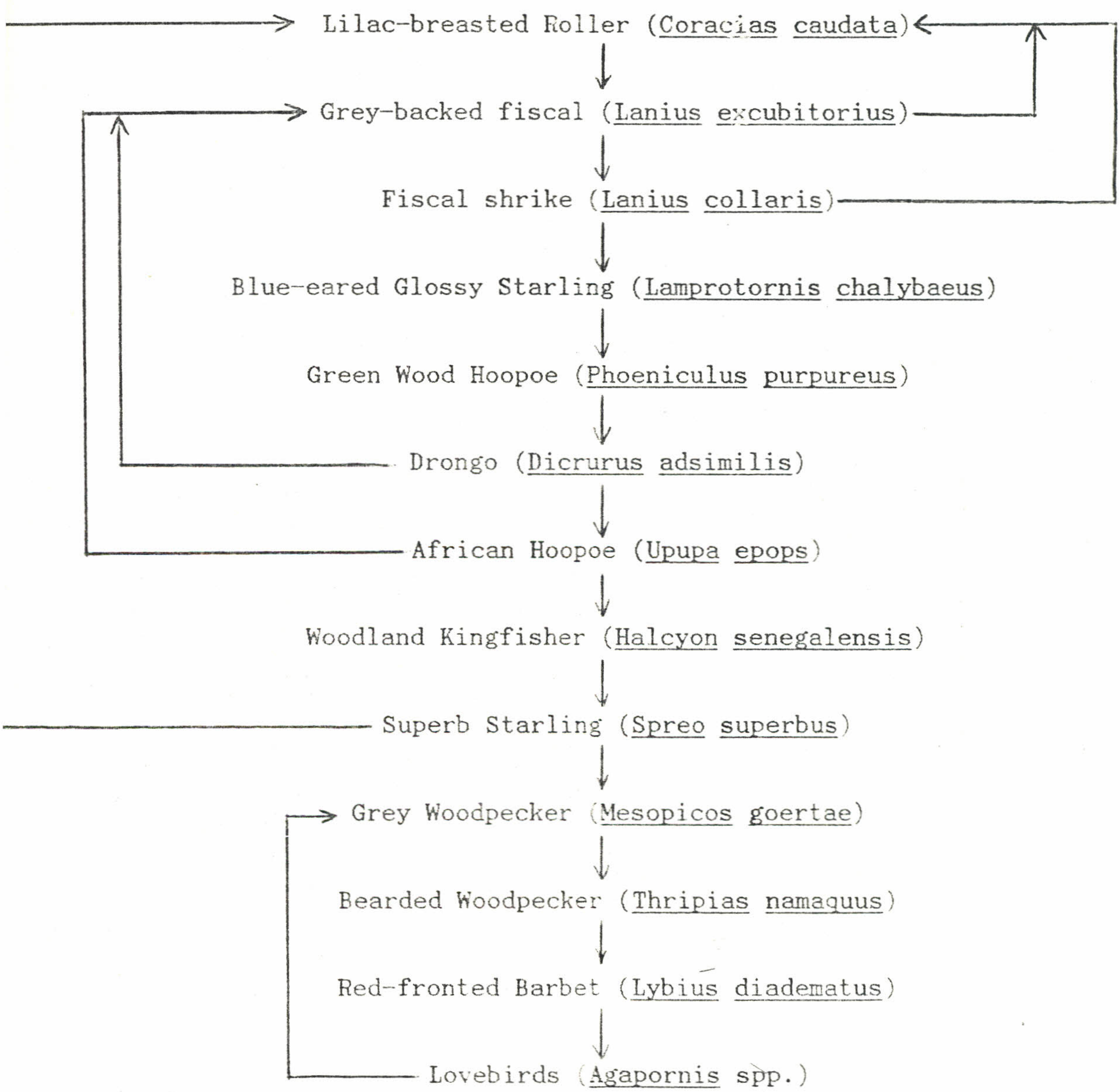
5.4.1 Interspecific Aggression Not Involving Lovebirds

As mentioned above, there are many causes for interspecific aggression, making the description of a reliable order of dominance difficult. The apparent reversal of dominance in different habitats or circumstances confuses the interpretation of aggressive encounters. Nevertheless the same individuals in many of these encounters between the same pair of species were always dominant, suggesting their clear superiority. As Nuechterlein and Storer (1985) have commented, the development of strong interspecific aggression povides a critical test for theories concerning the relationship between aggression and competition for resources. Difficulties arise however, with the interpretation of any apparent superiority. The Lilac-breasted Roller (Coracias caudata) is a good example since although an aggressive bird, it is shy at the nest. Therefore, even if a species is behaviourally dominant over another does not necessarily imply its overall superior competitiveness or fitness.

Figure 8 gives a flow diagram of interspecifically directed aggression for the species combinations more commonly observed. Species at the top are aggressively dominant over those below but, as shown, there were instances of birds low on the list aggressing on birds above. For example a Superb Starling (Spreo superbus) was seen once to aggress on a Lilac-breasted Roller. The order shown in Figure 8 does represent aggressive superiority in the majority of cases though. However, with so many species involved and such a large number of possible species combinations, the number of interspecific encounters for each pair are small so that Figure 8 remains only a tentative description of dominance until further observations are made.

Figure 8

Dominance hierarchy of some species at Lake Naivasha seen to interspecifically react aggressively



The apparent causes of interspecific aggression included nest-hole or territorial defence and anti-predator mobbing. However, most aggression was directed at the defence of localised food patches or elevated perches used by birds as convenient vantage points over food patches. Unlike many studies noting interspecific aggression and competition (Svardson 1949, Orians and Willson 1964, Cody and Walter 1976, Connor and Simberloff 1986) there was little relationship between the relatedness of species involved, similarity in diet or feeding techniques being the critical factor determining interspecific aggression. This implies a considerable overlap in feeding ecology, perhaps greater than normal, but what is the cause? In general there appeared to be more incidences of aggression in modified or agricultural habitats compared with virgin forest. In agricultural areas food supply (particularly for insectivores) is probably more abundant due to irrigation, cultivation and cattle stocking. For example, shrikes and starlings would commonly fight vigorously for "hunting rights" over cattle yards where a super-abundant supply of insects could be found in the manure. Such locally enhanced food supplies apparently heighten a bird's disposition towards foraging space defence despite the increased expenditure of time and energy involved. Obviously the costs are less than the benefits. Perhaps in a less agricultural habitat, food supplies are more evenly distributed as are species competing for them, thus reducing the incidence of aggressive encounters. Modified habitats, especially where the areas of modification occur in small patches as at Naivasha, are likely to contain a greater number of niches. Therefore, a greater variety of species are given the opportunity of successfully exploiting the area, resulting in increased contact and competition between more species having similar ecologies.

CHAPTER SIX

LOVEBIRD MOULT AND BREEDING

6.1 INTRODUCTION

During the mark-recapture experiment, the pattern of primary wing moult of captured lovebirds was recorded. The moult of the primary flight feathers is related to the moult of the whole plumage and can therefore be used as an index of total moult progress (Voitkevich 1966). The recapture of ringed lovebirds also allowed moult rate to be studied and since moult is preceded by breeding in parrots (Forshaw 1981) it can provide information on timing of breeding seasons.

6.2 METHODS

The moult score of each wing was scored separately by assigning a numerical value to each primary according to the internationally accepted 0-5 scale (Ginn and Melville 1983). A "0" was assigned to an old feather, "1" a missing feather or emergent pin, "2" a feather 1/3 grown, "3" 2/3 grown, "4" 3/4 grown and "5" a nearly complete or completely grown feather. In cases where the moult score differed between wings, the average of the two scores was used for moult rate calculations. By using the calculated average moult rate, the date of moult initiation in moulting birds was determined and therefore the theoretical date of breeding cessation.

Primary moult was considered as interrupted (Harper 1984) if all feathers were fully grown and no basal sheath was present on newly grown feathers. While moult interruption appears to occur for a variety of reasons in different species, it is usually associated either with breeding or migration (Harper 1984). This is generally thought to be due to the metabolic incompatibility of these processes so that they are programmed to occur at different times (Foster 1975, Payne 1969, Jones 1978, Miller 1961). Since lovebirds are not a migratory species, interruption of their moult is interpreted here as an indication of breeding activity.

6.3 RESULTS

6.3.1 Moult Pattern

Lovebirds, like all other parrots, renew their primaries from the centre outwards, usually beginning at the sixth primary. Taking the moult of both wings separately, out of 102 cases where initiation of primary moult could be observed, 0.9%, 15.6%, 82.3% and 0.9% of the birds began their moult at the fourth, fifth, sixth and seventh primaries, respectively. The usual pattern was then to progressively drop feathers on either side of the moult focus (Payne 1972) finishing by regrowing the inner-or-outer-most primary last.

6.3.2 Moult Rate

Five lovebirds were recaptured 4, 10, 16, 17 and 192 days after being ringed and their moult scores had progressed by 1.5, 1, 4, 4 and 24 points, respectively. This gives an average moult rate of 5.8 days per moult point with a standard deviation of 3.1 days per point. It is assumed that the relationship between the increase in moult score with time is linear so that on average the primary moult takes 290 days (5.8 x 50) for completion. The 95% confidence limits for moult rate (using the appropriate t statistic, d.f. = 4) is given by 5.8 $\pm$ 3.9 days per point or between 95 and 485 days for a complete moult cycle.

6.3.3 Breeding

Over the study period, a total of 164 moulting lovebirds were captured. Numbers caught and percentages of moulting birds in total monthly samples are presented in Table 12. Using the calculated average moult rate, the numbers of birds initiating their moult (and hence ceasing breeding) in each month are presented Figure 9(a). An adjustment to this histogram is necessary however, because, birds initiating their moult in some months had a longer period of time over which they could have been caught than others. For example, birds initiating their moult in June 1986 had available only one month over which they could have been caught whereas those initiating in May 1986 had two months. Since the average time to complete a moult cycle is 290 days (roughly ten months) the longest period of time available for capture while moulting is ten months. This would have corresponded to birds initiating their moult in August and September 1985 except that no

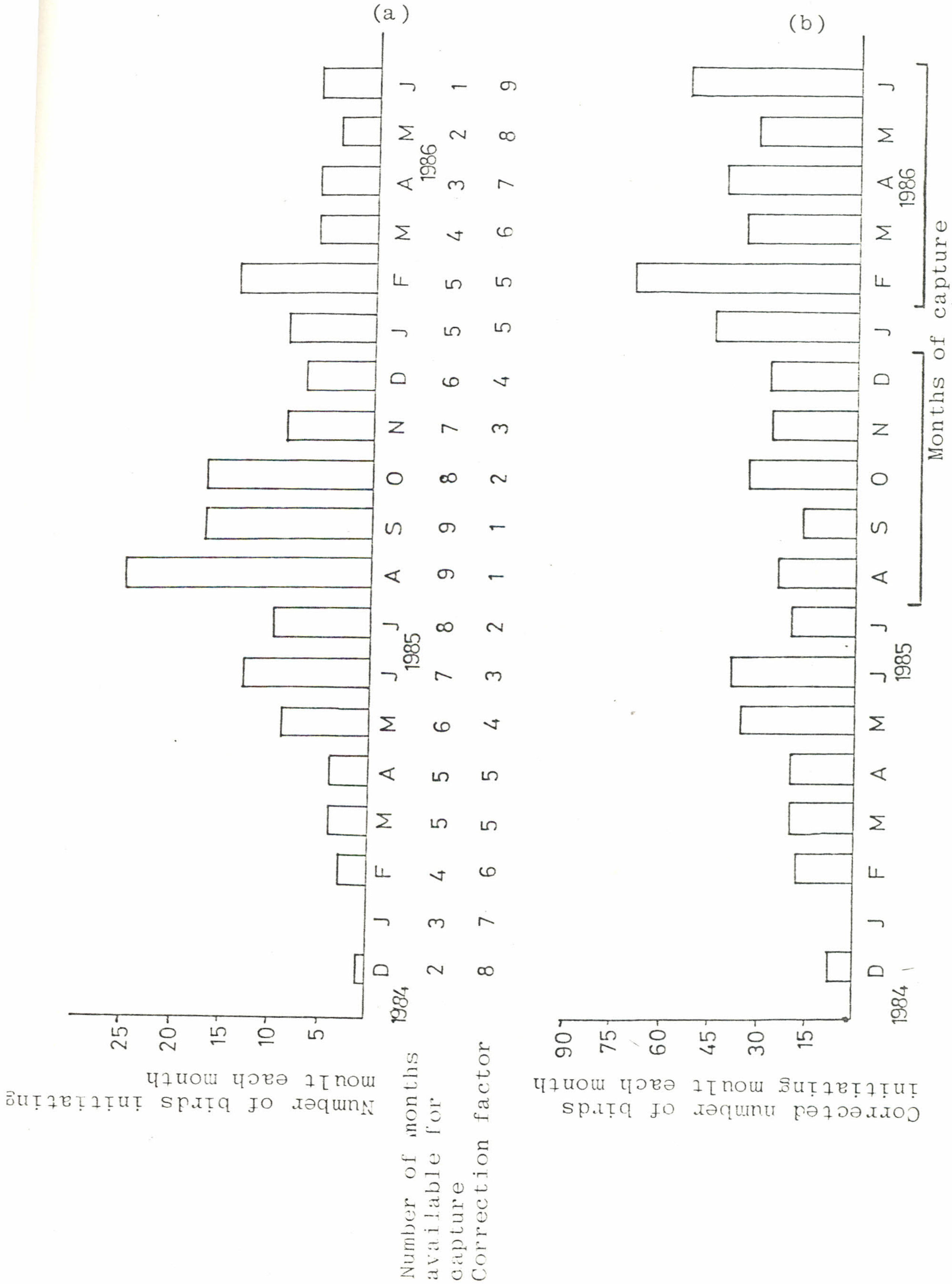
Table 12

Number of lovebirds caught and percentage moulting in each month over study period

Month	Number caught	Percentage moulting
August	58	16
September	94	14
October	109	28
November	120	37
December	31	13
January*	-	-
February	64	41
March	57	40
April	46	39
May	19	26
June	42	62

*No lovebirds caught in January

Figure 9. The use of moult to detect any breeding seasonality. The lower histogram gives the derived number of sampled birds in each month initiating their moult and hence ceasing to breed



collections were made in January 1986. Therefore, these August and September birds only had nine months available for capture instead of ten. The correction factor was derived from the number of months available for capture and the lower histogram generated by the multiplication of each month in Figure 9(a) by its correction factor. For example, the number of birds initiating their moult in August and September 1985 was multiplied by a factor of one, those in July and October by two and so on as shown in Figure 9(b). The resulting histogram gives an unbiased estimate of the proportion of lovebirds ceasing to breed in each month, as derived from moult data.

A runs test showed that the initiation of moult in captured lovebirds was not randomly distributed ($P < 0.05$ one-tailed test) with time, but was concentrated towards the latter half of the study period.

The percentages of captured lovebirds with interrupted moult in each month are presented in Table 13. A runs test showed that the percentage of lovebirds with interrupted moult did vary randomly throughout the study period.

A correlation analysis was performed on monthly breeding and rainfall data. To do this, breeding data from Figure 9(b) were shifted to the left by one month since these data represent the frequencies of birds ceasing to breed in each month rather than the frequency actually breeding.

Table 13

Monthly percentages of lovebirds with interrupted moult

Month	Percentage with interrupted moult
August	1.7
September	1.0
October	2.8
November	3.3
December	0
January*	-
February	6.3
March	1.8
April	3.1
May	5.3
June	21.4

*No lovebirds caught in January

Monthly rainfall was then compared with the following month's level of breeding cessation. The correlation (r = -0.185) was not significant at the 0.05 level of probability.

6.4 DISCUSSION

It is a pity that only five lovebirds were recaptured at different stages in their moult since the following arguments concerning breeding seasons are based on assumptions made about moult rate. Moult rate in lovebirds (and parrots in general) may be particularly variable due to its relatively slow progress. Nevertheless, while the details of Figure 9(a) and (b) may be subject to error due to the small sample size in moult rate calculations, there is little doubt that lovebirds will breed at Naivasha in any month of the year. In future, a detailed programme of nest examination should be performed to check results arrived at by moult examination as there can be no substitute for direct nest inspection in the proof of breeding.

The cause of the significant increase in breeding activity towards the end of the study period is unknown. A longer period of study is necessary to ascertain the cause of breeding peaks since, as Figures (9a) and (b) suggest , such patterns may be dependant on factors other than regular annual events, but rather on events which may occur over a longer period of time such as unusually high rainfall affecting food availability. The independence of breeding from regular seasonal events is further suggested by interrupted moult data since over the study period, the frequency of interrupted moult varied randomly. The lack of annual breeding peaks may be due to the agricultural nature of Naivasha's habitat since irrigation has probably caused food availability to be somewhat independent of rainfall, the most noticeable climatic effect in tropical regions (Brown and Britton 1980) likely to affect breeding.

It is likely that some variation in intensity of breeding occurs around the lake according to local conditions. Rainfall at the lake tends to be extremely patchy, especially in drier years, so that marked diffferences in food availability within short distances is possible. Patchy irrigation also enhances locally uneven food supplies. Since lovebirds have a short home range (chapter 4), their breeding behaviour may be dependent on their ability to forage outside these locally abundant food patches. In Panama, Kalma (1970) found quite different breeding patterns of the Rufous-collared Sparrow (Zonotrichia capensis) within a distance of only three kilometres depending on the condition and dryness of local grasslands. Since lovebirds were captured all around the lake, such local variation in breeding seasonality could explain their apparent ability to breed at any time of the year.

CHAPTER SEVEN

HYBRIDISATION

7.1 INTRODUCTION

The relatively recent geological origin of the genus *Agapornis* has created some conflict of taxonomic opinion due to their "borderline" stage of evolution (Moreau 1948, Dilger 1960). This particularly applies to the four white-eye-ringed forms *personata*, *fischeri*, *lilianae* and *nigrigenis* which have been treated as both separate species (Moreau 1948) or as subspecies of one species (Dilger 1960). While allopatrically distributed in the wild, they will readily hybridise in captivity forming morphological and behavioural intermediates.

The interest in this study was the opposite of most investigations into hybridisation. Instead of beginning with two distinct populations and studying the degree of hybridisation between them, it was assumed that all the founding birds at Naivasha were to some extent hybrids and the process of interest was one tending to either maintain an even polymorphism or to change the balance between the two sets of genes towards either extreme after twenty or more years of selection. The adaptive significance of hybridisation is important and other workers have shown how hybrids have been provided with additional genetic variation necessary for natural selection to produce a new adaptive form (Lewontin and Birch 1966, Greig 1980, Cade 1983).

7.2 METHODS

In addition to morphometric data recorded on wing and tail lengths and weight, a total of 311 captured lovebirds were assigned scores according to the colour of their head and chest plumage. Five categories were used, these being

A - depth and extent of black on the head
  - four point scale 0-3 (3 = maximum extent of black)

B - extent of yellow on chest and neck
  - four point scale 0-3 (3 = maximum extent of yellow)

C - extent of red on chest
  - four point scale 0-3 (3 = maximum extent of red)

D - shade of redness on forehead
  - three point scale 0-2 (0 = light peach)
    (2 = deep carmine)

E - extent of red on sides of face and neck
  - four point scale 0-3 (3 = maximum extent of red)

This body region has very distinctive plumage in the two forms, personata having a black head and yellow throat and chest while largely lacking the extensive red that is possessed by fischeri on the throat chest, sides of face and forehead.

A collection of nine study skins was prepared of either extreme and intermediate forms for comparison with live birds (Plates 13 and 14).

Plate 13. Lateral view of nine lovebird study skins

Plate 14. Ventral view of nine lovebird study skins

The Statistical Package for the Social Sciences (S.P.S.S) was used to calculate correlation coefficients and analyses of variance. The cluster analysis was performed on an "Acorn" BBC/B micro-computer. The cluster analysis package used Gower's coefficient of similarity (standardised by range) to produce a list of similarities. The single Linkage method was then used to generate dendrograms illustrating group affiliations or clusters.

7.3 RESULTS

Table 14 gives a summary of correlation coefficients between the various colour categories. All coefficients were significant except between characters C and D. In general, the extent of black and yellow was inversely correlated with the extent of red. Relative per cent frequencies for each character category are presented in Figure 10(a), (b), (c), (d) and (e).

Since after data collection, a strong negative correlation was found between characters A/B and C/E, these were grouped and analysed separately. Scores for characters A and B were simply summed while the reciprocal scores for characters C and E were summed. That is, for characters C and E, a score of 0, 1, 2 or 3 became 3, 2, 1 and 0 respectively. This allowed a maximum score of six for each summed category and transformed the correlation from a negative to a positive one as shown in Figure 11. A regression line for this grouped

Table 14

Correlation coefficients between colour categories.

	A	B	C	D	E
A	1.00	0.227	-0.242	0.314	-0.693
B		1.00	-0.668	0.189	-0.232
C			1.00	-0.086	0.381
D				1.00	-0.133
E					1.00

Figure 10. Relative per cent frequencies (R.P.F.) of each colour category in 311 lovebirds

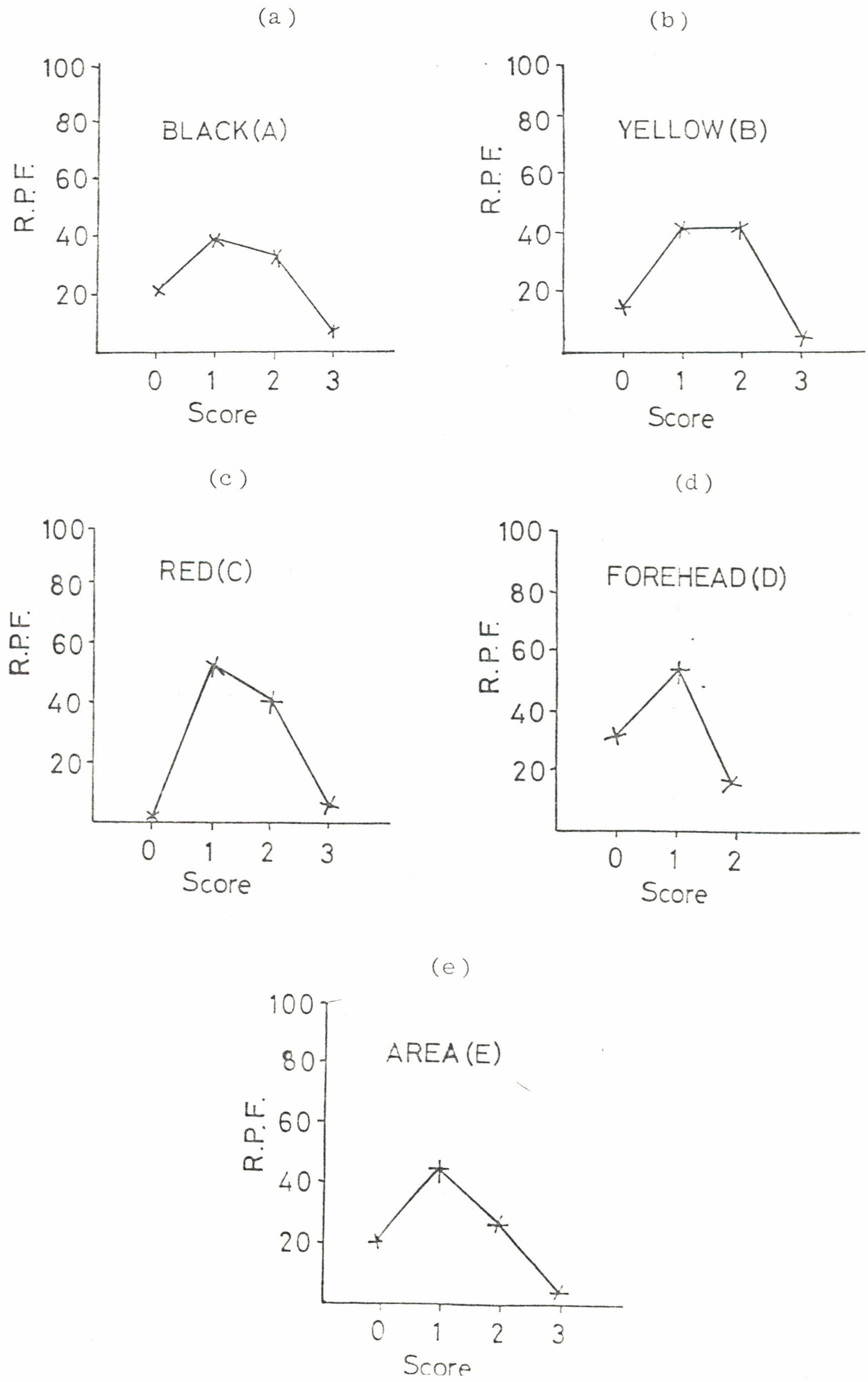
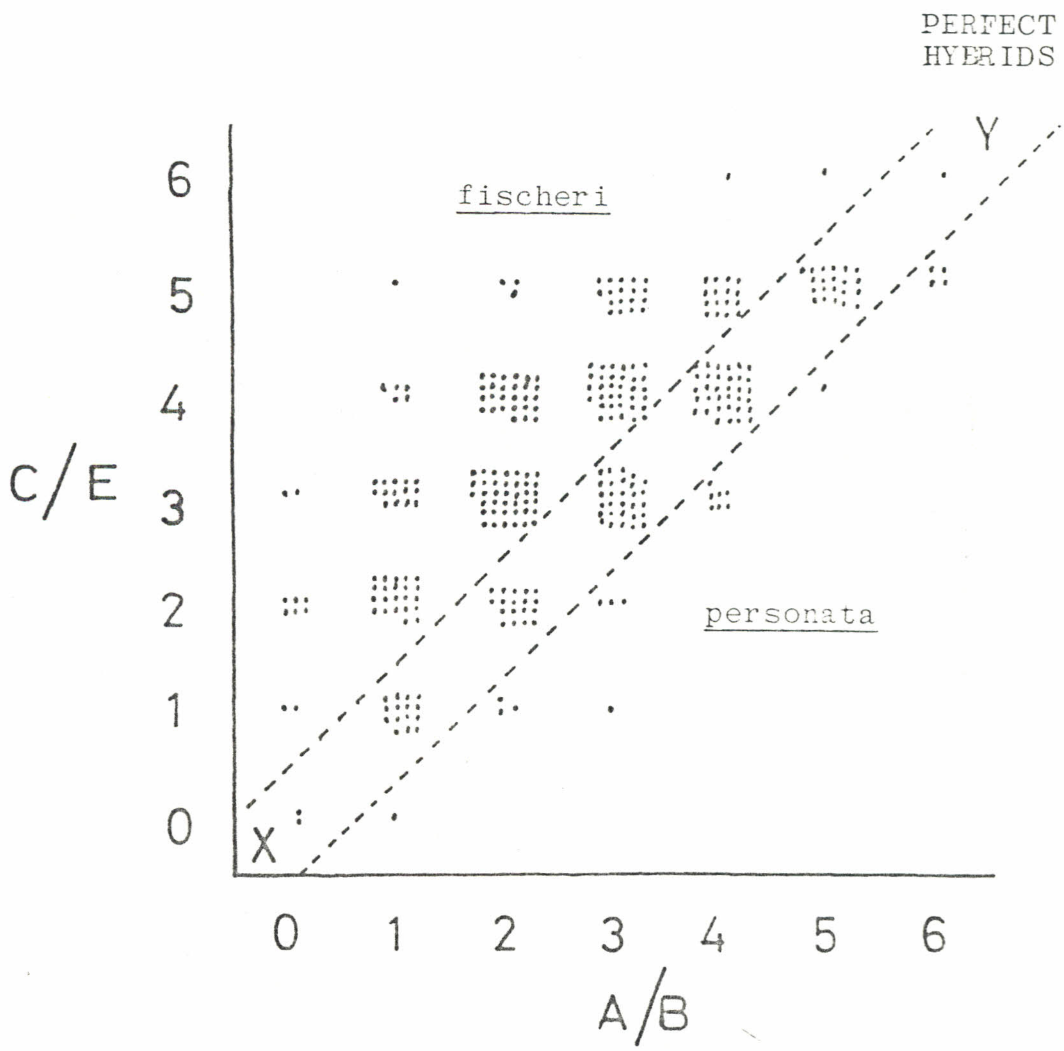


Figure 11. Scattergram of grouped adjusted scores for plumage colouration of 311 hybrid lovebirds



data was calculated and was significantly different ($P < 0.001$) from that expected had the characters A/B and C/E been perfectly correlated and all birds been perfect hybrids.

The points on Figure 11 can be divided into three categories depending on whether they fall on the hypothetical line XY of perfect correlation or fall above or below it. If above the line they more closely resemble the fischeri phenotype while if below, the combined characters are closer to the personata form. Hybrids with scores on the line of perfect correlation may be considered perfect hybrids with equal representation of fischeri and personata characteristics. Of all the points, 59.1% and 5.6% fall above and below the line of perfect correlation respectively, while 35.3% of the lovebirds had perfectly correlated hybridisation scores.

The difference in hybridisation scores between mist-netted and trapped birds was not significant at the 0.05 level of significance.

An analysis of variance was performed on the three groups of Figure 11 to determine if there were significant differences in morphology (wing and tail lengths and weight) according to plumage colouration. The differences were not significant so that external morphology was similar in the three groups.

Since the cluster analysis package was only able to handle 80 individuals simultaneously, a test run of the first 80 was performed to initially see if any obvious clusters were evident in the data. The resultant dendrogram analysing all the field characters is shown in Figure 12. Due to the lack of obvious groupings the data were split into binary and continuous variables and analysed separately. That is, the continuous morphologic measurements (wing and tail lengths, wights) were clustered separately from the binary colour categories (A, B, C and E). Character D was omitted from the latter analysis since it showed little importance judging from the correlation coefficient analysis. By splitting the variables to be analysed into two sets, the cluster programme should have separated any groupings more easily. As shown in Figures 13 and 14 however, individuals were not clustered into a few clear groups but appeared to be randomly related to one another. Figure 14 shows how individuals 74 and 78 were closely related according to their plumage colouration. These two birds did, in fact, possess colouration almost identical to that of a pure A. fischeri phenotype. Because of the lack of coherent clusters in this initial test, the remainder of the data analysis was discontinued.

7.4 DISCUSSION

7.4.1 Phenotypic Significance

While the results show that at present the Naivasha lovebird population is phenotypically closer to fischeri than

Figure 12. Dendrogram produced by cluster analysis with all fields active

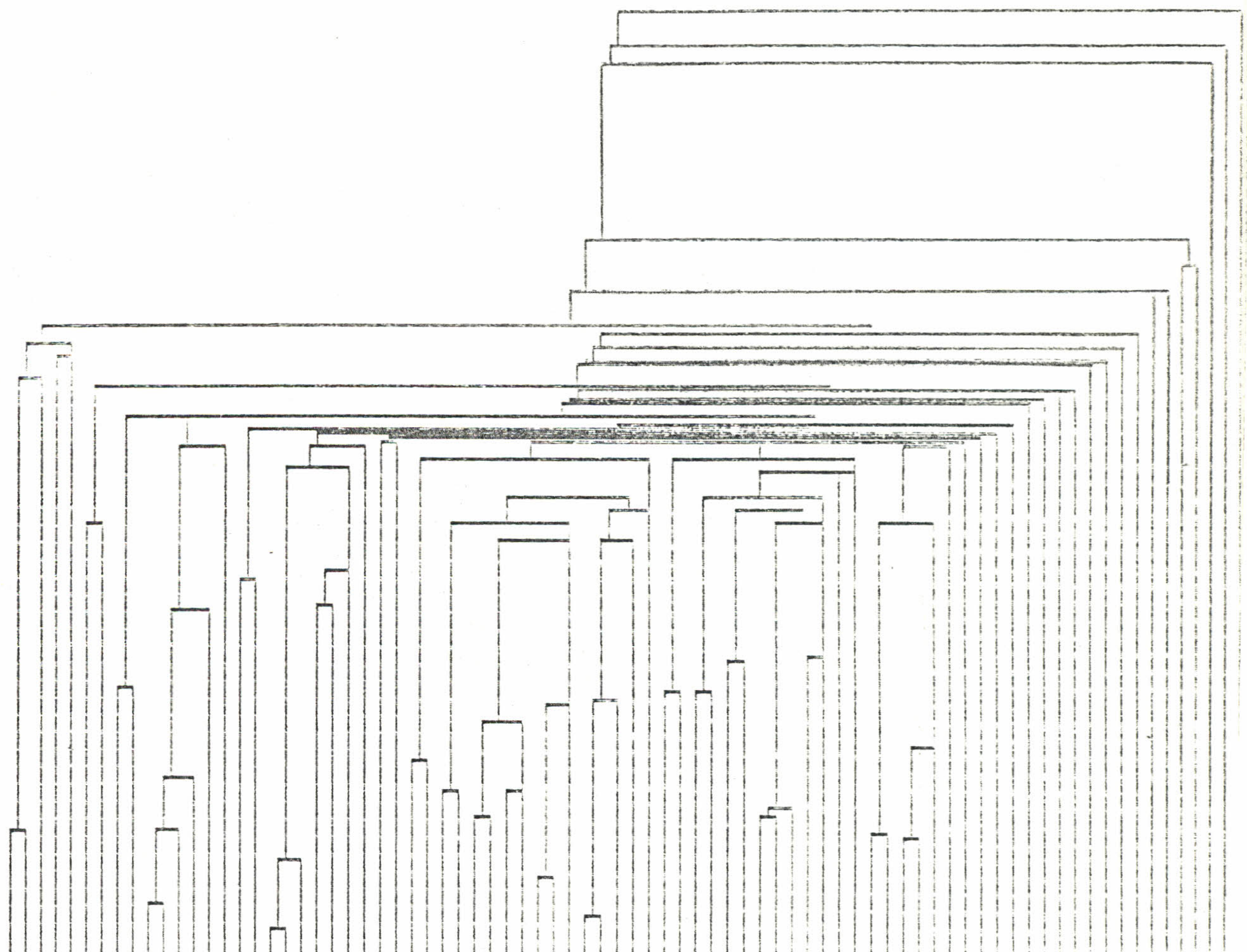


Figure 13. Dendrogram produced by cluster analysis with continuous (morphologic) fields active

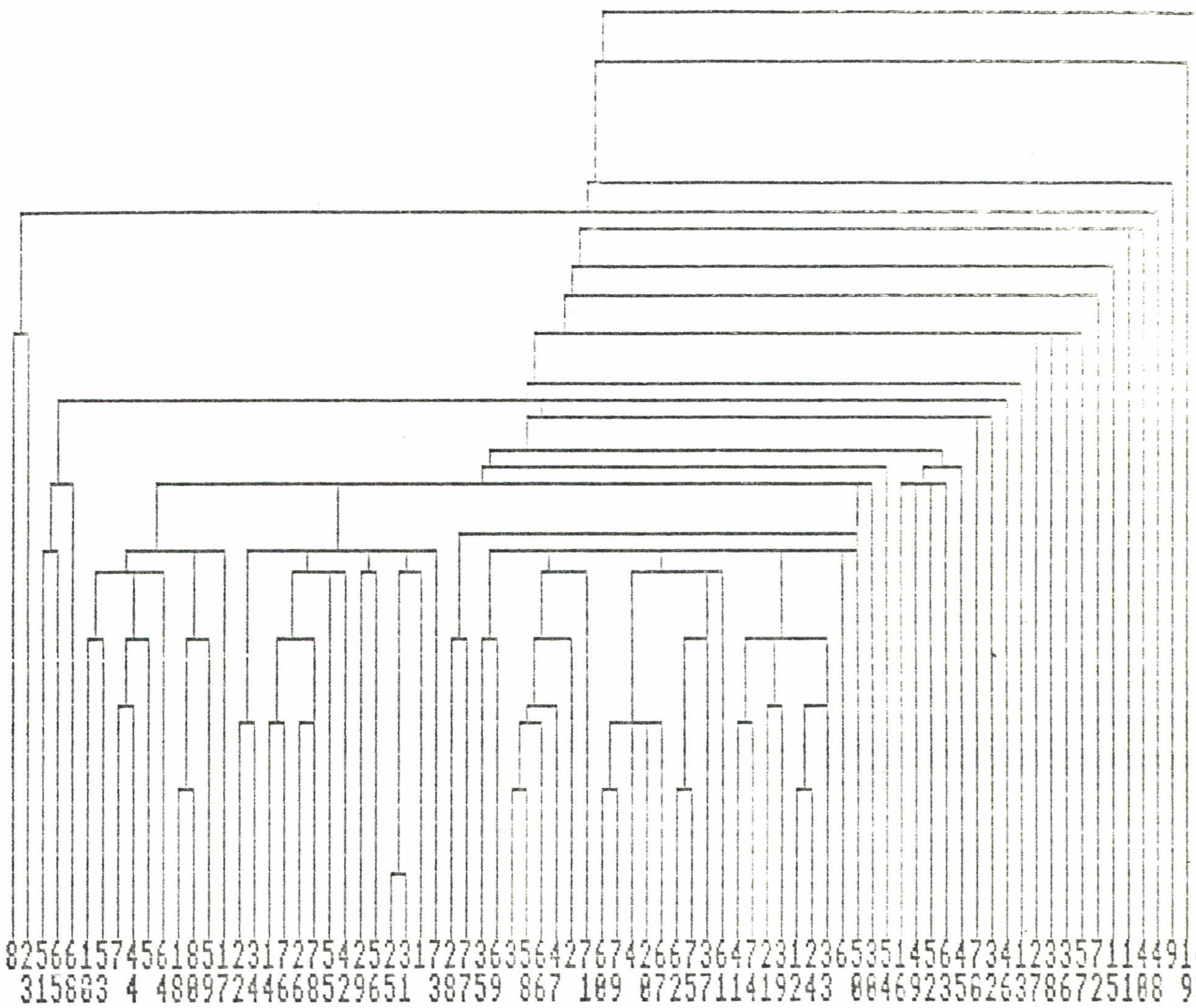
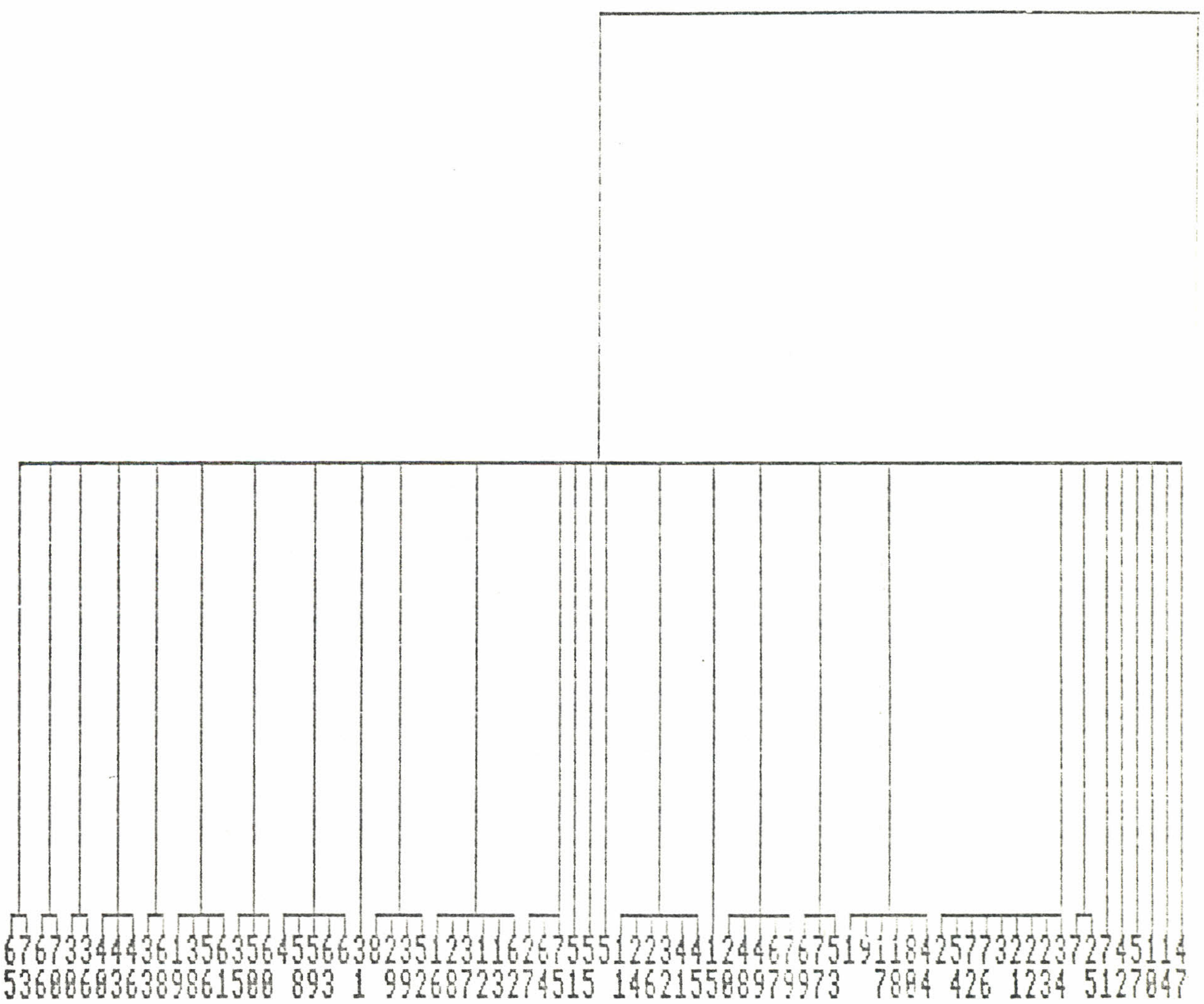


Figure 14. Dendrogram produced by cluster analysis with only binary (plumage colour) fields active



<u>personata</u> (Figure 11) the directional trend of any changes that may be occurring to alter this state is unknown and depends on what assumptions are made about the phenotypes of the lovebirds originally released at the lake. It is more likely that, phenotypically, the <u>fischeri</u> genotype is expressed more strongly than the <u>personata</u> genotype. This was noted by Moreau (1948) who pointed out that the progeny of <u>A</u>. <u>nigrigenis</u> and <u>A</u>. <u>personata</u> crosses (the two black-headed forms) are lighter than the two parental forms. Furthermore in their natural range, <u>A</u>. <u>fischeri</u> and <u>A</u>. <u>personata</u> have similar habitat requirements and it is difficult to see how one form could have superior fitness over the other. Assortative mating also seems an unlikely explanation since this would require <u>personata</u> types to assortatively mate with <u>fischeri</u> types. I therefore believe that although there is an apparent bias towards the <u>fischeri</u> genotype, this is more the result of an unbalanced genetic expression in plumage colouration resulting in greater numbers of the <u>fischeri</u> type.

Further evidence for the Naivasha lovebirds not being biased towards either pure type comes from plumage colouration morphological data. The lack of differences in body measurements according to plumage colouration suggests an even mixture of genes across the whole population. There is considerable overlap in these body measurements in the pure types (Forshaw 1981) and one would not necessarily expect there to be significant differences in a hybrid population.

The cluster analysis showed this clearly since no distinct groupings were detected. Individuals 74 and 78 were singled out as being unusual since they were particularly close to the plumage colouration of the _A. fischeri_ form. The vast majority of individuals though, were linked by intermediate forms with hybrid characteristics. Figure 10 also shows how the majority of lovebirds had colour characteristics intermediate in nature. The overall description of the Naivasha lovebirds therefore, is one of polymorphic variation between two extremes with the majority falling phenotypically in the mid-range but biased towards the _fischeri_ type.

7.4.2 Genetic Control of Plumage Colouration

The fact that most of the plumage characters were well correlated suggests a common genetic control mechanism. The exception, character D, is related to colour intensity rather than extent and may be controlled differently, although it did correlate well with characters A, B and E. The paucity of hybrids at either extreme of the hybrid spectrum suggests a co-dominance between genes controlling plumage colouration. This is because heterozygotes of co-dominant alleles should be phenotypically intermediate between the two homozygotes (Harrison _et al_. 1964).

On the other hand, the shapes of the curves in Figure 10 are reminiscent of curves for characters showing continuous variation such as human growth curves. Such characters have been shown to be under the control of a large number of genes (Harrison et al. 1964).

With the available data then, a definitive description of the genetic control of plumage colouration is not possible since there is the likelihood of it being under the control of multiple genes.

7.4.3 Consequences of Hybridisation

Anderson (1948) stated that "hybrid swarms can survive only in hybridized habitats". Although he largely referred to botanical examples, his ideas are applicable to the introduction of lovebirds to Lake Naivasha. The lake's forest has been subjected to increasingly intensive agriculture. By burning, tilling the soil and clearing, man has hybridised the habitat allowing lovebirds to inhabit the newly formed agricultural niche. Stebbins (1970) further emphasises the lasting effect of hybridisation in a "disturbed, rapidly changing habitat".

It has been shown with other bird species (Cade 1983) that hybridisation may inject genetic material from one species into another bestowing enhanced ecological and physiological capabilities and thus allowing the newly formed genotype to expand into previously unoccupied latitudes and altitudes. This has happened with hybrid lovebirds in other parts of Kenya. Although being confined to a narrow range of altitude of between 1100 - 1700 metres as the pure forms are in Tanzania, hybrids can be found from sea level in Coastal Kenya up to approximately 3000 metres at Molo in Central Kenya. Their range extension is still continuing.

7.4.4 Introgression with Pure Wild Agapornids

The mixing of genetic material from one closely related species with another has been noted in the past as a factor affecting species' integrity and survival (West 1962, Gill 1980, Greig 1980, Gillespie 1985). If hybrid lovebirds continue to spread within Kenya, the possibility that they will eventually meet and hybridise with Kenya's only native Agapornid, *A. pullaria*, should be considered.

An important factor determining the possibility of hybridisation between *A. pullaria* and hybrids is its specialised habits of nesting in arboreal ants' or termites' nests. This may reproductively isolate *A. pullaria* and reduce the chances of effective hybridisation. It is not stated in the literature however, that *A. pullaria* exclusively uses ants' or termites' nests. Therefore, there is still the possibility of some overlap in the types of nest-holes used and hence danger of hybridisation.

CHAPTER 8

THE MANAGEMENT OF HYBRID LOVEBIRDS IN KENYA

8.1 PRESENT STATUS AND FUTURE TRENDS

Although lovebirds are the principle avian pest of maize at Naivasha and encourage damage by other species, at present their impact on commercial production is insiginificant. Peasant farmers growing maize for their own consumption bear the brunt of the worst damage where lovebirds can severely depredate their small plots. At Naivasha therefore, the management of lovebirds, with respect to crop protection, would be aimed more at improving the plight of the poor farm labourer than increasing the production of marketable maize.

As the population of lovebirds increases in size at Naivasha, so will the levels of damage to maize. Their range extension will also increase the amount of damage attributable to them in the country, especially when they reach more important maize growing areas. However, the relative seriousness of their impact on maize at Naivasha is due to that area being a mosaic of forest and areas reserved for agricultural production. Therefore, lovebirds have an abundance of trees in which to nest nearby maize fields. In large areas used for commercial maize production though, hole-nesting opportunities will be fewer because of the lack of trees. Lovebird densities in these areas will always be lower and damage levels minimal.

The lovebird population at Naivasha has grown to a large size and it seems probable that other hole-nesting species have suffered. Some may even be disappearing from the lake altogether. Without comparative data though, it is impossible to estimate exactly how other species have been affected. Further monitoring of the situation at Naivasha will clarify this point. Furthermore, their range extension in Kenya threatens other hole-nesting populations. However, the apparent tendency of hybrid lovebirds to prefer modified or agricultural habitats may slow their entry into National Parks and Reserves.

In favour of lovebirds, many bird watchers (including tourists) appreciate the introduction of an attractive parrot to Kenya. Rather than admit to the competitive forces which lovebirds exert on other species, they prefer to turn a blind eye and claim that there is "room for everybody", as one Naivasha resident put it.. Some view the management of wild bird populations with disdain while others (including many farmers) simply don't care either way.

8.2 MANAGEMENT OPTIONS

8.2.1 Lethal Control

This would involve the capture of lovebirds by trap or mist-net around maize fields. To avoid the death of other species, a lethal control campaign should be carried out by properly trained ornithologists skilled in bird handling and the use of mist-nets. The use of poisons should be discouraged at all costs since their incorporation with the lake's hydrology would be inevitable as would be the unintentional poisoning of other animals and perhaps even man.

The Crop Protection Branch of the Ministry of Agriculture have the facilities to mount a control campaign but, in doing so, they would be diverted from more important problems within the country. Even if such a campaign were attempted, many birds would be caught initially but the costs of the campaign would quickly increase in relation to the number of birds able to be caught. Therefore, unless a considerable amount of money was spent, only minimal success would ever be achieved.

8.2.2 Exportation

The capture and export of lovebirds to international markets could be performed by either a Government agency or private individuals. This approach would avoid the wasteful killing of lovebirds, be a self-financing operation and be a source of foreign exchange for Kenya. The sale of lovebirds within Kenya should be prevented as this would only lead to their further spread within the country. Allowing the export of lovebirds should be viewed as an exceptional case, justified on the grounds of them being an introduced agricultural pest and competitor with indigenous species. On no account should their export be treated as a precedent, to be used as justification for the export of other bird species.

Weighed against this must be considered the issue of encouraging the international cage bird market. Some argue that by exporting birds in large numbers the market is increased, followed by demand for more birds, in turn affecting other species. Nevertheless, native lovebirds are already being exported from Tanzania and may even be endangered in parts of their range (Borner pers. comm.). Perhaps Kenyan lovebirds would take the pressure of lovebird export from Tanzania, especially if offered at competitive prices. Also, some bird exporters have earned themselves a reputation in the past for mishandling or overpacking birds in transit, resulting in large numbers dying. Although mortality can be reduced to a minimum by humane treatment, the death of a certain percentage of birds would be inevitable and a fact which would have to be accepted. Perhaps this is the lesser of two evils compared with lethal control campaigns.

8.2.3 Wait and See

At present, the status of hybrid lovebirds in Kenya as agricultural pests is minor and their harmful effect on other bird species, although likely, has not been proved conclusively. Furthermore, because of their wide distribution in Kenya today, even the most thorough efforts towards their removal will fail to eradicate them entirely. Therefore, a "wait and see" attitude would not make any difference as far as halting the problem before too late. Perhaps lovebirds will never prove to be enough of a problem to warrant attention.

8.2.4 Conclusions

It should be emphasised that these lovebirds have been introduced to Kenya, are a pest of Kenya's most important cereal crop, are competing with indigenous hole-nesting species and may even threaten the integrity of Kenya's only native Agapornid through introgression. Although it may make no difference to wait and see to what extent the problem increases, it also may not hurt to begin a feasibility study into methods and consequences of their control.

Lethal control campaigns would be the less cost-effective approach to control, leaving exportation as the only feasible option. An investigation into export techniques would be necessary to reduce in-transit mortality to a minimum. Continuous monitoring of the international market would also be desirable to assess any secondary effects of lovebird export on other species. An international approach is recommended to ensure cooperation and the flow of knowledge between countries because the export of birds from one country would be likely to have an effect on birds being exported from neighbouring states. If export proved a feasible control strategy, licences should be issued to the appropriate agencies or individuals.

8.3 FUTURE RESEARCH AT NAIVASHA

The status of lovebirds as a maize pest has been established here. Future research, in my opinion, should concentrate on their effect on other hole-nesting species. This is less quantifiable and a problem requiring a longer period of study. A more accurate estimation of the densities of other hole-nesting species is necessary along with a temporal record of hole use in a restricted study area. This will ascertain the extent of nest usurpation by lovebirds. Further density counts of lovebirds would be advantageous to monitor changes in the population size if no control measures are undertaken.

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Appendix I

Birds recorded in study area between August 1985 and June 1986

Common Name	Scientific Name
Cattle Egret,	*Bubulcus ibis*
Hammerkop,	*Scopus umbretta*
Marabou Stork,	*Leptoptilos crumeniferus*
Hadada Ibis,	*Bostrychia hagedash*
Sacred Ibis,	*Threskiornis aethiopica*
Egyptian Goose,	*Alopochen aegyptiacus*
Secretary Bird,	*Sagittarius serpentarius*
Augur Buzzard,	*Buteo augur*
Long-crested Eagle,	*Lophaetus occipitalis*
Fish Eagle,	*Haliaeetus vocifer*
Black Kite,	*Milvus migrans*
Black-shouldered Kite,	*Elanus caeruleus*
Coqui Francolin,	*Francolinus coqui*
Helmeted Guineafowl,	*Numida meleagris*
Crowned Crane,	*Balearica pavonina*
Blacksmith Plover,	*Vanellus armatus*
Crowned Plover,	*Vanellus coronatus*
Speckled Pigeon,	*Columba guinea*
Ring-necked Dove,	*Streptopelia capicola*
Red-eyed Dove,	*S. semitorquata*
Laughing Dove,	*S. senegalensis*
Hartlaub's Turaco,	*Tauraco hartlaubi*

appendix I contd.

Common Name	Scientific name
Didric Cuckoo,	Chrysococcyx caprius
Klaas' Cuckoo,	C. klaas
Great Spotted Cuckoo,	Clamator glandarius
African Cuckoo,	Cuculus gularis
Red-chested Cuckoo,	C. solitarius
White-browed Coucal,	Centropus superciliosus
Verreaux's Eagle Owl,	Bubo lacteus
*Pearl-spotted Owlet,	Glaucidium perlatum
Speckled Mousebird,	Colius striatus
Narina's Trogon,	Apaloderma narina
*Giant Kingisher,	Ceryle maxima
*Pied Kingfisher,	C. rudis
*Woodland Kingfisher,	Halcyon senegalensis
*White-fronted Bee-eater,	Merops bullockoides
*Lilac-breasted Roller,	Coracias caudata
*African Hoopoe,	Upupa epops
*Green Wood Hoopoe,	Phoeniculus purpureus
*Grey Hornbill,	Tockus nasutus
*Ground Hornbill,	Bucorvus cafer
*Red-fronted Barbet,	Lybius diadematus
Lesser Honeyguide,	Indicator minor
Scaly-throated Honeyguide,	I. variegatus
*Red-throated Wryneck,	Jynx ruficollis
*Nubian Woodpecker,	Campethera nubica

appendix I contd.

Common Name	Scientific Name
*Cardinal Woodpecker,	*Dendropicos fuscescens*
*Grey Woodpecker,	*Mesopicos goertae*
*Bearded Woodpecker,	*Thripias namaquus*
House Martin,	*Delichon urbica*
Striped Swallow,	*Hirundo abyssinica*
African Rock Martin,	*H. fuligula*
Drongo,	*Dicrurus adsimilis*
African Golden Oriole,	*Oriolus auratus*
Black-headed Oriole,	*O. larvatus*
Pied Crow,	*Corvus albus*
Cape Rook,	*C. capensis*
*White-bellied Tit,	*Parus albiventris*
African Penduline Tit,	*Remiz caroli*
Arrow-marked Babbler,	*Turdoides jardineii*
Black-lored Babbler,	*T. melanops*
Black Cuckoo-shrike,	*Campephaga flava*
Common Bulbul,	*Pycnonotus barbatus*
Anteater Chat,	*Myrmecocichla aethiops*
Northern Olive Thrush,	*Turdus abyssinicus*
Yellow-breasted Apalis,	*Apalis flavida*
Cisticola's	*cisticola* spp.
Grey-capped Warbler,	*Eminia lepida*
Red-faced Crombec,	*Sylvietta whytii*
White-eyed Slaty Flycatcher,	*Melaenornis chocolatina*

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Common Name	Scientific Name
Chin-spot Batis,	Batis molitor
Paradise Flycatcher,	Terpsiphone viridis
African Pied Wagtail,	Motacilla aguimp
Tropical Boubou,	Laniarius ferrugineus
Grey-headed Bush-shrike,	Malaconotus blanchoti
Northern Brubru,	Nilaus afer
Black-headed Tchagra,	Tchagra senegala
Fiscal Shrike,	Lanius collaris
Grey-backed Fiscal,	L. excubitorius
Wattled Starling,	Creatophora cinerea
*Blue-eared Glossy Starling,	Lamprotornis chalybaeus
*Ruppell's Long-tailed Glossy Starling,	L. purpuropterus
Red-winged Starling,	Onychognathus morio
*Superb Starling,	Spreo superbus
Beautiful Sunbird,	Nectarinia pulchella
Golden-winged Sunbird,	N. reichenowi
Scarlet-chested Sunbird,	N. senegalensis
Variable Sunbird,	N. venusta
Yellow White-eye,	Zosterops senegalensis
Red-headed Weaver,	Anaplectes rubriceps
White-winged Widow Bird,	Euplectes albonotatus
Yellow Bishop,	E. capensis
Baglafecht Weaver,	Ploceus baglafecht

appendix I contd.

Common Name	Scientific Name
Black-headed Weaver,	*P. cucullatus*
Masked Weaver,	*P. intermedius*
Spectacled Weaver,	*P. ocularis*
Chestnut Weaver,	*P. rubiginosus*
Red-billed Quelea,	*Q. quelea*
Chestnut Sparrow,	*Passer eminibey*
Rufous Sparrow,	*P. motitensis*
Pin-tailed Whydah,	*Vidua macroura*
Red-billed Firefinch.	*Lagonosticta rubricata*
Red-cheeked Cordon bleu,	*Uraeginthus bengalus*
Purple Grenadier,	*U. ianthinogaster*
Yellow-rumped Seed-eater,	*Serinus atrogularis*
Streaky Seed-eater,	*S. striolatus*
Brimstone Canary,	*S. sulphuratus*

*Hole-nesting species