# THE IMPACT OF MAN ON BIRDS OF PARADISE IN THE JIMI VALLEY

CHRISTOPHER J. HEALEY

## INTRODUCTION

In this paper I discuss the impact of man on populations of several species of Birds of Paradise (Paradisaeidae) in the Jimi Valley, Western Highlands area of Papua New Guinea. Although the importance of Bird of Paradise plumes in the cultures of New Guinea people is well known, little systematic attention has been given to the effects of human alteration of habitat and predation on the birds. It is often supposed that the greatest single threat to the survival of Birds of Paradise is the clearing of forest for food gardens to support a growing rural population and to make way for commercial ventures. Some authorities assert that hunting pressure seems to have little impact on the numbers of birds (e.g. Schodde 1973).

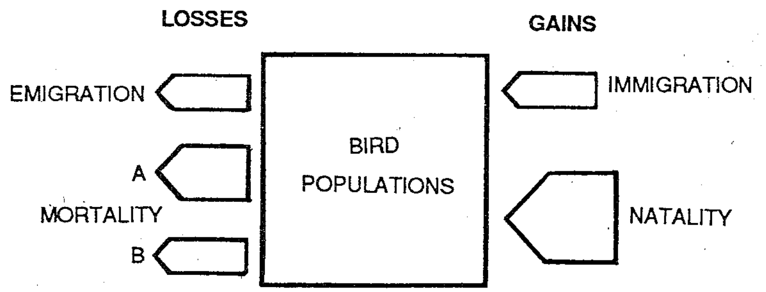
Elsewhere (Healey 1980) I have documented in some detail the regions where Bird of Paradise plumes are most intensively used as items of decoration and ceremonial wealth, and also the extent of the area in which hunting occurs to supply plumes. Plumes are most intensively used in only a few major valleys of the central highlands of PNG, especially the densely populated Simbu and eastern Wahgi Valleys. Relatively little hunting occurs locally in these valleys, as much of the original forest has long given way to grassland and fallow re-growth. Most hunting for plumes occurs in less densely settled areas of the highlands, especially on the northern and southern fringes, and in the surrounding foothills. Complex and extensive trading networks, some hundreds of kilometres long, funnel plumes from numerous peripheral communities towards the limited region of ultimate consumption. There are two consequences of this trading system. First, central highlands can exert a high demand for plumes without intensifying predation locally. This tends to spread hunting pressure over a very wide area. Second, hunting in peripheral areas is stimulated in part by a demand for plumes in central areas of consumption, so that in these supply areas, hunting pressure may actually be increased above the requirements of local demand. In other words, the intensity of hunting in peripheral areas with relatively low human population density is not simply a function of local demographic conditions, but is influenced by demographic and economic factors in distant regions.

These conditions complicate analysis of Bird of Paradise population dynamics. Since man does not depend upon the birds even marginally for biological survival, one cannot treat man and birds as interdependent populations of predator and prey. Hunting by man, unlike other predators, is a cultural activity. As such, models of predator-prey relations developed by Errington (1934), Klein (1970), Krunk (1972), Lack (1966), Mech (1970), Schaller (1967, 1972), Slobodkin (1961) and others are clearly inadequate to describe predation by man on these birds. Nonetheless, such models may have some relevance to the response of bird populations to predation by man.

I adopt Slobodkin's (1961:134ff.) steady state or homeostatic model of populations, in which density-dependent factors tend to control populations around a steady (but not necessarily optimum density) figure. "The effect of predation on the size of the prey populations is either to substitute one cause of mortality for another or to lower the survival at some particular age in the population, or both". Sources cited in the preceding paragraph give empirical support to Slobdkin's model. That the model also applies to Birds of Paradise subjected to predation by man can only remain a working hypothesis in the absence of sufficient data on the ecology and population dynamics of Birds of Paradise.

Predation on the birds to supply the plume trade is both sex- and age-specific: adult males are selected by the hunter, even if females and immature males are taken incidentally for food or in uncontrolled traps. I propose that in populations of Birds of Paradise subjected to selective predation, recruitment and/or loss rates will be adjusted so as to maintain population densities around a steady state. These adjustments should be manifest by age and sex structures differing from those of populations free from human predation. Factors involved in the dynamics of Bird of Paradise populations are illustrated in Figure 1.

FIGURE 1: MODEL OF BIRD OF PARADISE POPULATIONS



Mortality factor A. = loss from age, natural predators, parasites, disease, starvation stress.
Mortality factor B. = loss from human predation.

Similar models applied to populations of large prey species, such as wildebeest (Kruuk 1972), buffalo (Sinclair 1977), and deer (Klein 1970; Mech 1970) can be tested by the reconstruction of age/sex composition over time by the examination of such factors as dentition, height and weight of living and dead animals. Similar analyses of bone and tooth remains have been used to examine the population dynamics of prey species found in archeological remains of human hunters (Smith 1974; Davis and Wilson 1978).

Data on age-specific characteristics of Birds of Paradise are lacking, except for some fragmentary material on captive specimens. Thus there is no basic material to permit a study of the diachronic operation of the model by the examination of the birds themselves. However, one aspect of the model is amenable to diachronic analysis, and that is mortality from human predation.

Non-literate people commonly have impressive memories. Hunting successes told to me in detail provide a means of reconstructing an index of past hunting rates. Remembered kills can be compared for different time periods and be taken as indices of predation rates, using the assumption that standard proportions of actual kills are forgotten. Such comparison can be further refined by proposing that the proportion of forgotten kills increases with time. I hypothesize that human hunting success is partially density-dependent: where birds are common, the hunter is more likely to kill birds; where they are uncommon, he is less likely to exert himself or meet with success. Thus, reconstructions of past hunting rates based on these indices allow me to make inferences about the stability of actual hunting over time, and thus the approximate density of suitable prey (adult male's birds).

The aims of this paper are:

1. To examine the present structure of Bird of Paradise populations in a defined area, and to relate this structure to empirically determined levels of human predation and alteration of habitat in the past.

2. To examine the diachronic operation of the model through a reconstruction of past levels of predation. The effects of this predation on past populations will be inferred in relation to the present relationship between man and birds, as outlined in 1 above.

Methods. This paper is based on 16 months fieldwork in the Jimi Valley. In 1972 I spent three months visiting 13 settlements, including a nine-day stay in Tsuwenkai. Twelve months fieldwork in 1973-74 and another month in 1978 were all spent in Tsuwenkai village. This research was directed towards formulating and testing the model outlined above. This was an anthropological study of the ecology and economics of a regional trade system (Healey 1977). An examination of the hunting of Birds of Paradise to provide plumes for trade provided a focus for the study. An attempt was made to discover the dynamic operation of the trade system and its local basis in the production of plumes, by adding a time dimension.

All quantitative data and ornithological material reported here were obtained during 1973-74. Data on human interaction with Birds of Paradise were obtained by observations and conversations on bird lore. In addition, I collected detailed histories of hunting of valuable birds and mammals from 57 resident adult men. These records, which stretch back to the 1920s, provide data to reconstruct past predation rates. In addition, with the help of three local assistants, I kept a record of all kills of Birds of Paradise in Tsuwenkai during the year.

Eleven men were questioned in detail about their hunting of female-plumaged (i.e. adult females and immatures, either male or female) Birds of Paradise, since the 57 hunting histories concentrate mainly on adult males killed.

During 1973-1974 a record was kept of the location and altitude of all Birds of Paradise seen or heard. I also noted similar records provided by my three full-time field assistants, and selected other informants if I judged their reports to be reliable. Of particular value were the reports of one of my assistants, Lucien Yekwai, a local hunter of considerable skill, and an acknowledged village expert on natural history. All these records by age, sex, or plumage-type, were entered onto a map (scale 1:20000) which had been prepared from air photographs prior to my 1973-74 fieldwork. The map was divided into 400 $m^2$ grids which, in conjunction with a dense pattern of ridges and streams, allowed for fairly accurate placement of records in most cases.

Over the 12 month period of fieldwork I made numerous single day excursions to various parts of Tsuwenkai territory, as well as several extended drier-season trips lasting up to four days. For these latter, six forest camps were established (see Map 2 in Appendix).

The rugged terrain, poor visibility in the forest, and constraints of time and other duties prevented me from developing appropriate techniques for censuses along transects. However, I established three census areas (Map 2) within which I attempted to record all individuals of two species of Birds of Paradise. Area 1 was a strip 200 m wide and 800 m long, spanning the boundary between primary and secondary forest. Areas 2 and 3 were deep in the primary forest. Area 2 was 16 ha in extent and 400 $m^2$, located at the bottom of a major valley. Area 3 included Area 2, but extended 2000 m to the ridge-crest at about 2450 m, and was 80 ha in area.

I was unable to make a conclusive test of the model of bird populations as the amount of quantitative data gathered on birds remained limited. The necessity of gathering a broad range of ethnographic material to discover the cultural use and management of Birds of Paradise precluded more exhaustive censusing or the use of more time-consuming techniques for observing and recording ecological data on birds.

## THE ENVIRONMENT

Location of the Study. This study was based in the village at Tsuwenkai, Western HIghlands Province, PNG, which is inhabited by the Kundagai people who speak the Maring language. The village centre lies at 5°25'S, 144°38'E, at an altitude of 1680 m on the north wall of the Jimi Valley (see Map 1 in Appendix). The village is accessible only by foot track which connects to a mission airstrip several hours walk away. A vehicular road to link the village with major highland centres was being built with local labour in the 1970s. It is possible this project will never be completed.

Tsuwenkai lies close to the crest of the Bismark Range, extending westward from Mount Wilhelm (4509 m). The range forms the northern wall of the Jimi Valley, which is separated from the densely populated Wahgi Valley to the south by the Sepik-Wahgi Divide, which rises to over 3700 m in places. The Jimi River rises on the north-west slopes of Mount Wilhelm and flows roughly west-north-west in the northern part of the valley to drain into the Sepik River. The Jimi thus provides a corridor from the northern lowlands into the central highlands. The total area of Tsuwenkai territory is 25 km$^2$.

Climate. The average yearly rainfall, for a six year period, at Tabibugo government station south of the Jimi is 3124 mm. The Tsuwenkai rainfall is probably somewhat higher. Rain is rather seasonal, the wetter period lasting from November to April, the drier period from May to October.

Temperatures show no clear seasonal variation. The average daily maximum recorded during fieldwork at Tsuwenkai was 23°C, and the average minimum, 15°C.

Terrain. Tsuwenkai and environs are located in the valley of the Kant, a major feeder stream of the Jimi. The Kant Valley is narrow, with short, steep, lateral spurs and intervening streams. Tsuwenkai territory ranges in altitude from about 1220 m to abut 2800 m. The loose shales and clays are prone to landslips, even in primary forest.

Vegetation and Ecological Zones. Four major ecological zones can be delineated, each characterized by particular floral communities.

1. The montane zone extends down from the mountain peaks to the forest edge, mainly between 1700 and 1850 m. Most of this zone is of mixed floristic composition, although *Castanopsis* and *Lithocarpus* oaks are common at the lower edge, and *Nothofagus* beech on some of the highest peaks. Informants stated that oak forest formerly extended to lower altitudes, before being cleared to make way for food gardens. Montane forest has a more or less continuous canopy about 30 m or more above the ground. One, usually two, substages are present. The ground level is fairly clear, except below openings in the canopy. The montane zone covers 16 km$^2$ or 64% of the Tsuwenkai area.

2. Below this zone lies the zone of human habitation. This is a patchwork of secondary forest in all stages of development, food gardens, small coffee plantations, homesteads, and groves of ornamental and shade trees. The following subzones can be identified.

Secondary forest: ranging from tall forest merging into primary montane forest to lower, more open-spaced woodland on drier sites. Secondary forest approaches the characteristics of montane forest in 40 to 70 years after initial clearing.

Bush fallow: composed of lower, scrubbier growth. This may reach a height of 18-20 m in six years, and if left uncleared will develop into secondary forest.

Homesteads: coffee and casurina groves: these tend to be semi-permanent sites, dominated by planted vegetation. Tall secondary forest trees may also shade these areas, and provide attraction for birds when in fruit or flower. Tsuwenkai village consists of about forty home-steads or single house sites scattered for 2 km on the west flank of the Kant valley.

These three subzones together cover about 5.8 km$^2$ (23.2% of the total area).

Gardens; the Kundagai practise slash and burn agriculture, clearing gardens mainly from secondary forest. Gardens are kept in production from a little over one year to two years after planting. The average fallow period for garden sites is 15-16 years (range 6-16 years (range 6-22 years, mode 12 years). Excluding small homestead gardens, the total area under production in 1974 was about 0.5 km$^2$ or 2% the total area.

3. The third major zone is grassland, comprising some 2 to 2.5 km$^2$ or 9% of the total area. Grassland is interspersed in the zone of human habitation, and is more extensive in the southern part of the area, towards the Jimi. Oral traditions indicate that most of this grassland has been stable for 200 years.

4. A fourth zone is found in lower altitudes beyond Tsuwenkai territory. This is lower montane rainforest, which is extensive near the Jimi itself.

Birds of Paradise are found in all these zones except the grassland. Of the thirteen species recorded in Tsuwenkai, six are confined to the montane zone, five occur in both montane and human habitation zones, and two are confined to the latter, but extend to the lower montane zone beyond Tsuwenkai (Table 3). Narrow strips of grassland do not act as barriers to the movement of Birds of Paradise. However, extensive grasslands beyond Tsuwenkai's southern borders may have prevented the entry of the Lesser Bird of Paradise *Paradisaea minor* into the lower altitude secondary forest. This species is common elsewhere in the Jimi Valley (Healey 1978b).

Effect of Human Activity on the Environment. Under the present agricultural regime, there appears to be no expansion of the zone of human habitation. Until recently, there was probably some shrinkage following population decline through epidemics in the

1940's and 1950's. The collection of wild plants for building and other purposes, and foraging domestic pigs undoubtedly affect the speed of regeneration and the floristic composition of secondary forest, in more accessible parts of primary forest. Fires spreading from garden sites also damage the adjacent forest, and help maintain grassland communities.

This apparently stable situation may not continue long, as Kundagai population growth appears to be accelerating. Although reserves of secondary forest in excess of present needs will allow for the expansion of food gardens to feed the growing population, new clearing of primary forest may eventually become necessary. This situation may be hastened as increasing areas of land are lost to subsistence agriculture by the planting of semi-permanent groves of coffee as a cash crop in old garden sites.

The population of Tsuwenkai in 1974 was 304 people. The overall population density is 12 people per km², while the density of people to area of land currently under cultivation and fallow is 48. These densities are low by New Guinea highlands standards. I estimate that with present agricultural techniques, the Tsuwenkai area could support almost double the present population. My data are insufficient for suggesting when this growth might be achieved.

For the present, the Kundagai consider that they have sufficient agricultural land. They are generally reluctant to bring large areas of primary forest into production, as these are harder to clear and do not give such high yields as gardens cut in secondary forest. The clearing of some areas of forest, believed to be the abode of ancestral spirits, is specifically tabooed (see Healey 1977: 83-92 for a fuller discussion of these issues).

## HUNTING AND ITS REGULATION

The Kundagai are divided into several clans. Clans and their sub-divisions are important land-owning groups. Three clans jointly own most of the land north of Renmapai Creek and east of the Kant River. The land between Renmapai and Punk Creek is owned by a fourth clan. All four clans have equal rights of access to the land south of Punk Creek.

The Kundagai use the plumes or skins of 53 species of birds in their head-dress decorations on festive or ritual occasions. Nine of these species are Birds of Paradise, all but one of which occur in Tsuwenkai forests. Most plumes are obtained by gift or loan from friends and relatives, or by trade. Bird of Paradise plumes and other forest products are the only resource locally available to the Kundagai which are valuable trade items and in high demand elsewhere in the highlands. They are therefore heavily involved in both hunting to provide plumes for trade, and in importing plumes from their northern and western neighbours, and re-exporting them towards the central highlands to the southeast. In return they receive steal tools, decorative shells, live pigs, and money.

No one in Tsuwenkai owned a gun, and all hunting involved bow and arrow or trap. Birds of Paradise are shot or trapped at fruiting trees or at baits set by the hunter. Baits used are the fruit of the *Trichosanthes* vine or the wild banana (*Musa* sp). Hides are sometimes built in the branches of fruiting trees and beside baits. Birds are also shot from hides at forest pools and display trees.

Most hunting occurs in the drier season, mainly for reasons of comfort. Some men do not enjoy hunting, and many lack sufficient skill and knowledge to make it a rewarding pastime. Of the approximately 70 men of active hunting age (15 to 55 years), only 11 are considered by the Kundagai to be particularly skillful and successful.

A Kundagai may ideally hunt in any part of Tsuwenkai land, including areas not owned by his own clan. However, he may only kill valuable birds on land owned by his own clan. The species considered valuable are listed in Table 1.

TABLE 1. RESTRICTED GAME IN TSUWENKAI

Species which may be killed only on the clan land of the hunter.

| | |
|---|---|
| *Casuarius bennetti* | Dwarf Cassowary |
| *Charmosyna papou* | Papuan Lorikeet |
| *Epimachus meyeri* | Brown Sicklebill |
| *Epimachus fastosus* | Black Sicklebill |
| *Astrapia stephaniae* | Stephanie's Astrapia |
| *Lophorina superba* | Superb Bird of Paradise |
| *Pardisaea minor* | Lesser Bird of Paradise (Not present in Tsuwenkai) |
| *Pteridophora albertii* | King of Saxony Bird of Paradise |

In addition to confining his hunting of these species to his own clan land, a man may lay personal claim of ownership to Birds of Paradise he discovers. Usually he claims such birds at their display trees. Consequently, some hunters inadvertently kill birds that have been claimed by others, and become involved in informal court cases.

Sites where generations of birds have displayed communally are a valuable resource for their finder, as birds can be killed over extended periods. Such sites may be passed on to sons on the death of the owner. The only species displaying communally in Tsuwenkai is Stephanie's Astrapia *Astrapia stephaniae* although display sites of the Lesser Bird of Paradise *Paradisaea minor* are widespread at lower altitudes.

Most highly successful hunters tend to concentrate their hunting in a favourite area that they know well. Such men owning *Astrapia* display sites, for example do much of their hunting for other species in the vicinity of display sites. These favoured areas are know to most other Kundagai, who rarely seek valuable birds there on the assumption that they have already been discovered and claimed. Favoured hunting regions of successful hunters in effect become *de facto* personal hunting territories. In 1974 the Kundagai recongised six such territories, owned by eight men (two territories being jointly owned by two men each). Together, these territories comprised about one fifth of all montane forest.

Whilst territorial restrictions limit the number of hunters who may operate in some areas, various other restraints apply to all hunters. The fear that forest-dwelling spirits will be angered and send sickness on the hunter who kills too much game on any expedition possibly acts as a limit on the bag of hunters. Perhaps more importantly, the Kundagai adopt various restraints for reasons of conservation. Many hunters consider it unwise to kill all adult male Birds of Paradise in a region, and female-plumaged and immature male birds are often spared by hunters. These measures are to ensure a continued breeding stock to produce plumed males for the future.

The Jimi Local Government Council, established in 1966, has adopted traditional rights and restrictions as rules for hunting valuable birds. The Council has also endorsed the national law forbidding the killing of Birds of Paradise by other than traditional means.

## EFFECTS OF HUNTING RESTRICTIONS ON INTENSITY OF PREDATION

The number of active hunters operating in an area must have some effect on hunting productivity. Where there are many hunters in a given area of hunting land their effects on prey populations will no doubt be greater than where there are few. Many hunters combing the area for game are more likely to secure a high total bag than a few, even where each individuals has limited success as game becomes scarcer through intensive predation. By contrast, where the ratio of hunters to area of hunting land is low, individual hunters can achieve high productivity while the total bag of all hunters remains relatively low. In short, predation may be extensive rather than intensive.

These propositions can be examined by a comparison of hunter:land area ratios in several different Maring territories, using data set out in Table 2. This table compares ratios of males over 15 years of age to areas of primary forest in nine village territories (see Map 1 for locations). The actual ratio of hunters to forest land will be lower than indicated for two reasons. (1) population figures include small numbers of absentee males and (2) include old men who no longer hunt. I can correct for these factors only in the case of the Tsuwenkai population. Nonetheless, these ratios can serve as an index of the maximum potential hunting pressure expressed as the number of hunters operation in a given area.

Assuming game is equally dense in all territories listed,it is evident that game will be subjected to less intensive predation in Tsuwenkai because there are fewer hunters there. The inference is that each hunter in Tsuwenkai, having a larger area in which to hunt, competes less with his fellow hunters, and thus may be able to secure more birds in a given time. Men of all settlements probably have roughly equal demands on their time to participate in social and subsistence activities. This places an upper limit on the amount of time they are able to devote to hunting. Tsuwenkai hunters may be more inclined to approach the maximum time available for hunting, because the returns will be greater, making hunting a more rewarding activity in economic, nutritional and psychological terms.

TABLE 2: Ratio of Hunters to hunting land in Maring communities[1]

| Population | Numbers of hunters | Area of primary forest in km² | No of hunters/km² |
|---|---|---|---|
| Tsuwenkai[2] | | | |
| a. | 58 | 16.0 | 3.8 |
| b. | 89 | 16.0 | 5.6 |
| Tsembaga | 68 | 3.9 | 17.4 |
| Mondo | 81 | 5.9 | 13.7 |
| Gai | 125 | 4.4 | 28.4 |
| Nimbra | 97 | 4.3 | 22.6 |
| Tsenggamp | 57 | 5.6 | 10.2 |
| Kompiai | 315 | c.2.7 | c.116.7 |
| Total | 832 | 42.8 | |
| Mean | 118.9 | 6.1 | 19.5 |

Note: 1 For sources see Healey 1977:235
2 a. = resident population in November 1974;
2 b. = resident population plus absentee males. The latter to be compared with other populations.

Since the amount of hunting time is similarly limited in all settlements, it also follows that game is subjected to less hunting pressure where the density of hunters is low. For example, six Tsuwenkai per square kilometre of hunting land will have to work much harder to exert the same hunting pressure in the same period of time as 117 in Kompiai.

Aside from the time available for hunting and competition from other hunters, the efficiency of a hunter is further limited by his knowledge of game, skill in hunting techniques, and the efficiency of his weapons. Available time and other limitations set an upper limit on the productivity of hunting. Where the ratio of hunters to hunting land is high, these additional limitations become less significant in reducing hunting pressure. Where the ratio of hunters to hunting land is low, as in Tsuwenkai, additional limitations become more important in reducing overall hunting success, so that while each hunter may be highly productive, the sum of all hunter's efforts is lower. This may be so even if the total number of prey killed by each hunter exceeds the total killed by each man in populations with a high hunter to area ratio, because prey species may remain more numerous, in turn sustaining continued high productivity.

The assumption of an even distribution of game is, however, false, and the preferred prey varies in relation to what is locally available. Feral pigs and large lower montane marsupials are especially sought in all territories other than Tsuwenkai listed in Table 2. These animals are absent from Tsuwenkai, where hunters concentrate on montane forest marsupials and birds. I have no good data on relative abundance of game animals in different territories. Informants' subjective opinions nonetheless offer a rough guide.

Kompiai men told me that Birds of Paradise were less numerous in their territory than in Tsuwenkai. In a survey of the contribution of game to the diet, Buchbinder (1973:132) found that those questioned had eaten little meat in the week prior to her investigation, and that all had been from small animals, rather than the preferred larger prey. Such small game appeared fairly common according to Nimbra and Tsenggamp people, but the Gai people, with a higher ratio of hunters to land, said there was little game available and apparently had difficulty in locating it. By contrast, the Kundagai consider that their preferred prey species are mostly quite common, and while a hunter may not always find what he is searching for, he seldom has much difficulty in locating game of some sort. His problem, rather, is actually killing it.

This material is inconclusive but lends some support to the hypothesis that game is more plentiful, and individual's hunting productivity is greater, in those territories where there is a low ratio of hunters to land area.

Aside from these demographic effects on the intensity of predation, other factors serve to reduce hunting pressure in all territories. It is questionable whether fear of spirit anger actually inhibits a hunter enjoying good fortune. However, despite often considerable knowledge of his prey and skill in hunting techniques, the simple technology of hunting often leads to failure.

Since little hunting occurs in the wetter months, Birds of Paradise suffer little molestation from man during their breeding season, and annual recovery rates of their population are not directly affected by human activity.

I conclude that various hunting restrictions outlined in the preceding section tend to limit human predation. Joint rights held by members of a group to hunt valuable birds in certain areas, the exclusive rights of individuals to hunt at certain sites or make use of hides or baits they have constructed, and *de facto* personal hunting territories, all limit the number of men who may hunt in certain areas or at specific sites. This results in a reduction of the intensity of hunting to which birds may be subjected.

Voluntary restraints on killing female and immature male birds, and the practice of leaving some adult males alive at a communal display site may have beneficial effects aside from limiting the number of birds shot. Sparing female-plumaged birds helps maintain the reproductive pool of females and the number of immature males to reach maturity.

There is no direct evidence for the benefits of hunting techniques and restrictions in limiting the intensity of predation. There is some inferential evidence for reduced hunting pressure at communal display sites of *Astrapia*, as noted below. However, in the absence of comparative material from human communities that do not observe the restrictions summarised here, it is not possible to demonstrate the conservatory benefits of these beliefs and practices.

## DISTRIBUTION AND BREEDING BIOLOGY

Here I make some general remarks on the distribution of Birds of Paradise and aspects of nesting display and moult. More detailed species accounts are given in the section on effects of human predation on populations.

TABLE 3: Paradisaeidae of Tsuwenkai

| Species | Habitat[1] | Altitudinal range (m) | Status | Hunting[2] |
|---|---|---|---|---|
| *Loria loriae* | Second,montane | 1660-2070 | Common | - |
| *Loboparadisea sericea* | Second,montane | 1700+ | ? | - |
| *Manucodia chalybatus* | Second | 1620-1640 | Uncommon | - |
| *Paradigalla brevicauda* | Montane | 1800-1900 | ? | - |
| *Epimachus fastosus* | Montane | c2000+ | Very rare | (+) |
| *Epimachus meyeri* | Montane | 2060-2250 | Rare | (+) |
| *Astrapia stephaniae* | Montane | 1630-2250 | Common | + |
| *Parotia carolae* | Second,montane | 1730-2000 | Common | (+) |
| *Parotia lawesii* | Second,montane | ?1730-2000 | Uncommon | (+) |
| *Lophorina superba* | Second,montane | 1450-2200 | Common | (+) |
| *Diphyllodes magnificus* | Second | 1450-1600 | Common | (+) |
| *Pteridophora alberti* | Montane | 2050-2400+ | Common | + |
| *Paradisaea rudolphi* | Second-montane edge | 1700 | Rare | (+) |

Notes: 1. Second = second growth; montane = primary montane forest.; 2 Intensity of hunting pressure: + = adult males activity sought for plumes; (+) = plumes used by little deliberate hunting; - = plumes not used, no special hunting efforts.

Distribution and Biological Cycles of Birds of Paradise in Tsuwenkai. There are least 13 species of Birds of Paradise in Tsuwenkai land (Table 3). Like other birds, all may be killed for food. The plumes or skins of eight species are used in decorations, but only three species are deliberately sought for their plumes and subjected to intensive predation of adult males.

Only two of the locally represented Paradisaeidae are lower lowland montane species: *Manucodia chalybatus* and *Diphyllodes magnificus*. Other low altitude forms are found in neighbouring areas: *Manucodia keraudrenii, Cicinnurus regius*, and *Paradisaea minor*.

Diamond (1972) has noted some sorting by sex and age in the altitudinal range of the general *Loria, Loboparadisea, Epimachus, Lophorina, Diphyllodes* and *Pteridophora*. Displaying males tend to be concentrated in the upper part of the range with females in the lower part. Immatures are often most common in the lowest reaches of the range. I noted similar segregation by sex in Tsuwenkai of *Lophorina* and, most clearly, in *Astrapia*, where adult males appear to be confined to the top 200 m of the range, females and immatures being found throughout the 630 m range of the species.

Birds of Paradise are largely frugivorous, although some species feed on invertebrates and small vertebrates also. My data on the diet of birds derives mainly from information provided by Kundagai hunters, who listed local names for trees and shrubs at which Birds Paradise fed (Table 4). The list is probably incomplete, especially for those species not hunted for their plumes. It is possible that there are significant differences (unknown to the Kundagai) in the diet of the two *Epimachus* and two *Parotia* species. Even given these shortcomings, the table suggests that *Pteridophora* has the most restricted diet (one recorded fruit food) and *Lophorina* the most diverse diet (fourteen fruit foods). In terms of the variety of fruits available, the food supply is roughly constant throughout the year, with perhaps a slight peak in supply with the onset of the drier season.

TABLE 4: Fruit eaten by paradisaeidae in Tsuwenkai[1]

| Bird Species | Fruit Family | Genus &/or Species | Form | Fruiting time[2] |
|---|---|---|---|---|
| *Loria loriae* | Araceae | | Wild taro | A |
| | Urticaceae | *Cypholophus* | Tree | ? |
| | | *Maoutia* | Tree | A |
| | | *Procris* | Tree | ? |
| *Paradigalla brevicauda* | Araceae | | Wild taro | A |
| | Musaceae | *Musa* | Wild banana | A |
| | Palmae | *Calamus* | Palm | A |

TABLE 4 cont: Fruit eaten by paradisaeidae in Tsuwenkai[1]

| Bird Species | Fruit Family | Genus &/or Species | Form | Fruiting time[2] |
|---|---|---|---|---|
| *Epimachus fastosus/ meyeri* | Araceae | | Wild taro | A |
| | Araliaceae | *Schefflera* | Tree | D |
| | Cucurbitaceae | *Trichosanthes* | Climber | A |
| | Ericaceae | *Rhododendron macgregoriae* | Tree | D |
| | Musaceae | *Musa* | Wild banana | A |
| | Pandanaceae | *Freycinetia* | Climber | A |
| | | *Freycinetia* | Climber | ? |
| | Rubiaceae | *Timonius* | Tree | A |
| *Astrapia stephaniae* | Araceae | | Wild taro | A |
| | Araliaceae | *Schefflera* | Tree | D |
| | Cucurbitaceae | *Trichosanthes* | Climber | A |
| | Ericaceae | *Rhododendron macgregoriae* | Tree | D |
| | Musaceae | *Musa* | Wild banana | A |
| | Pandanaceae | *Frycinetia* | Climber | A |
| | Rubiaceae | *Timonius* | Tree | A |
| | Ulmaceae | *Trema orientalis* | Tree | A |
| | Unident | | Tree | D |
| *Parotia carolae/ lawesii* | Araliaceae | *Schefflera* | Tree | D |
| | Cucurbitaceae | *Trichosanthes* | Climber | A |
| | Euphorbiaceae | *Homolanthus* | Tree | W,I |
| | Palmae | *Calamus* | Palm | A |
| | Pandanaceae | *Freycinetia* | Climber | D |
| | Piperaceae | *Piper* | Tree | A |
| | Sapindinaceae | *Harpullia* | Tree | D |
| | Ulmaceae | *Trema orientalis* | Tree | A |
| | Urticaceae | *Maoutia* | Tree | A |
| *Lophorina superba* | Araceae | | Wild taro | A |
| | Araliaceae | *Schefflera* | Tree | D |
| | Cucurbitaceae | *Trichosanthes* | Climber | A |
| | Ericaceae | *Rhododendron macgregoriae* | Tree | D |
| | Euphorbiaceae | *Homolanthus* | Tree | W,I |
| | Musaceae | *Musa* | Wild banana | A |
| | Myrtaceae | *Decasperum* | Tree | I.W |
| | Palmae | *Calamus* | Palm | A |
| | Rubiaceae | *Timonius* | Tree | A |

TABLE 4 cont: Fruit eaten by paradisaeidae in Tsuwenkai[1]

| Bird Species | Fruit Family | Genus &/or Species | Form | Fruiting time[2] |
|---|---|---|---|---|
| *Lophorina superba* cont: | Rutaceae | *Evodia crispula* (&/or Sapindinaceae q.v.) | Tree | D |
| | Sapindinaceae | *Arytera* (or Rutaceae q.v.) | Tree | ? |
| | | *Harpullia* | Tree | D |
| | Ulmaceae | *Trema orientalis* | Tree | A |
| | Urticaeae | *Maoutia* | Tree | A |
| *Diphyllodes magnificus* | Piperaceae | *Piper* | Tree | A |
| | Ulmaceae | *Trema orientalis* | Tree | A |
| *Pteridophora alberti* | Rubiaceae | *Timonius* | Tree | A |
| *Paradisaea rudolphi* | Araliaceae | *Schefflera* | Tree | A |
| | Musaceae | *Musa* | Wild banana | A |
| | Piperaceae | *Piper* | Tree | A |
| | Ulmaceae | *Trema orientalis* | Tree | A |

<u>Notes</u>: 1 All identifications are tentative. No species were collected, but identifications were made by matching Kundagai names for plants to vernacular names listed against scientific determinations (by the National Division of Botany) provided by W. Clarke (personal communication and 1971), Manner (1977) and Rappaport (1968).

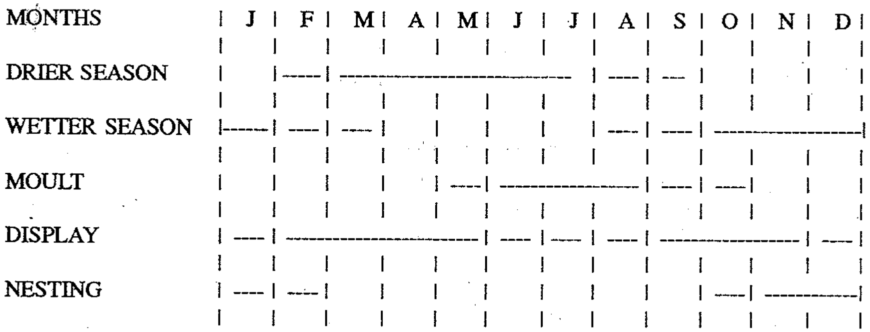
2 Symbols: A = at any time during the year; D = in drier season; W = in wetter season; I = between seasons.

Diamond (1972: 86) states "that breeding is almost entirely confined to times of local wet conditions in most (New Guinea) fruit-eating birds", including Birds of Paradise. I found no evidence of breeding during extended visits to the forest, which occurred mainly in the drier season. Informants claimed that all Birds of Paradise, along with most other birds, breed in the wetter season. Various men claim to have found nests, or seen juveniles being fed, of *Epimachus meyeri, Astrapia stephaniae, Parotia carolae, Lophorina superba* and *Pteridophora alberti*. Only one egg, nestling or juvenile was seen in each case, and all sightings were confined to the wetter season, especially between November and February. Female birds are said to care for fledglings until about May or June. The few such records suggest that the Kundagai seldom encounter evidence of breeding, supporting the claim that the birds breed in the wetter season, when hunting activity is diminished.

Displays I have observed in five species (*A. stephaniae, P. carolae, L. superba, D. magnificus* and, elsewhere in the Jimi, *Paradisaea minor*) all indicate that the behaviour may occur in the absence of females. Such displays may be territorial in solitary displaying species, and to determine a dominance hierarchy in communal-displaying species, and perhaps also among those species occupying exploded arenas (display sites of solitary males in auditory contact, [Gilliard 1969]). The occurrence of display does not therefore necessarily indicate that breeding is imminent or in progress. The Kundagai claim that displays continue throughout the year. However, the intensity of display does seem to vary over the year. Several *Diphyllodes* males displaying within earshot of my house increased the vocal intensity and frequency of display with the onset of the wetter season. On the basis of limited observations of *Astrapia* in the drier season months of July, August and September, it appears that display activity declines in the latter month when the birds are in moult immediately preceding the wetter season. Draffan (1978) noted a similar decrease in display activity in *Paradisaea guilielmi* preceding the wet season on the Huon Peninsula.

Informants state that Birds of Paradise moult their ornamental plumes from about the winter solstice in June, and that moult is complete by the summer solstice. I have seen evidence of moult in *Astrapia* (missing central tail feathers in September), *Parotia* (missing a pair of occipital plumes in October) and *Pteridophora* (one occipital plume not reached full length in August). None of these records is conclusive, although made prior to breeding, when moult of ornamental plumes might be expected Figure 2 depicts the biological cycle of Birds of Paradise.

FIGURE 2: Timing of nesting, moult and display in Birds of Paradise at Tsuwenka



<u>Effects of Forest Clearing on Distribution.</u> Before Tsuwenkai was settled by pioneering immigrants about 50 years ago there was only a small human population and much of the present zone of human habitation was under primary forest. South of Danmarak Creek clearing for food gardens on the western slopes of the Kant and Pint Valleys has destroyed all primary forest from near the valley bottoms up to 1700-1850 m. Prior to this clearing, various mid-montane Birds of Paradise probably occupied the more extensive forests.

Schodde (1973: 138) states that *Epimachus meyeri*, *Astrapia stephaniae* and *Pteridophora* are largely confined by habitat preference to montane forests above the frostline, which he identifies at about 2200 m. He concludes that their habitat is seldom encroached upon by agriculture, and that habitat availability is therefore not a limiting factor in their distribution. While it is true that sharp ground frosts are a critical climatic factor in limiting the upward spread of subsistence agriculture, the actual level at which this occurs varies with climatic and topographic influences, from about 1980 m to almost 2600 m (Brookfield 1964). My own data indicate that the three species mentioned by Schodde extend well below 2200 m (see also Diamond 1972) and might therefore be in danger of encroachment by agriculture. Schodde's remark is based upon the present distributions of these species, which are best known from the mountain ranges flanking the densely populated Wahgi Valley. I would suggest that these birds are confined above the frostline not by habitat preference as Schodde argues, but because human interference in the form of agriculture and intensive hunting have forced them to retreat to the higher ranges.

Clearing of Tsuwenkai forests below 1800 m has undoubtedly reduced habitat availability. Thus, with the extensive destruction of oak forest in the Kant Valley *Paradisaea rudolphi* is now confined to a few remaining stands of oak at the edge of the montane zone. An increase in inter-specific competition may have attended the compression of the montane zone, with some species squeezed out of habitat occurring within their altitudinal range. This may explain the confinement of *Epimachus fastosus* to the highest ranges which support greater altitudinal belts of montane forest with sufficient habitat to support this species and its congener, *E. meyeri*. As the forest edge was extended upwards, and oak forest destroyed, *E. fastosus* may have been eliminated. This scheme is supported by informants' statements that both *Epimachus* species were formerly more common, and were found close to settlement areas and therefore at lower altitudes before forest clearing was so advanced.

Similar, but downward, compression of habitat may explain the absence of *Paradisaea minor* from Tsuwenkai, even though there are relict patches of advanced secondary forest within its altitudinal range.

*L. superba*, *D. magnificus* and, to a lesser extent, *Parotia carolae*, are well adapted to secondary growth, and may have benefited by the increase in disturbed habitat, as have *Paradisaea raggiana* and *P. minor* elsewhere (Diamond 1972; Healey 1978b). These three species are found in young fallow, and even visit taller trees shading homesteads and coffee groves, although they appear to require fairly well-advanced secondary forest for display and nesting sites.

There is little present need to clear additional primary forest, although this may become necessary in the future. I detected no obvious increase in forest clearing over the period 1974 to 1978. Encroachment of agriculture on montane forest is most liable to affect distribution of *Paradigalla*, *Loboparadisea*, *Astrapia* and *Pteridophora*. However, much of the montane zone has little or no agricultural potential under present Kundagai methods of production, and unless disturbed by forestry or mining, extensive areas of habitat will remain. Under these conditions, hunting assumes importance as a possible limiting factor on bird population.

## EFFECTS OF HUMAN PREDATION ON BIRD POPULATIONS

There are no published comparative data on the population ecology of Birds of Paradise. The effects of intensive age- and sex-selective human predation on population dynamics cannot therefore be assessed by comparison with unmolested control populations of the same species. However, comparison with other species of Birds of Paradise in Tsuwenkai give some indication of the effects of intensive and selective predation. None of these control species is totally free from human predation, although hunting pressure is low, and there is little if any selectivity of adult males over immatures and females in contrast to hunting of valuable birds. Since my data on control populations of Birds of Paradise are limited, I also use data on several species of Neotropical birds with apparently similar ecological requirements and behaviour patterns to Birds of Paradise.

Various studies have shown unequal sex ratios among Passerines. Tertiary sex ratios (among fledged birds) are generally unequal in favour of males (Dow 1973; Mayr 1939; Selander 1965). Dow (1973) and Selander (1965) note that sex ratios may vary between different locations and seasons for one species. Dow also reviews some of the problems in accurately determining tertiary sex ratios in the field, even in sexually dimorphic species. Both Dow (1973) and Selander (1960) conclude that, contrary to the general Passerine trend, unequal sex ratios in favour of females do occur, but that they are largely confined to polygynous or promiscuous breeding species. Gilliard (1969) considers that most of the sexually dimorphic species of Birds of Paradise are polygynous. It is not clear if he intends the restricted meaning for this term of the male forming a pair-bond with several females. Field observations suggest that at least one communally displaying species, *Paradisaea decora*, is actually promiscuous with no pair bonding, and a single female may copulate with several males (LeCroy *et al.* 1980), and this may be a general pattern among sexually dimorphic species with elaborate displays.

Selander (1965) notes that delayed maturation is common in non-monogamous breeding species, although females generally breed at a younger age than males. This is presumed to occur in Birds of Paradise (Gilliard 1969), where males are thought to take at least 5 years to attain full adult plumage. In captivity, males of *Paradisaea rubra* are known to take at least 6 years to attain adult plumage (Frith 1976), while G. George (per. comm.) suggests that 7 years may be a more realistic estimate for most species. There is evidence (reviewed below) that males are capable of breeding while in sub-adult plumage. There are no indications of when females achieve sexual maturity. Since in their first few years immature males are indistinguishable in plumage from females, one cannot determine secondary or tertiary sex ratios in Birds of Paradise by sight. In the following discussion I therefore deal with plumage-type ratios (adult male-and-female-type plumage) as indices of tertiary sex ratios.

Clutch size is not known in many Birds of Paradise species. Most species seem to lay a single egg, but in the genera *Manucodia, Phonygammus, Ptiloris, Cicinnurus,* and *Diphyllodes* two eggs are laid, while at least three *Paradisaea* species lay one or two eggs (Cooper and Forshaw 1977). With the exceptions of *Diphyllodes magnificus* and *Paradisaea rudolphi*, all Birds of Paradise in Tsuwenkai probably lay a single egg, as Kundagai testimony also suggests. Informants were of the opinion that each female lays only one egg each breeding season.

Populations Free from Intensive Predation. From these considerations a theoretical model of the structure of unmolested Bird of Paradise populations can attempted. In a population of adult birds with an equal sex ratio the plumage-type ratio will also be equal. For purposes of model building I make a series of assumptions: 1). that there is an equal mortality of the sexes at all ages; 2). that each adult female rears one young each year, and 3). that the sex ratio of nestlings is equal from which it follows that the tertiary sex ratio will remain equal while the plumage-type ratio will be biased in favour of female-type because of delayed maturity in males. If females breed at younger ages than males, then the sex ratio for breeding birds will be biased in favour younger of females and unequal plumage-type ratios will be further accentuated by younger females producing chicks while their male age-mates are still in female-type plumage.

Clearly these assumptions are invalid for wild populations. In particular, mortality will tend to reduce the number of female-plumaged birds, as mortality in birds is commonly highest within the first year of life (Lack 1966). Destruction of unhatched eggs and nestlings is particularly high especially in the tropics where snakes are the major predators (Skutch 1966).

The following notes give details on sightings of species not subjected to intensive predation with particular attention to plumage-type ratios. Sight and call records include some birds noted only by assistants accompanying me on forest surveys. I also list reports of birds seen or heard by my assistants or others on other occasions. All records other than my own are included only if I could plot the birds onto a map of locations with reasonable accuracy. These records are compiled over the twelve months from November 1973. My own observations and opinions of Kundagai experts on bird lore indicate that individuals of most sexually dimorphic species are relatively sedentary. Birds repeatedly seen in the same locality were therefore treated as the same individual. Clearly there remains a danger of counting an individual more than once. I cannot claim to have eliminated this difficulty, except in areas visited only once. If I was in any doubt that a bird was already recorded I omitted later records. I add some notes on the results of interviews with eleven hunters whose kills of adult male and female-plumaged birds were recorded.

The following abbreviations are used: PTR = plumage-type ratio; M = adult male(s); I = immature male(s); F = females(s); f = female-plumaged bird(s). Maring bird names are given after English vernaculars.

*Loria loriae* Loria's Bird of Paradise, *mambaruo*.

Sight records: 1M in company of 1f at about 2070 m in primary forest; 1 possible 2 other f seen in secondary growth.

The Kundagai consider this a common bird, though I found it retiring. I have insufficient sightings to suggest a PTR or sex ratio, although in the nearby Kaironk Valley f probably greatly outnumber M (Majnep and Bulmer 1977: 72).

*Loboparadisea sericea* Yellow-breasted Bird of Paradise, *chengbamai*.

Sight records: One bird indistinctly seen in a tall primary forest tree, tentatively identified as a male.

*Manucodia chalybatus* Crinkle-collared Manucode, *mungunt*.

Sight records: Four unsexed individuals on two different occasions in secondary growth. This species appears to be more common at lower altitudes beyond Tsuwenkai.

*Paradigalla brevicauda* Short-tailed Paradigalla, *balbalmai*

Call records: heard on two occasions in primary forest.

*Epimachus fastosus* Black Sicklebill, *Kalanch gi yondoi*.

Sight records: None.

Call records: 1M

Reports: The specimen heard is said to range from Mounts Kumbant to Karenmai, and one man has laid claim of ownership to it. One I is known to live on the Kombaku range.

This is exclusively a bird of the montane forest, and is evidently rare, largely, it seems, replaced by the congener *E. meyeri*. Nowhere common in the Jimi, it seems to have a patchy distribution along the Bismark flanks. This may be partly due to declining areas of mixed oak forests, its preferred habitat (see also Majnep and Bulmer 1977: 57).

Calls of males are audible over long distance, and if more vocal males were present I would expect Kundagai hunters to know of them. The above two records therefore probably constitute the total resident population of males. The sex ratio may therefore approach equality. However, any hunting successes would have a comparatively great effect on the population structure, and with a high mortality of young birds the potential for population increase would be low.

The hunting histories I collected of 57 men include only one record of an *E. fastosus* being killed, in about 1930-35. This species is said to have been more common in the early 1900s when one man is credited with killing two males in one day. Other birds may have been shot since then by men now dead, but the paucity of recorded kills suggests that the present rarity of this bird is not due to predation, at least over the last 30 or 40 years.

*Epimachus meyeri* Brown Sicklebill, *Kalanch gurunt*.

Sight records: 2f,1I. 3 *Epimachus* f were seen by my assistants, but since the Maring do not distinguish between the two female-plumaged *Epimachus*, it is not certain that they were *E. meyeri*.

Reports: 1 possible 2M, in forests south and west of the Kant River. One male allegedly displays in the upper Anyen Valley.

These records and reports are all from about 2060 m (female-plumaged birds) to around 2250 m (adult males). This species is uncommon in Tsuwenkai. Where both *Epimachus* species are present elsewhere in New Guinea, *E. meyeri* is usually found at higher altitudes than *E. fastosus* (Diamond 1972: 328). Bulmer (1968: 634) notes that in the nearby Schrader Ranger *E. meyeri* is generally confined to *Nothofagus* beech forest above about 2300 m. In Tsuwenkai the species extends below this level into mixed forest, and where this occurs *E. fastosus* seems to be absent. Diamond (1972) has noted a similar pattern in the south-eastern highlands. It is possible that the expanded altitudinal range of *E. meyeri* has led to the exclusion of *E. fastosus*. Both species occur together only on the highest ranges of the flanks of the main Bismark Crest north of the Kant River where the wider altitudinal belt of forest may allow sufficient room for each species.

The above records suggest a PTR of 1 or 2M:6f. Informants state that individuals range widely, and the seven or eight birds recorded may represent the total population south and west of the Kant.

Hunting histories include only one adult male shot in Tsuwenkai.

*Parotia carolae* Carola's Parotia, *Kiawoe*

Sight records: 3M, 3f.

Call records: 1M.

This is a fairly common bird of primary and secondary forest between about 1730 and 2000 m. Males clear display bowers on the forest floor (Healey 1980). Some informants claim that several males may display at the same bower (cf. Schodde and Mason 1974).

Call and sight records are too few to suggest a PTR or sex ratio. However, the PTRs of birds killed by three of the sample of eleven hunters are suggestive:

Hunter 1 killed 3M, 6f in various places at different times.
Hunter 2 trapped 1M, 3f at one display bower over a brief period.
Hunter 3 shot 1M, 3f at various times and places.

Other hunters had not killed the species or had killed only one or two birds of either plumage type. The PTR may thus be between 1M:1f and 1M:3f. The latter ratio may represent a sex ratio approaching equality.

*Parotia lawesii* Lawes' Parotia, *kiawci*

Sight records: 1f.

This was a bird that visited a bower of *P. carolae* (Healey 1976). The species is apparently uncommon.

*Diphyllodes magnificus* Magnificent Bird of Paradise, *pengaluo*

Sight records: a). At display bowers: 1M at each of 3 bowers: b) Away from bowers; 3M, 5f. Some of these may also have been seen at bowers.

This is a common bird in its restricted habitat of secondary forest and woodland below about 1600 m. Several males each maintain bowers within auditory contact, forming an exploded arena. Bowers are in dense thickets, and may even be located in narrow tongues of growth in steep gullies on grassy slopes.

Limited observations at bowers suggest a sex ratio of breeding birds of 1M:2F (cf. Thair 1977). One hunter told us that he had shot a male at a bower which was visited by three female-plumaged birds at one time. The PTR of birds seen away from bowers of 1M: 1.6f suggests that the sex ratio in the population as a whole may be biased in favour of males, since some female-plumaged birds are likely to have been immature males.

*Paradisaea rudolphi* Blue Bird of Paradise, *aweng*.

Sight records: 1, possibly 2M, 1f.

Reports: 1I seen in an area away from where my own sightings were made.

Several birds which I did not locate to determine plumage-type were regularly heard calling from particular areas of the forest edge. Although one hears this species call almost every day on the edge of the settlement, there are only a few individuals, apparently occupying limited territories centred on relict stands of *Lithocarpus* and *Castanopsis* oak at the forest edge. I never saw or heard the species in the depths of montane forest, nor in secondary growth less than about twenty-five years old. The species appears to have a patchy distribution in the Jimi, Simbai and Kaironk Valleys, probably due to progressive destruction of habitat (cf. Majnep and Bulmer 1977:72). There are insufficient records to suggest the PTR or sex ratio.

These scanty data are clearly inconclusive. They are, however, comparable with data on valuable plume-bearing species in that at least *Parotia, Diphyllodes, Epimachus* and *Paradisaea* are highly sexually dimorphic, with cryptically coloured female-plumaged birds, and ornate, eye-catching adult males. One might expect the above relatively unmolested species to be as noticeable to the observer as the intensively hunted species to be discussed below.

For seldom-hunted species, the PTR seems generally to be only slightly unbalanced in favour of female-plumaged birds, suggesting a sex ratio of 1:1 or slightly favour males.

Non-Paradisaeidae Free from Human Predation. A consideration of the population structures of several other birds gives some comparative data to aid in the evaluation of the effects of predation on Bird of Paradise populations. Two species of Manakin (*Pipridae*) studied by Snow (1962a,b) on Trinidad can be compared with Birds of Paradise. These little birds are remarkably similar to Birds of Paradise in their habits and habitat.

Snow found an equal sex ratio in the Black-and-white Manakin *Manacus manacus* and assumes this is also true of the Golden-headed Manakin *Pipra erythrocephala*. In *Manacus* populations the PTR is about 1M:2f and in *Pipra* 1M:2.2 to 2.3f.

*Manacus* generally lays two eggs, and more than one brood may be laid in a season. In common with many other tropical forest species *Manacus* has a high nest failure rate (cf. Skutch 1966). Sixty percent of all nests started fail to produce hatched young. Of the 40% of successful nests, almost 50% failed to produce fledged young (81% of all nests started). The average number of fledglings per nest was 0.33. Snow estimates that each female lays an average of three broods per year, resulting in each female producing one surviving fledgling each year. Only one third of these subsequently reach breeding age, so that each female contributes 0.33 individuals to the next season's breeding population. About half of these are males which do not breed in their first year, and which may be unsuccessful in securing advantageous locations at leks, and so fail to breed in succeeding years.

Low reproductive success in tropical birds in general has been correlated with high adult survival rates (Skutch 1955; Snow and Lill 1974). While in *Manacus* the number of nests producing fledged young is only 19%, and two thirds of these young die in their first year, the adult survival rate is about 89% per annum. Snow and Lill (1974) have shown that *Manacus* males may survive at least 14 years, females for 12.5 years. Female *Manacus* breed until at least 10 years old, males possibly until 12 or more. *Pipra* breeding life appears to be almost as prolonged.

Data on the breeding success (numbers of fledged young to eggs laid) of seven tropical lowland forest birds in Trinidad give an average of 25% (range 17-33%) (Snow and Snow 1963; 1973; Snow 1974). This is close to Skutch's (1966) figure of a 21% breeding success in lowland Panama. Skutch notes that in general breeding success increases with altitude in the tropics. He found that Central American birds nesting in disturbed habitats between about 1500 to 1800 m had breeding success of 53%, although those nesting between about 1980 to 2280 m had a success rate of only 44%. The average for both regions is 48.5%. Skutch goes on to show that Central American forest breeders generally have a lower nest success, probably because loss of eggs and young is higher.

In the absence of any satisfactory data on Birds of Paradise these data on Neotropical birds provide the basis for the following assumptions on breeding of Birds of Paradise in Tsuwenkai.

Paradisaeidae Species Subjected to Intensive Predation for Plumes. Most Birds of Paradise in Tsuwenkai breed in primary forest between the 1500 and 2280 m limits mentioned by Skutch. Snakes are the main nest predators implicated by Skutch (1966) and Snow (1952b), though these may be less numerous in Tsuwenkai than in Central America. Nonetheless, conclusion for the Americas cannot simply be applied to New Guinea, though they serve as a useful guide. I shall err on the side of caution and assume that Bird of Paradise breeding success is towards the lower limit indicated by Skutch for birds breeding at comparable altitudes in Central America. I assume that only one attempt is made to lay one egg, and that the sex ratio in unmolested birds is about equal or biased in favour of males. In fact, small clutch size and high nestling mortality may be compensated for by repeated nestings.

Survival of adult Birds of Paradise is probably high, but since nesting success is possibly higher than in lowland Manakins, adult survival may be lower than the almost 90% of Snow's (1962a) Manakins. Deferred maturity of males for 5 or more years would, on comparative evidence from tropical America, argue for a long life. Each bird therefore has a long reproductive life to compensate for low breeding success rates resulting from small clutch size and probably high mortality rates in at least the first year of life. My only evidence for the age of a wild Bird of Paradise is highly circumstantial. An adult male *Astrapia* was wounded by a hunter at a communal display site, and consequently deserted the site. The bird took up residence in a small area of forest where it had remained for 5 or 6 years prior to my sighting of it. If this bird was shot soon after assuming full adult plumage it must be at least 10 - 12 years old.

Two factors may operate among Birds of Paradise to maintain a steady-state population in the face of increased human predation. This first is that other birds may quickly compensate for heavy mortality by increased reproductive output or by predation replacing other forms of mortality. The latter consequence is less likely in the case of human predation on birds for their plumes, as the hunter will tend to prefer well-plumed, active adults. Non-human predators, on the other hand, tend to select young or weak prey which might otherwise succumb to other forms of mortality (e.g. Mech 1970; Krunk 1972). Campbell *et al.* (1973) provide material on compensatory reproduction in response to predation. They found that human predation on one population of *Callipepla squamata* Scaled Quail in New Mexico was over 17 times more severe than the general level for all populations in the state. The harvest of quail bagged per square mile was eight times greater than the statewide harvest. Even when quail populations in their experimental area were greatly decreased through predation and other mortality factors, numbers built up to densities similar to those on a control, unhunted area, within a single season. Campbell *et al.* (1973: 26) conclude that it appears that proportionally more young quail were added to the treatment area (where hunting was encouraged) than to the control area (where hunting was prohibited), thus accounting for the relative increase on the former". Similar increases in reproductive success to compensate for increased mortality have been noted for other vertebrates, as noted in the introduction.

The particular relevance of the study by Campbell *et al.* is that it shows the response to massive predation can be fast. Since the predation on Birds of Paradise is biased to adult males, the reproductive population of females remains relatively unchanged. Because the species to be considered below are polygynous or promiscuous breeders, a large number of females can be fertilised by a small number of males. The reproductive rate, therefore, may be more dependant on the number of breeding females, so that levels of reproduction can be maintained with only a few breeding males (see e.g. Wynne-Edwards 1962). Even where tertiary sex ratios are equal, the effective sex ratio of breeding birds can be heavily skewed in favour of females through direct female selectivity of mates, or indirectly, by exclusion of males from contact with females at leks or exploded areas.

The second factor which may operate in conjunction with, or in place of, the first to maintain a steady-state population is that in the partial or even complete absence of adult males, subadult males may breed. Schodde (1973: 139) notes that unplumed males in ten genera examined were sexually mature. Cooper and Forshaw (1977) report evidence of the capacity of subadult males, mostly captive specimens, to breed. Diamond (1972:340) suggests that subadult male *Paradisaea raggiana* regularly breed in the Karimui Basin where fully plumed males are rare. The most convincing evidence of the acceptability of unplumed males as mates is provided by LeCroy *et al.* (1980), who observed unplumed birds mounting females even in the presence of fully plumed displaying males.

With these considerations in mind, I turn to an examination of the effect of hunting on the population numbers and structures of individual species. The following calculations should be regarded as approximations only. Given the insufficiency of reliable data I have attempted to err on the side of under-estimation.

*Astrapia stephaniae* Stephanie's Astrapia, *Kombam*

Sight records:
a. At display sites:
Gachambo: 4M, 2f (maximum numbers during six observation periods).
Gandakai: 3M, 2f.
Bombong: 4M, 1I, 1f
b. Away from display sites:
i. Including known or suspected repeated sightings of some birds: 6M,20f(PTR 1M: 3.3f).
ii. Single sightings excluding birds known or suspected to have been previously encountered at or away from display sites: 2M,4I,13f (PTR 1M:8.5f).
Reports: Alyunk display site: 3M (subsequently abandoned the area).

This is a fairly common bird. Adult males are confined entirely to montane forest between 2050 m and 2250 m or higher. Females and immature males occupy this range and also occasionally visit the forest edge, exceptionally down to 1630 m.

Adult males display communally at traditional sites composed of one or more trees (Healey 1978a). The Kundagai know of four widely dispersed sites (Map 2): Gachambo, Gandakai, Bombong and Aiyunk. I visited the first three. Birds ceased displaying at Gandakai shortly before I visited this site, allegedly because the owner of this area had wounded a bird there. However, males congregated near the display trees, and local experts considered that displays would recommence in time.

The Gachambo site was originally found, between 1944-49, close to the Kant River. Around the mid 1950s birds gathered in trees higher on the slopes of Mt. Gonggia. The Gandakai site has been in use since at least the late 1950s. *Astrapia* have been known in the Bombong area since the early to mid-1940s, but the display site was only discovered between 1962 and 1964.

The Aiyunk site is owned by an old man, who found it between 1910 and 1915 when he was a boy. He has never shot birds there, although his relatives have. Poachers are also suspected to have taken many birds at the display area. One of my assistants, Lucien Yekwai, an acknowledged expert on *Astrapia*, spent two days searching for the birds associated with the Aiyunk site with which he was familiar. Although birds had been seen displaying here early in 1974, all trace of them at the display trees and in the surrounding forest had vanished by the time of Yekwai's search in August. Yekwai concluded that the males had either wandered to another part of the rocky and treacherous Aiyunk slopes or crossed the Bismarck Crest into the Simbai.

Display sites may be visited by several generations of birds. The locations of sites may shift over time, and the actual trees used by displaying birds may also change. Allegedly, not all adult males display at communal sites. Yekwai claims that one male he once wounded at Gachambo deserted that site permanently, and now maintains a solitary existence at a lower level near the Kant River. During the day males associated with particular sites disperse loosely in the neighbouring forest. I am unsure how far birds wander. Some are found well away from known display areas, where they possibly display alone or not at all.

Sight and report records (at display sites and single sightings of category b, ii above) yield a total known population of 39 birds (16M, 23f, of which 5 are distinctive I), with a PTR of 1M:1.4f and a sex ratio of at least 1M:0.86F. These ratios include males seen at display trees which females seem to visit only occasionally and in small numbers. Thus the sex ratio is probably less biased in favour of males in the population as a whole. As indicated in entries for sight records above, the PTR's of birds seen away from display sites give different results. The ratio of about 1M:6f based on single sightings of 19 birds is probably the most reliable, though based on a small sample, and I use it to project estimates of the minimum total population.

Assuming this ratio holds for all 11M observed at display sites, then 88f are associated with them, giving a total population of some 100 birds. If the 3 Aiyunk males remain in Tsuwenkai, the total would be 142 birds. I will work on the smaller figure which can stand as the minimum population in land west of the lower Kant and Goimbang Creek.

Of the 19 birds seen away from display sites 4 were distinguishably I. Thus, 6 males and 13 apparently female birds were seen. Assuming an equal secondary sex ratio the 2M will be balanced by 2 adult F, and the 4I by 4 younger F which will be at least 2 years old (since immature male plumage is distinguishable from female plumage only in the second year (Gilliard 1969:157) and possibly capable of breeding. This leaves 7f of undetermined sex. Some of these will be young males. It is therefore likely that the actual sex ratio is about equal. This breakdown also implies a large proportion of young birds in the population which is at odds with comparative data suggesting a population composed mainly of older birds. In other words, a relatively large fraction of the 9 or 10 female birds in this sample should be capable of breeding. I will assume that 6 females (31.6%) of the sample fall into this category: this may be an underestimate. Projecting this proportion onto the estimated population of 100 birds, about 31 may be breeding females. With a 33.3% nesting success there will be 10 surviving young each season with an equal sex ratio.

Hunting histories at the Bombong and Gachambo display sites indicate that males are shot at the rate of one every 2 to 2.5 years. Hunting histories of 57 men include *Astrapia* kills by 21 men. They had together shot 49 male *Astrapia* since 1930, at a rate of 1.1 per annum. Three of these men own display sites and have shot 6, 7 and 8 birds, not all at display sites. Men not owning display sites shoot birds less frequently. One such man had shot five, others only one or two. For the years 1965-73 for which records of kills are most reliable, a minimum of 17 birds (almost 2 per year) have been shot. Seven of these were shot at display sites, six at Bombong and Gachambo. Omitting the later, the predation rate away from display sites was about one male killed each year. During 12 months fieldwork two males were killed, one near a display site.

Rates of predation on males are therefore around two per year, but vary from about one away from display sites to one killed every 2 to 2.5 years at display sites. These rates are within estimated limits of the reproductive rate of the population.

However, these rates are calculated from kills everywhere in Tsuwenkai, while recruitment rates are based on the projected population of only part of the area. Actual breeding output may therefore be somewhat higher.

Of the eleven men questioned about their hunting of female-plumaged birds, six had killed from one to three *Astrapia* females each. Eight of them had killed from one to eight males. In all, they had killed 17 males and 11 female-plumaged birds, some of which would be immature males. Hunting of *Astrapias* therefore not as age- and sex-selective as might be expected of a species primarily sought for its plumes. Most hunters must shoot *Astrapia* away from display sites, where adult males are less commonly encountered than female-plumaged birds. On the other hand, predation rates on males are lower at display sites where mating presumably occurs. The reproductive potential of the species may therefore not be unduly affected.

*Lophorina superba* Superb Bird of Paradise, *yenandiok.*

Sight records: 13M, 1I, 13f.

Call records: 4M, 4F, 19 unsexed. Assistants claimed to be able to determine the sex of a bird by its calls, and I have relied upon their opinion.

This is the most common of the valuable Birds of Paradise. It is numerous in the lower reaches of montane forest and at the forest edge. Female-plumaged birds and, less commonly, adult males, can be found in the zone of human habitation. I have encountered this species from the bottom of the Kant Valley at 1450 m up to 2200 m in the montane forest. This last record seems to be exceptional both for Tsuwenkai (one record) and for the eastern highlands in general (cf. Diamond 1972: 331). *Lophorina* mainly occurs between 1630 and 1940 m, that is, spanning the transition area between secondary and primary montane forest. Adult males are more common in the upper part of this range, being mainly found above 1830m.

Each male customarily calls and displays alone from the crowns of one or more trees within a confined territory. Males seem to be highly sedentary, spending much time in the vicinity of calling or display trees. Unlike *Astrapia* display sites, *Lophorina* trees are usually loosely clustered within auditory range of one another.

Sight and call records indicate a PTR of 1M:1.08f, which suggests an unbalanced sex ratio in favour of males, but this may be influenced by a disproportionate recording of highly visible and very vocal males. Accounts of the eleven men whose hunting of M and f birds were recorded suggest that PTRs in five small areas where some men had trapped and shot birds varied from 1M:3f to 1M:8f (mean 1M:5f), suggesting a sex ratio close to 1:1. The eleven hunters had shot 38M and at least 43I in nine years, although some men said they could not remember all birds shot. Predation is thus not markedly sex selective. Assuming a PTR of 1M:5f, the 17M seen or heard are part of a total population of 102 birds. This is clearly an underestimate for Tsuwenkai as a whole, as parts of the territory were minimally surveyed.

Results of censuses in Areas 1 and 2 (Map 2) projected to the total available habitat give a higher estimate of the population. In the primary forest Area 2 there were 6 *Lophorina*, or a density of one bird per 2.7 ha. In the forest edge Area 1 there were 9 birds, for a density of one every 1.8 ha. Observations suggest that this greater density of *Lophorina* in such disturbed habitats as Area 1 is general in Tsuwenkai. I estimate the minimum total area of habitat for *Lophorina* at about 6 km$^2$. Over half of this area is primary forest with lower densities of birds. The overall average density will therefore be between one bird to 2.7 ha and one every 1.8 ha. I assume a density of one bird every 2.3 ha. The total area of available habitat would then support about 260 birds.

Of the conservative estimate of 102 birds, at least half the population will be females, assuming a near equal sex ratio. With high mortality of young birds, and high adult survival rates, most of these females would be adults capable of breeding (say 80% of all females). I will assume that about 40 females are in breeding condition (39.2% of the total population). With a 33.3% nesting success, these females produce about 13 fledged young each year, half of them males. Applying the same assumption to the estimated total of 260 birds, 120 breeding females produce 34 fledged young each year, including 17 males.

In the nine years 1965-73, at least 16M or almost 2 per year were killed. In the 12 months of fieldwork 8M were killed. This higher rate is within the recruitment rate of the larger estimated population. Since estimates of population densities and available habitat used to compute total numbers are deliberately conservative, annual recruitment rates may exceed variable predation rates of 2-8M by an even greater margin.

*Pteridophora alberti* King of Saxony Bird of Paradise, *balpan*.

Sight records: 7M, 6I,16f.

Call records: 2M, 2I, 18f, 2 unsexed. Assistants claim that calls of adult and immature males and of females are distinguishable, and I have relied upon their opinion.

This common bird is found only in undisturbed primary forest mainly between 2050 and 2260 m. In the nearby Kaironk Valley it extends up to at least 2400 m (R. Bulmer pers. comm.) and Diamond (1972: 339) recorded males at 2740 m on Mt. Karimui. A record of an immature male and several female-plumaged females at 1860 m may have been due to particular conditions in a valley noted for its peculiarly low temperatures.

*Pteridophora* and *Lophorina* seem to displace one another altitudinally, with the former being most common in the lower part of its range.

Adult males maintain several customary calling trees within their individual territories (see also Majnep and Bulmer 1977:74), although nuptial displays probably occur in the forest substage (Beach 1975; Healey 1975). Plumed males appear to be highly sedentary, spending long periods resting or calling in customary trees.

The PTR of sight records is 1M:3.1f (including I in the latter category). The sex ratio probably does not diverge markedly from equality.

In census Area 3, 15 *Pteridophora* were located (3M and 12f), at a density of one bird to 5.3 ha. No birds were recorded in the upper 16 ha of this area, which is probably above the altitudinal limit of the species. Omitting this section of the census strip raises the density to one bird every 4.3 ha. Approximately 8 to 9.5 km$^2$ of Tsuwenkai land is primary forest within the altitudinal range of *Pteridophora*. This area would support 160-190 birds at a density of one every 5 ha or 199-237 at a density of one every 4 ha. I shall work with a mean estimate of 200 birds.

Female-plumaged *Pteridophora* are rarely killed and the species is not attracted to fruit baits or caught in traps. Most birds killed are therefore the results of deliberate effort. Males are usually shot high in calling trees. Female-plumaged birds are seldom shot because hunters spare them, but also because they are seldom encountered in males' calling trees (cf. Beach 1975). Predation is therefore more sex- and age-selective than is apparent for other species, so one might expect greater skewing of the population in favour of female-plumaged birds.

Of the 53 birds seen or heard 17 were males (including 8 immatures), and 18, or 34% were females. A larger proportion may actually be capable of breeding, for some of the remaining 18 unsexed birds would have been adult females. Projecting these figures to the estimated population of 200 birds there would be at least 68 adult females. With a 33.3% nesting success rate their reproductive output would be 22 birds, or 11 males each year.

Over the period 1965-73, 24 birds were killed at a rate of 2.7 per year. During the 12 months of fieldwork 5 males were killed. Both are within the projected annual reproductive rate of the species.

A nearly equal sex ratio in the face of more marked sex-selective predation than in any other species suggests that either *Pteridophora* has compensated for this predation, or that the tertiary sex ratio in unmolested populations is biased in favour of males.

## PREDATION RATES AND HOMEOSTASIS OF THE BIRD POPULATIONS

Calculations for some individual species in the preceding section are based on rather few observations over a limited period. Predation rates, however, are based on records over longer periods, and show fluctuations between the periods 1965-73 and 1973-74. Annual rates appeared to be higher in the latter period, probably because some informants had forgotten kills in the earlier period. Predation rates of individual hunters vary considerably over time (Healey 1977: 254ff), but since the numbers of hunters and their identities and skills vary over time, any fluctuations in predation rates by individuals is not necessarily reflected in their combined rates. Nonetheless, one might expect the predation rates on Birds of Paradise of the Kundagai as a whole to vary somewhat over time, in response to the irregular occurrence of ceremonies requiring decorative plumes. Potentially this could mean that the reproductive capacity of the population would also fluctuate.

Trade in bird plumes has increased since 1956 when the Kundagai were first contacted by the government, and an imposed peace ensured greater safety for traders. One might expect hunting rates to have increased in this time to sustain intensified trading, and the Kundagai claim that this is so. Analysis of the hunting histories, which extend back to the 1920s, shows that there has been no appreciable increase in predation rates on the three most commonly killed Birds of Paradise.

Table 5 provides hunting rates pre and post 1956, as well as gross numbers killed in 1973-74. There is no way of knowing whether the latter figures are representative of average predation levels, nor whether the variation from year to year is accurate. It is not possible to reconstruct past absolute predation figures. Thus, the number of birds recorded as killed in the two earlier time periods are not gross figures but only the totals killed by <u>men still living</u> in 1973-74. Since most active living hunters have been operating mainly since 1955, the data are biased towards more recent hunting. Consequently, pre 1955 rates must have been somewhat higher, so that the slight increases in predation rates of *Astrapia* and *Lophorina* are more an artefact of the method of analysis than a reflection of the real situation. The conclusion is that, whatever the actual levels of predation prior to my fieldwork, they do not appear to have increased since pacification and the attendant intensification of trade in the mid 1950s.

TABLE 5: Annual predation rates pre and post 1956, and 1973-74.

| | Pre 1956 (25 year period) | | Post 1956 (19 year period) | | 1973-74 |
|---|---|---|---|---|---|
| SPECIES | No. of birds killed | Rate/year | No. of birds killed | Rate/year | No. of birds killed |
| *Astrapia stephaniae* | 16 | 0.6 | 19 | 1.0 | 2 |
| *Lophorina superba* | 24 | 1.0 | 29 | 1.5 | 8 |
| *Pteridophora alberti* | 28 | 1.1 | 22 | 1.1 | 5 |

In fact it is probable that hunting rates prior to 1956 were actually higher than at present. Since that date the Kundagai have greatly increased their import of plumes. This has allowed them to export more plumes and consequently increase imports of pigs, shells and other valuables flowing in the reverse direction (see Healey 1977 for discussion of these changes). This presumed post-1956 decline in hunting may be simply because increasing import of plumes has made the Kundagai less reliant on local hunting to provide themselves with feathers for decoration and export. It may also be a response to an increasing scarcity of wild birds. Oral traditions indicate that there were fewer people living in Tsuwenkai two to three generations ago and that the forests were more extensive. It is therefore quite possible that there were larger populations of wild birds which could sustain higher rates of predation. It is also possible that these populations declined under pressure of hunting and forest clearing, although there is no evidence for this.

Present hunting rates appear to be within the rate of annual recruitment; that is, under its present organisation, hunting does not pose a threat to the survival of the birds in Tsuwenkai. However, there is no way of knowing if the present balance between recruitment and mortality in bird populations is representative of the past. Thus, while bird populations appear to be stable now there are no grounds for assuming that this circumstance can be projected into the past, much less into the future. Since the birds still exist, it is reasonable to conclude that hunting rates over time have remained within the limits of reproductive potential. This conclusion does not rule out the likelihood of past decline; that is, of periodic over-exploitation without a full recovery of population levels.

## CONCLUSION

This study suggests that the Kundagai can maintain long-term production of feathers on a sustained-yield basis.

The model described in the introduction is based on an assumption of a steady state in population dynamics. In terms of this assumption, homeostasis in bird populations has been maintained, albeit with probable fluctuations, for several decades.

Clan and individual rights to territories and specific resources, as well as new, if informal, Council rules and personal restraints accepted by hunters, all limit the intensity of predation. Nonetheless, one cannot actually specify any positive links between these social and cultural constraints and the population ecology of the birds. However, as long as trade in bird plumes remain an important part of the local economy, hunters in Tsuwenkai will be motivated to observe restrictive rules of access to wild birds. This does not preclude the possibility that these rules will be subject to changes which may serve the short-term interests of some individuals or groups, but may be to the long-term detriment of Birds of Paradise. The "age old traditions" of preliterate tribal peoples are vulnerable to subtle changes and reinterpretations over time. The maintenance of customary rules regulating hunting partly depends on the continuing high demand for plumes in the central highlands, over which the Kundagai have no control, and on continuing lack of opportunity for the development ventures which might be highly destructive of the environment, such as large scale cash cropping, forestry or mining. Even if such developments do not directly lead to destruction of habitat, the attendant changes in social organisation and cultural conceptions of man's relationship to the environment may make Jimi people less inclined to conserve their forest resources.

I noted that there is little present incentive to clear additional areas of forest to meet subsistence needs. Additional clearing will almost certainly become necessary in the future as the population grows, and planting of cash crops increases. Much of the climax forest remains above the limits of agriculture, although the Kundagai entertain the hope they will be able to engage in some commercial logging when the road connecting them to Tabibuga and the Highlands Highway is completed. Even so, it is likely that large continuous tracts of forest should remain as retreats for Birds of Paradise. Further, some species, notably *Lophorina superba*, would seem to benefit by the creation of disturbed habitat.

Undoubtedly, the greatest threat to wildlife in the area is from mining. A national subsidiary of a major multinational company has recently taken out exploration permits for gold and other minerals in a large area of the Jimi and Simbai Valleys, and a particularly promising region is centred right on Tsuwenkai. Clearly, a large mining venture in such terrain would have radical effects on the local environment.

Whether mining will go ahead in the region is not yet known. Apart from this threat, the future of most species of Birds of Paradise seems reasonably secure in Tsuwenkai. However, this conclusion cannot be drawn for the Jimi as a whole, other parts of which show a higher hunter to hunting land ratio, and higher overall human population densities. It is likely that bird populations in these areas are subject to more intensive predation, and are more liable to suffer from destruction of habitat than in Tsuwenkai. Local extinction of Birds of Paradise may occur in some of these areas if forest clearing increases to support a growing population, or if mining is developed. More detailed studies are still needed to determine the current and project status of Birds of Paradise in the Jimi and to assist in their conservation.

Field research in 1972 was supported by a grant from the University of PNG, and in 1973-74 by grants from the New York Zoological Society, The Myer Foundation, and the PNG Department of Natural Resources. The research was designed in consultation with officers, in particular Max Downes, of the PNG Wildlife Division (then in the Department of Agriculture, Stock and Fisheries, now in the Department of Environment and Conservation). The object was to provide basic data on the cultural significance of Birds of Paradise and to assist those responsible for the development of a programme for the conservation of Birds of Paradise.

A number of people have give me assistance in the interpretation of data and preparation of this paper. Professor Bill Clarke gave tentative identifications of some plants, and Mr Graeme George provided information on various aspects of Bird of Paradise biology and ecology. Professor Ralph Bulmer was instrumental in the planning stages of my research, and commented generously and profusely on its results. Mary LeCroy and Dr Jim Menzies made very helpful comments on a draft of this paper.

For general assistance in the field, companionship, and help in pursuing birds through the forest I am indebted to Felicity Healey, Mathew Deimang Kuk of Kwiop, and Phillip Amang and Lucien Tekwai of Tsuwenkai. Without the generous and amiable guidance and instruction in natural history by Lucien my results would have been much poorer.

My sincere thanks to all these individuals and institutions. Any errors or misrepresentations in this report are entirely of my own making.

BEACH, J. 1975. Display and mating of the King of Saxony Bird of Paradise. **PNG Bird Society Newsletter,** 109: 1-2.

BROOKFIELD, H.C. 1964. The ecology of highland settlement: some suggestions. **Amer. Anthropologist** (Special Publication) 66: 20-38.

BUCHBINDER, G. 1973. **Maring microadaptation: a study of demographic, nutritional, genetic and phenotypic variation in a highland New Guinea population.** PhD. thesis, Columbia University, U.S.A.

BULMER, R. 1968. Worms that croak and other mysteries of Karam natural history. **Mankind** 6: 621-639.

CAMPBELL, H., D.K. MARTIN, P.E. FERKOVICH & B.K. HARRIS. 1973. Effects of hunting and some other environmental factors on Scaled Quail in New mexico. **Wildlife Mon.** 34: Washington Wildlife Soc.

CLARKE, W.C. 1971. **Place and People: an Ecology of a New Guinean Community.** Canberra: Australian National University Press.

COOPER, W.T. & J.M. FORSHAW. 1977. **The Birds of Paradise and Bowerbirds.** Sydney: Collins.

DAVIS, L.B. & M. WILSON (Eds.). 1978. Bison procurment and utilization: a symposium. **Plains Anthropologist,** Mem. 14.

DIAMOND, J.M., 1972. Avifauna of the eastern highlands of New Guinea. **Pubs. Nuttall Orn. Club.** No. 12.

DOW, D.D. 1973. Sex ratios and oral flange characteristics of selected genera of Australian honeyeaters in museum collections. **Emu** 72: 41-50.

DRAFFAN, R.D.W. 1978. Group display of the Emperor of Germany Bird of Paradise *Paradisaea guilielmi* in the wild. **Emu** 78: 157-159.

ERRINGTON, P.L. 1934. Vulnerability of Bob-White populations to predation. Ecology. 15: 110-127.

FRITH, C.B. 1976. Displays of the Red Birds of Paradise *Paradisaea rubra* and their significance, with a discussion of displays and systematics of other Paradisaeidae. **Emu** 76: 69-78.

GILLIARD, E.T. 1969. **Birds of Paradise and Bowerbirds.** London, Weidenfeld and Nicolson.

HEALEY, C.J. 1975. A further note on the display and mating of *Pteridophora alberti*. **PNG Bird Society Newsletter.** 110: 6-7.

__________. 1976. Sympatry in *Parotia lawesii* and *Parotia carolae*. **Emu.** 76: 85.

__________. 1977. **Maring hunters and traders; the ecology of an exploitative, non-subsistence activity** PhD dissertation. University of PNG, PNG.

__________. 1978a. Communal display of Princess Stephanie's Astrapia *Astrapia stephaniae* (Paradisaeidae). **Emu** 78: 197-200.

__________. 1978b. Effects of human activity on *Paradisaea minor* in the Jimi Valley, New Guinea. **Emu.** 78: 194-155.

__________. 1980. Display of Queen Carola's Parotia *Parotia carolae* (Paradisaeidae). **PNG Bird Society Newsletter** 163/164: 6-9.

KLEIN, D.R. 1970. Food selection by North American deer and their response to over-utilization of preferred plant species. In **Animal Populations in Relation to Their Food Resources.** A Watson (Ed). Oxford and Edinburgh: Blackwell Scientific Publications: 25-44.

KRUUK, H. 1972. **The Spotted Hyena: a Study of Predation and Social Behaviour.** Chicago: University of Chicago Press.

LACK, D. 1966. **Population Studies of Birds.** London: Oxford University Press.

LECROY, M., A. KULUPI, & W.S. PECKOVER. 1980. Goldie's Bird of Paradise: display, natural history and traditional relationships of people to the bird. **Wilson Bull.** 92: 289-301.

MAJNEP, I.S. & R. BULMER. 1977. **Birds of my Kalam Country.** Auckland: Oxford University Press.

MANNER, H. 1977. Biomass: its determination and implications in tropical agro-ecosystems: an example from montane New Guinea. In **Subsistence and Survival: Rural Ecology in the Pacific.** T.P. Bayless-Smith & R.G. Feachem (Eds). London: Academic Press: 215-241.

MAYR, E. 1939. The sex ratio in wild birds. **Amer. Nat.** 73: 156-179.

MECH, L.D. 1970. **The Wolf: The Ecology and Behaviour of an Endangered Species.** New York Natural History Press.

RAPPAPORT, R.A. 1967. Pigs for the Ancestors: **Ritual in the Ecology of a New Guinea People.** New Haven: Yale University Press.

SCHALLER, G.B. 1967. **The Deer and the Tiger: A Study of Wildlife in India.** Chicago: University of Chicago Press.

__________. 1972. **The Serengeti Lion: A Study of Predator-prey Relations.** Chicago: University of Chicago Press.

SCHODDE, R. 1973. General problems of fauna conservation in relation to the conservation of vegetation in New Guinea. In **Nature Conservation in the Pacific.** A.B. Costin, and R.H. Groves (Eds). Canberra: Australian National University Press: 123-144.

SCHODDE, R. & I.J. MASON. 1974. Further observations on *Parotia wahnesi* and *Parotia lawesii* (Paradisaeidae). **Emu** 74: 200-201.

SELANDER, R.K. 1960. Sex ratios of nestlings and clutch size in the Boat-tailed Grackle. **Condor** 62: 34-44.

__________. 1965. On mating systems and sexual selection. Amer. Nat. 99: 129-141.

SINCLAIR, A.R.E. 1977. **The African Buffalo: A Study of Resource Limitation of Populations** Chicago: University of Chicago Press.

SKUTCH, A.F. 1966. A breeding bird census and nesting success in Central America **Ibis** 108: 1-16.

SLOBODKIN, L.B. 1961. **Growth and Regulation of Animal Populations.** New York: Holt, Rinehart and Winston.

SMITH, B.D. 1974. Predator-prey relationship in the south-eastern Ozarks - A.D. 1300. **Human Ecol.** 2: 31-43.

SNOW, B.K. 1974. Lek behaviour and breeding of Guy's Hermit Humming Bird. *Phaethornis guy*. **Ibis** 116:278-297

SNOW, D.W. 1962a. A field study of the Black and White Manakin, *Manacus manacus,* in Trinidad. **Zoologica** 47: 65-104.

__________. 1962b. A field study of the Golden-headed Manakin, *Pipraerythrocephala,* in Trindad. **Zoologica** 47: 183-198.

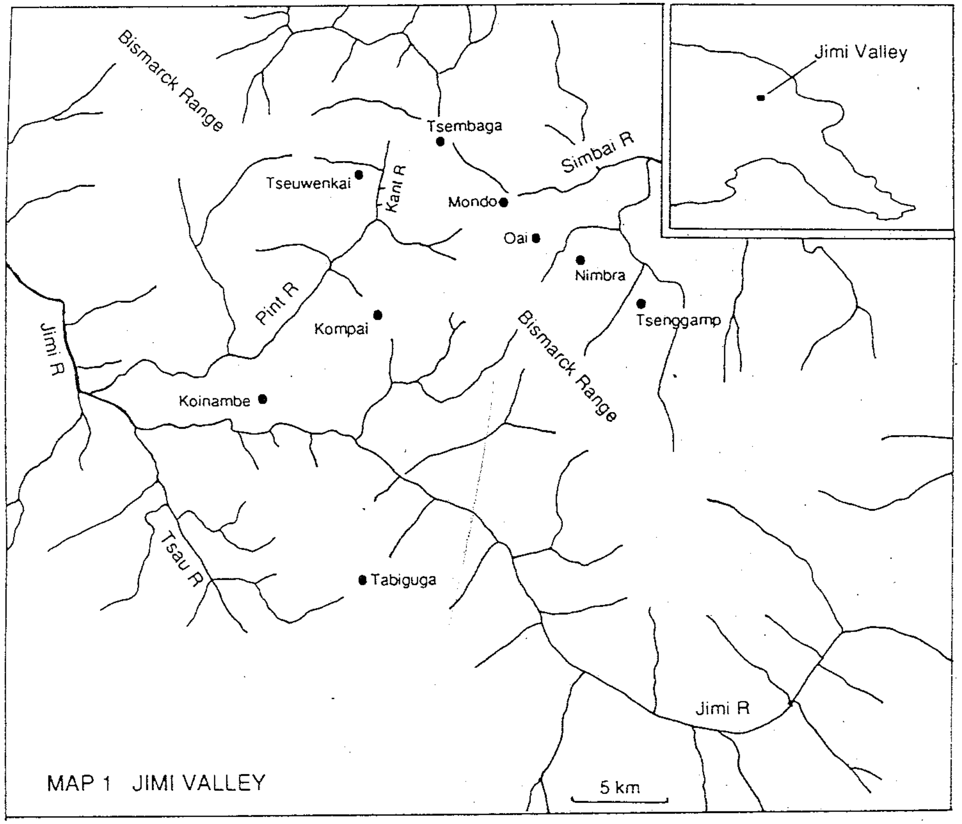
SNOW, D.W., & A. LILL. 1974. Longevity records for some neotropical land birds. **Condor** 76: 262-267.

SNOW, D.W., & B.K. SNOW. 1963. Breeding and the annual cycle in three Trinidad thrushes. **Wilson Bull** 75: 27-41.

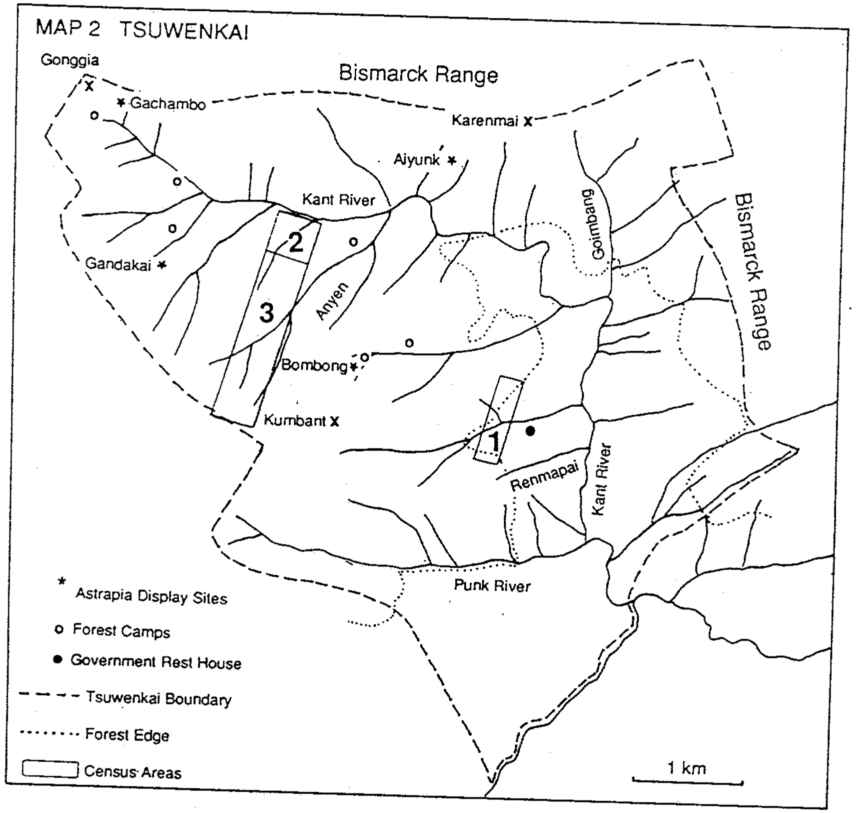
__________ & __________. 1973. The breeding of the Hairy Hermit *Glaucis hirsuta* in Trinidad. **Ardea** 61: 106-122.

THAIR, S., & M. THAIR. 1977. Report on display of Magnificent Bird of Paradise. **PNG Bird Society Newsletter.** 128: 13.

WYNNE-EDWARDS, V.C. 1962. **Animal Dispersion in Relation to Social Behaviour.** Edinburgh: Oliver & Boyd.



MAP 1 JIMI VALLEY



MAP 2 TSUWENKAI