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THE SOCIAL STRUCTURE, BREEDING AND POPULATION DYNAMICS OF PARADISE SHELDUCK IN THE GISBORNE-EAST COAST DISTRICT

By MURRAY WILLIAMS

ABSTRACT

The breeding biology of the Paradise Shelduck *(Tadorna variegata)* was studied on hill-country farmland west of Tokomaru Bay, New Zealand, during 1973-1976.

Throughout the breeding season the shelduck population comprised territorial pairs, which occupied areas of pasture surrounding stock ponds or other water bodies, and flocks, which were mostly of juveniles and which remained at specific sites on river terraces or hillsides. Breeding was attempted only by the territorial pairs.

Prospecting for nest sites started in late June and 62% of 47 nests found were in hollow logs on the ground. Laying began in August and the mean size of 36 clutches was 9.4. Of 282 eggs, 5% were infertile and 87% of the fertile eggs hatched. Only 20% of the pairs which lost their clutches re-nested.

Ducklings were reared on stock ponds, in streams or rivers, and in swampy soaks on hillsides. About 60% of the ducklings reaching the rearing areas survived the 8-week fledging period. The main causes of duckling mortality were bad weather and predation by feral cats. During their first week, ducklings fed mostly on aquatic insects, and thereafter on plant material. Of 677 ducklings which fledged, 54.7% were males, and, after fledging, males dispersed more widely than females .

Ten (13%) of the 78 territorial pairs studied during 1973-1975 did not attempt to breed, 46 (59%) appeared with ducklings, and the nesting attempt of 22 (28%) failed. Each pair of territorial shelducks which attempted breeding produced 2.6-2.8 ducklings annually. The mean percentage annual survival of territorial shelducks was 64%, while about 50% of the flock birds survived their first year and 55% their second. In most cases, birds first attempted to breed when two years old.

The number of flock birds doubled each year between July and October as mostly males arrived from nearer the coast. The number of territorial pairs fluctuated from year to year: only 15 of the 37 territories were occupied in all four years of the study. Few locally-reared young were recruited back into the local breeding population, and changes in the density of territorial pairs did not seem to reflect positively the breeding success two years previously. Recruitment into the breeding population may be determined by competition amongst juvenile pairs when they attempt to establish preliminary territories.

INTRODUCTION

The Paradise Shelduck *(Tadorna variegata)* is one of the few endemic birds to have benefited from European Man's drastic alteration of the New Zealand landscape. Restricted in pre-European times to lowland short-tussock grasslands and swamplands, a scarce native habitat, the Paradise Shelduck has extended its range dramatically in the wake of the conversion of forest to pasture (Williams 1971). The extensive construction of small watering ponds for stock throughout hill-country farmland has created a habitat which the species has successfully exploited (McAllum 1965) and the introduced pasture grasses are now its main food (Bisset 1976).

This increase in numbers and range has been accompanied by an increase in exploitation (Williams 1972). Although the Maoris formerly caught large numbers of moulting birds for food (Buller 1893, Beattie 1920), an activity which undoubtedly affected local populations for a time, sustained hunting by sportsmen has had a more dramatic effect both locally and nationally. Since 1950, as their numbers declined, the species has been periodically removed from the list of hunted waterfowl in many districts and only a sustained period of protection has enabled recovery. The Paradise Shelduck is easily over-exploited and if it is to be managed wisely, its biology needs to be better understood.

Little research to assist the wildlife managers has been done. Extensive banding to determine rates of mortality and patterns of dispersal commenced in 1961 (Williams 1972, 1975) and showed that (a) district populations, defined as birds moulting at particular sites, were relatively discrete and rarely intermingled, and (b) mortality rates varied between districts. However, there is no published information on breeding output to complement these studies. Therefore, the present

study began with the principal aim of determining the productivity of a Paradise Shelduck population.

The literature on this species (Buller 1888, Henry 1907, Oliver 1955, McAllum 1965) and other shelducks (Dementiev & Gladkov 1952, Delacour 1954, Hori 1964, Frith 1967), the comments of hunters and others, and my own previous observations suggested that Paradise Shelduck populations contained both large flocks and scattered pairs. A first step, therefore, was to determine precisely this social structure, to establish which birds attempted to breed and examine the behaviour of birds in these social categories, and determine how and when birds moved from one social category to another. My findings are presented in the section on social structure.

Having identified the breeding birds I then followed their nesting activities. Much of the published information on Paradise Shelduck breeding behaviour is fragmentary and conflicting. I have included in the section on breeding, therefore, details of nest sites, egg size and weight, incubation behaviour and duckling development, etc., as well as data relevant to the study's principal aim (e.g. clutch size, hatching success and duckling survival) so that the breeding biology of this species is more completely documented.

In the section on population dynamics, where the productivity of my study population is calculated, I have tried to compile a life equation for the species, that is, relating the average annual production of ducklings to the numbers of adults and non-breeders which die each year. This allows the productivity to be estimated and a statistical description of the important stages in the life cycle.

This study had as a secondary aim the identification of those aspects of the species' biology which the wildlife manager could beneficially influence. It is not my intention to discuss management procedures in this paper. This and a discussion of the communal moult gatherings will appear separately. However, in compiling this paper I am aware that my secondary aim has substantially influenced the quantity of data collected on some topics, e.g. behaviour of flock birds, incubation, duckling development, while others such as adult food, territory size, and territorial behaviour have gone unstudied. In approaching my study, the needs of the wildlife manager have been uppermost in my mind, and those aspects of Paradise Shelduck biology which he cannot economically, practically or beneficially influence have therefore received lesser attention.

STUDY AREA

The study was conducted on Huiarua Station and adjacent farms, an extensive region of hill-country farmland about 30 km west of Tokomaru Bay (38°05′ S, 178°00′ E) (Fig 1). It is a geologically unstable area with spectacular badland erosion. The northern part of the study area, roughly north of the divide between the Mata and Waitahaia rivers,

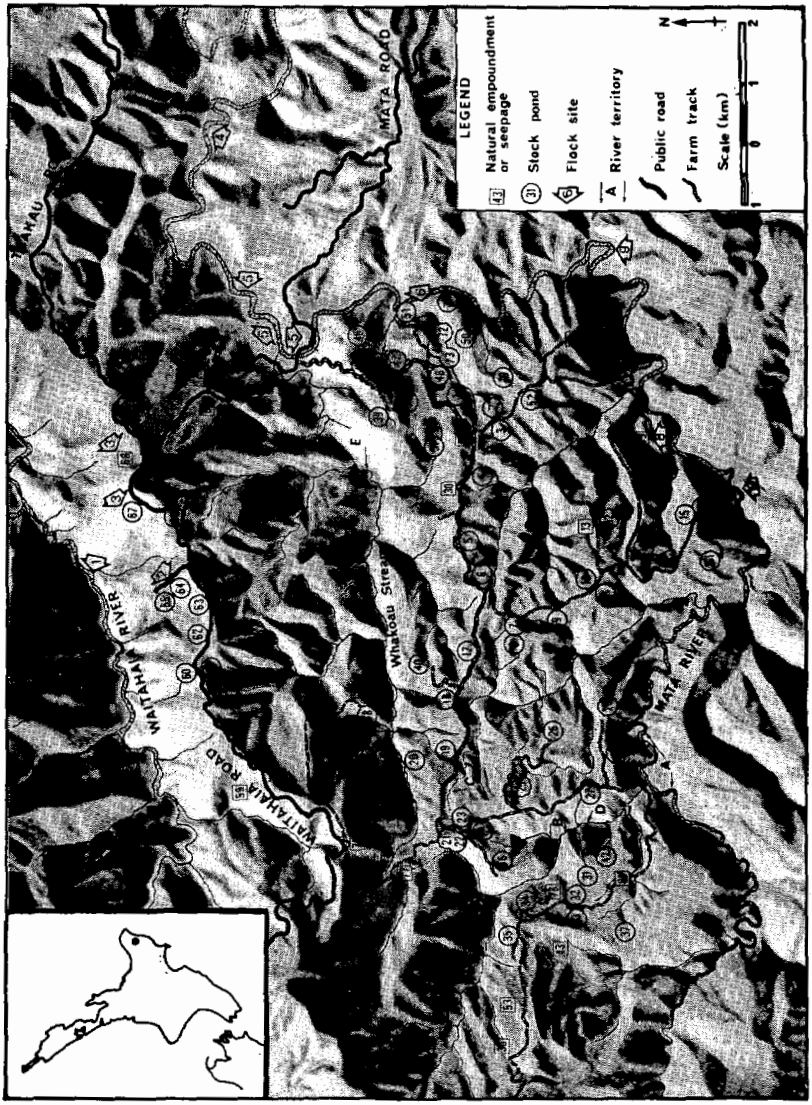

FIGURE 1 — The study area on Huiarua Station, Tokomaru Bay, showing topography, location of stock ponds, natural empoundments, river territories, vehicle tracks and flock sites.

and the westernmost part are underlain by rocks from the Clarence to Dannevirke Series (Kingma 1965), which span the interval from 100 to 50 million years ago. These rocks vary in hardness and in grain size from mudstone to coarse sandstone and conglomerate, and most units are broken by faults and fault movement. The southern part of the study area is formed mostly of soft, grey sandy siltstone of Upper Tertiary (Southland Series) age, often known as " papa." Thus, the land throughout is unstable, landslides are frequent and temporary ponds common.

The study area varies from 420 m a.s.l. in the Mata River valley to the east, to 1000 m toward the Raukumara Ranges to the west, and throughout is heavily dissected by deep valleys with steep hillsides (Fig. 2). Small creeks which drain these hillsides have cut deep into the soft underlying strata, causing extensive erosion and depositing huge sediment loads which in some parts form large river terraces. Small sadly depleted remnants of the original forest cover occur in patches on hillsides or in gullies but are seldom larger than 5 ha. Otherwise the entire area is covered by high-class pasture dominated by white clover *(Trifolium repens)* and rye grass *(Secale repens)*. Supplementary feed crops of turnips *(Brassica rapa)* were grown on a limited scale each year after which new grass was sown, providing Paradise Shelduck flocks with a highly preferred food for several years thereafter.

Scattered throughout the station were numerous stock ponds ranging in size from about 300 m^2 to 2 ha and located in a wide variety of situations from deep in gullies to high on exposed hillsides. Most had no marginal vegetation and had heavily eroded margins, the result of stock trampling. The numerous temporary empoundments and swampy soaks also provided feeding and rearing habitat for shelducks.

Breeding pairs were studied on Huiarua Station, an area of 125 km^2. Approximately 87 km of farm roads and tracks provided vehicular access close to most of the 66 stock ponds, 16 naturally-created empoundments and to various sections of the Mata River. Some pairs within this area lived where access was difficult, and so they were not studied intensively. The intensive observations were restricted to those pairs which could be easily observed. To increase the sample of 'easy' pairs I included some resident alongside the Waitahaia Road (Fig. 1).

In addition to observing the survival and dispersal of ducklings reared by the intensively observed pairs, data were also collected on broods reared on a series of stock ponds alongside the Tuakau and Mata Roads (Fig. 1).

Data on flock birds were gathered at all flock sites within the study area.

METHODS

Capture

I have previously described the techniques used to capture moulting shelducks (Williams 1972).

Ducklings reared on small ponds or on swampy flats were caught

FIGURE 2 — The heavily eroded and slumped pastoral landscape of Huiarua Station. A — looking south-west up the Mata River valley from pond 54. B — looking south-east from pond 75.

by hand as they hid amongst emergent vegetation. Those reared on ponds with no escape cover usually attempted to avoid danger by diving. To catch these, a 10 cm mesh gill net, very lightly weighted, was hung in the water and the diving birds became entangled.

Five females were captured on their nests during the last five days of their incubation period. After banding they were returned to their nests and, although they all departed almost immediately, all resumed incubation within 3 - 4 hours and successfully hatched their clutches.

Banding

From 1970 to 1972, ducklings were caught throughout the study area and banded with numbered stainless steel bands and a coloured plastic band to denote year class. In addition, birds moulting at four sites elsewhere in the Gisborne-East Coast district were caught and banded with colour combinations which denoted locality and age. As a result, 11 birds from 10 of the 25 pairs studied in 1973 could be identified individually.

In January 1974, 196 birds moulting on Pond 20 (Fig. 1) were caught and banded, each with a unique colour combination. The following breeding season, 16 birds from 14 of the 21 intensively-observed pairs could be individually identified.

In January 1975, a further 958 moulting birds were caught on Ponds 20 and 69 (Fig. 1) and banded with individual colour combinations. In the subsequent breeding season, 38 individuals from 28 of the 32 pairs could be identified.

In each of the 1973, 1974 and 1975 seasons, all ducklings reared within the study area (and some reared outside) were banded with numbered plastic colour bands which allowed both year-class and individual identification.

The numbered stainless steel bands used on all birds were 12 mm high with an internal diameter of 14 mm. Colour bands were made from " Darvic " plastic of similar dimensions to the metal bands. Numbered plastic bands were also made of " Darvic " plastic, 20 mm high and 12 mm internal diameter. The engraved digits (the engraving filled with black enamel paint) were 12 mm high and the two digits were vertically offset so as to avoid confusion about which was the first.

Observations

All observations were made using 10 x 40 binoculars and 40 x spotting scope. Birds throughout the study area were tolerant of farm vehicles and I used a landrover as a mobile hide. In difficult terrain or weather, work was done on foot, and careful stalking allowed me to approach close enough to read colour combinations and engraved band numbers.


B

Throughout the breeding season (August to early November) all pairs were observed on average once every two days, although some pairs near my field base (near Pond 47, Fig. 1) were sometimes seen three times daily. Only in dry weather were all parts of the study area visited in a single day. Each pair was observed long enough to record its identity, location and behaviour, but for some special studies pairs were observed continuously for several hours.

Outside the breeding season, visits lasting about one week were made in various months to build up a picture of the species' annual cycle.

ANNUAL CYCLE

Paradise Shelducks gather in large flocks for their annual wing moult. Their numbers at the traditional moulting sites build up rapidly in late December when non-breeding juveniles (birds in their first year) and yearlings (birds in their second year) arrive, followed later by the failed breeders and finally the successful breeders, often accompanied by their fledglings. Each bird is flightless for 3-4 weeks but remains with the flock for longer, and it is not until early March that the first adults leave to return to their breeding areas. The previous year's territories are then reoccupied; pairs which may have lost contact during the moult are re-united while the newly fledged young (now juveniles), together with juveniles of the previous year (now yearlings) remain together as a flock.

From April to July, pairs defend their territories against neighbours and previously non-breeding individuals which are attempting to establish territories. Mates lost are replaced by new partners at this time.

The large flock remaining at each moulting site gradually fragments as small groups of birds move away to prime feeding areas nearby where they remain throughout the rest of the year. However, in September-November some juvenile pairs temporarily leave the flocks and begin to visit areas which are potential territory sites and some preliminary attachments to sites are made. By December, the various flocks return to the moulting sites and the first juveniles are flightless in mid-December.

During July, nest prospecting begins, with pairs spending much of the day, particularly the morning, away from their principal resting and feeding areas while the female looks for a suitable nesting site in hollow logs or holes in the ground or in trees. The first eggs are laid in August, laying reaching a peak toward the end of the month. Ducklings first appear toward the end of September and are taken from the nest to nearby water, usually the stock pond within their parents' territory, where they are reared for eight weeks until fledged. After fledging, the young and parents remain as a family group on the territory for up to two months while the adults undergo most of their body moult. Later (usually late January or February), the adults migrate to their moulting site to complete the wing moult.

SOCIAL STRUCTURE

During the breeding season the population comprised two distinct social categories:

(a) Those birds which, as pairs, were spatially separated from all others, occupying an area from which all other shelducks were excluded and in which almost all of their activities were confined. These were the territorial pairs, most of which attempted to breed.

(b) Those birds, some of which were paired, which associated with numerous others and spent most of their time in flocks at specific localities. These were the flock birds, none of which attempted to breed.

Outside of the breeding season, this clear separation did not occur. When, in March and April, the large moulting flocks fragmented, small groups formed on the breeding areas. These comprised some previous breeders (mostly males), some younger birds approaching breeding age and which later in the year would attempt breeding, as well as a few juveniles and yearlings. The experienced breeders were awaiting the return of their previous year's mates and so the flock with which an experienced breeder was associated was invariably that which had formed closest to its territory of the previous year. Once re-united, the pair left the small flock to reoccupy their territory. If however the flock was resident on the pair's former territory, much fighting ensued before the flock was driven away. Gradually, these small flocks disintegrated, and by June the experienced breeders were back on their former territories, newly mature pairs were on unclaimed areas, and the juveniles and yearlings were drifting away to rejoin large flocks at the moulting site or at specific flock areas nearby.

THE FLOCK

The following discussion refers to the flock during the breeding season, unless otherwise stated.

Flock sites

The flocks of juveniles and yearlings did not move throughout the study area; instead, they were almost always to be found at 10 specific areas, shown in Fig. 1 and 3. All flock sites had two principal characteristics:

1. A wide-open aspect so that feeding birds had an uninterrupted view of a large area; and
2. Proximity to a concentration of territorial pairs.

Only one of the ten sites was not close to or associated with the river. This site (No. 7, Fig. 1) was on rolling pasture in the midst of territorial pairs. Here flock birds fed mainly on pasture grasses on a large flat area and roosted on tops of hillocks from which they had an extensive view. Seven sites were on the riverbed or on low flats adjoining the river where the birds fed mainly on high-quality

FIGURE 3 — Paradise Shelduck flock sites. A — site 6, a riverside flat of new grass. B — site 8, comprising a natural empoundment of about 1.5 ha on which moulting occurs. Flat swampy pasture extends further to the right of this view and behind the trees in the centre. The Mata River is visible at top left.

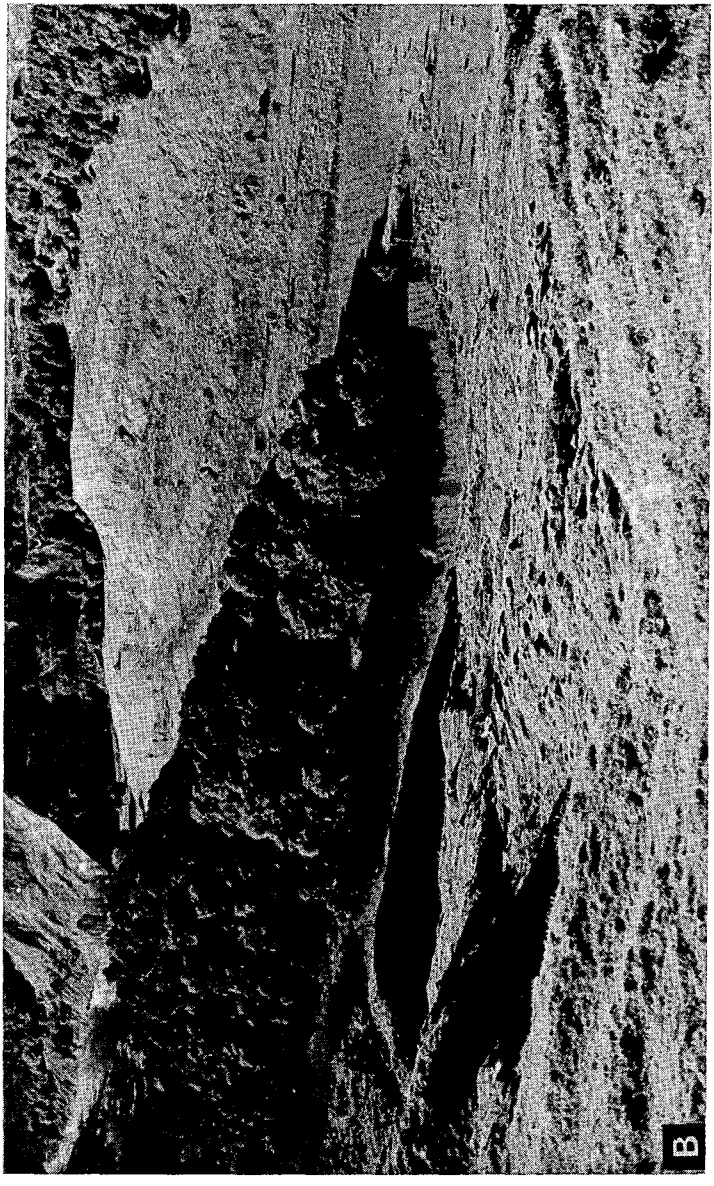
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TABLE 1 — Characteristics of flock sites.

Site location (from Fig. 1)	Terrain	Feeding area	Associated water area	Usage
1	river flat	pasture/swamp	river	constant
2	hillside	swamp	ponds	limited
3	hillside	swamp	ponds	limited
4	river flat	pasture	river	limited
5	river flat	pasture	river	limited
6	river terrace	pasture	river/ponds	limited
7	paddock	pasture/swamp	ponds	constant
8	river terrace	pasture/swamp	river/ponds	constant
9	river bed	swamp	river	limited
10	river bed	swamp	river	limited

young pasture and in associated swampy soaks (Table 1). Sward height determined the use of the pasture; once grass stood 8-10 cm high the birds avoided it, and so farming practices such as removal of stock or closure of a paddock for hay could change the distribution of flocks.

The two hillside flock sites were both in the Waitahaia River valley but were over 350 m above the river. The birds concentrated about two ponds, using them for bathing and drinking and the adjacent swampy soaks for feeding. When these soaks dried up in late spring the birds joined the flock at the river flat nearby.

Choice of flock sites

Although there were 10 flock sites in the study area, they may be regarded as forming four distinct units: sites 1,2,3; 4,5,6; 7; and 8,9,10. This division is based on the behaviour of marked birds. Of four males and 27 females seen in flocks four or more times during their first year of life, only two females were observed in more than one of these unit areas. Of another 10 males and 14 females seen two or three times in the flocks, only six of the males were seen in two of the unit areas.

All of the above 41 juvenile females were most frequently seen at the flock site which was closest to their natal territory. This was not so for males. Eight of the above 14 males were seen at flock sites well away from their natal area.

These observations suggest that females almost continuously remain close to their area of birth whereas males are more mobile, a feature of the species' biology which may account for seasonal changes in the sex ratio within the study area (see Sex Composition of Flock) and the lack of examples of males breeding near their natal area (see Population Dynamics).

Age composition

No adults were seen in flocks at the moulting sites after April. Although the small flocks on the breeding areas included adults, juveniles and yearlings, no adults were ever seen in flocks at the 10 flock sites. The breeding season flock was therefore a separate social entity by May.

Most birds observed in the breeding-season flocks were juveniles: of 161 banded individuals identified there during 1973-1975, 143 (89%) were juveniles, the rest yearlings. No adults, paired or unpaired, with previous breeding histories or birds three years of age or older were seen in these flocks.

Towards the end of the breeding season (November), the number of yearlings in the flocks increased. Some had occupied territories but apparently had not attempted to breed. They abandoned their territories and rejoined the flocks before the annual moult. Adults whose breeding attempts had failed associated with flock birds only at the moulting sites and were never seen at any of the main flock sites.

The breeding-season flock therefore comprised juveniles and yearlings only.

Sex composition

The numbers of males and females in some of the flocks encountered from February to October were recorded. Because newly fledged young resemble adult males and cannot readily be distinguished from them when viewed from a distance, no data were collected from November to January.

Post-moulting flocks in February and March contained significantly more females than males (Table 2). This was probably caused by a difference in the timing of departure of males and females from the moulting sites (the male of a breeding pair was usually the first to be recorded in the small flocks on the breeding areas), and the dispersal of juvenile males may also commence then.

TABLE 2 — The percentage of female Paradise Shelducks seen in post-moulting flocks (February to April) and in breeding-season flocks (May to October). A chi-square value greater than 3.82 indicates significantly more females than males.

Month	No. of flocks	No. of birds	Female %	Chi-square value
February	28	2676	52.2	5.2
March	80	4270	53.9	25.5
April	16	238	49.6	0.2
May	11	227	50.7	0.04
June	43	1357	60.2	56.5
July	30	389	64.8	34.0
August	85	1453	61.3	73.6
September	131	3301	60.4	143.4
October	150	3558	55.3	39.3

There was no difference in the number of each sex encountered during April and May and because of the small samples, the percentage of females recorded then was not significantly different from that recorded in February and March. However, the percentage of females seen in June was significantly greater than that seen in May ($X^2 = 7.3$, $0.01 > p > 0.001$). This rather sudden increase in the percentage of females may have resulted in part from the effects of the May shooting season. Williams (1972) has recorded that males are more likely to be shot than females — 53% of the shooter's bag were males. However, there must be other contributing factors. One possibility is that yearling males may pair with older females, leaving a surplus of yearling females in the flocks. Only one banded yearling male was identified in a flock during June to September but four in October, a time when the percentage of females in the flocks decreased when yearling and juvenile pairs, which for part of the breeding season may have temporarily occupied territories, returned to the flock.

Courtship behaviour of flock birds

Within the flock, some juveniles and all identified yearlings associated in pairs. Many of these associations were temporary; one male, for example, kept company with four different females at various times. Courtship and the making and breaking of these temporary associations was the major non-feeding activity within the flocks.

The dominant female courtship display was Inciting (Heinroth 1911). Females typically incited their actual or potential mates to attack less preferred males or other females, thus choosing the male whose response was the strongest.

Inciting occurred on land or water from a posture which varied with the intensity of the display. On water, low intensity Inciting was characterised by a forward-stretched neck and head, both being inclined at an angle of 20°-30°. The head was frequently downturned so that the bill was close to the water. High-intensity Inciting (Fig. 4A) results in the outstretched body lying almost flat along the water surface, the head and neck stretched as far forward as possible. Postures intermediate between these extremes, indicative of differing intensities, may be recognised. This display was accompanied by a loud, rapidly repeated high-pitched note uttered continuously. When displaying, the female pointed to and frequently swam toward the " offending " bird(s), swinging the body from side to side, the swinging movement and the calling increasing before she charged.

On land, the posture also varied in intensity. At low intensities the body axis was held at about 25° to the ground, the head and neck held low and stretched well forward (Fig. 4B). With increasing intensity the head was further lowered and a charge usually followed.

The male's initial response was to move close alongside his female, uttering a monosyllabic note, best described as a honk. If Inciting persisted, the male call changed to a higher-pitched disyllabic

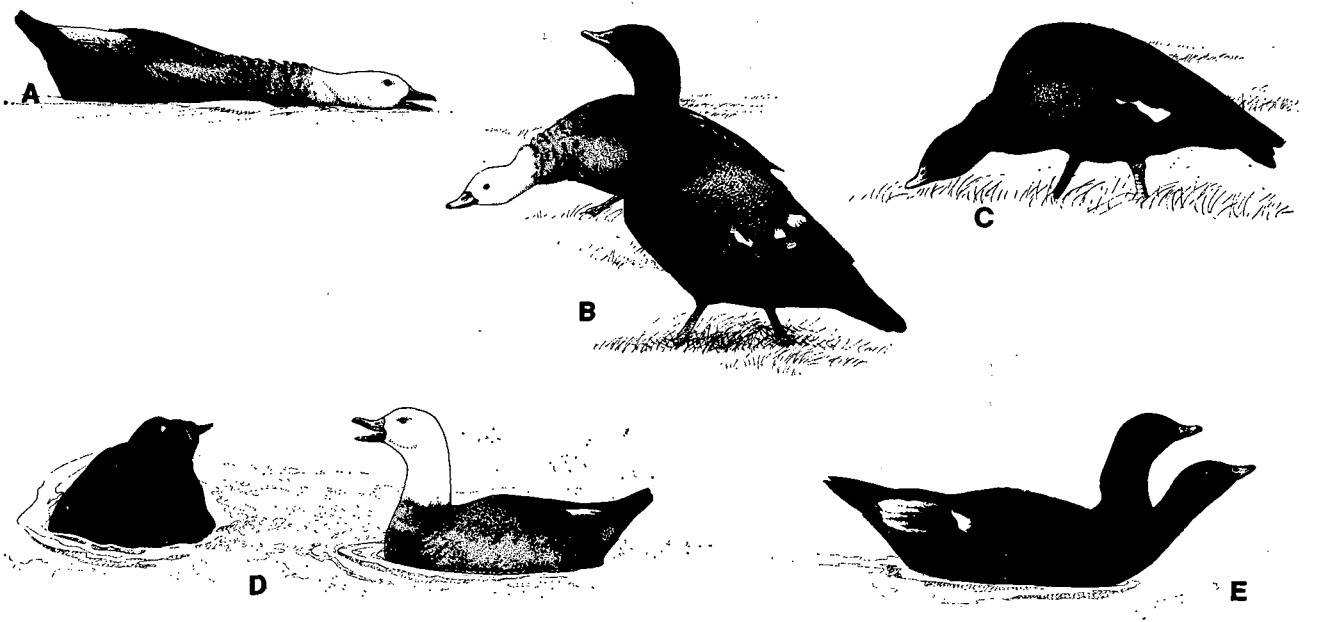


FIGURE 4 — Courtship displays of the Paradise Shelduck. A — high-intensity Inciting on water by the female. B — Inciting on land by female, male in the High-and-Erect posture. C — male Threat posture. D — Mutual Trumpeting Ceremony. E — male Triumph posture. Del. Rod Morris.

note, and he adopted a High-and-Erect posture in which the head and neck were stretched forward and upward and the lower neck feathers raised (Fig. 4B). The call was uttered in rapid succession and while calling the male pivoted first toward the threatened bird, then back to his mate. This was usually followed by the adoption of the Threat posture and a charge (Fig. 4C).

Following a successful chase, the pair usually indulged in a Mutual Trumpeting Ceremony; the male adopting the High-and-Erect posture and giving the disyllabic call, repeated rapidly, the female adopting the Erect posture with the neck vertically up-stretched, the head horizontal and calling continuously (Fig. 4D). When the female ceased calling the male note changed to the Triumph call — a disyllabic note similar to that previously uttered although more protracted, with a distinct break between the syllables and the second syllable declining in amplitude and volume. There was an associated Triumph posture; the short first syllable of the call was associated with a rapid upward jerking of the head, the longer second by a forward movement of the head, still with the neck fully stretched (Fig. 4E).

The success of the male in repulsing challenges from others seemed to be the basis on which the pair bond was maintained. Females changed mates when the male was unable to curtail the persistent presence of others and was beaten in the fights which occurred. The Mutual Trumpeting Ceremony was not always performed after the male was beaten in these fights and its absence probably indicated an impending change of association.

Territory prospecting by flock birds

As pairs, many juveniles and most yearlings left the flock for varying periods and attempted to occupy and settle at or near the female's natal area. Sometimes these excursions were for only a few hours, for the natal territory was usually occupied by a breeding pair which drove the pre-breeders away. If, however, the natal pond or an area close by was unoccupied, the flock pair often spent most of the day there before returning to the flock in the evening. Eventually, occupation of this area became continuous and the pair began to defend it against other flock pairs.

These yearling or juvenile pairs on their territories tended to decoy others from the flock and it was common to encounter several pairs and individuals with them. Inciting and fighting were common in these situations with usually one pair constantly attacking others, both on the ground and in aerial pursuits. As a result of clashes on these potential territories, changes in pairings occurred.

Most of this prospecting for territories occurred during September and October. On 46 occasions from July to November 1974, I saw juvenile pairs prospecting, three during July, eight in August and November, 12 in September, and 15 during October.

Small groups of females only were sometimes seen flying and landing at various localities amongst the territories, often near to or alongside adult males waiting alone on their territories. Usually these groups of females were immediately attacked and forced away.

TERRITORIAL PAIRS

Territorial birds are defined as those which, as pairs, were spatially separated from others, exclusively occupying and defending a fixed area of habitat to which almost all of their activities were confined.

This definition includes pairs, one or both members of which were juveniles, pairs which, although of breeding age apparently did not attempt breeding, and pairs which bred. A distinction was therefore made between those territorial pairs which attempted to breed and those which did not. A breeding attempt was identified by one of the following criteria:

1. The pair appeared with ducklings. All adults guarding broods were known to be the parents of some or all of the ducklings in their charge.
2. The nest of a pair was found.
3. The male of a pair was seen alone on his territory.

I have no records of members of pairs conforming to criteria 1 and 2 being separated from each other during the breeding season except when the female was at the nest. While the female was nesting the male remained alone on the territory, and for most breeding pairs there were numerous such sightings. Furthermore, the behaviour of breeding females was distinctive. During egg laying she was absent from the territory one to three hours each day; when incubating she was present on the territory for about one hour, two or three times daily, feeding in a characteristically avid manner. Immediately prior to egg laying, females developed a conspicuously distended abdomen (Young 1970) as the ovaries and oviduct enlarged. The minimum evidence upon which a breeding attempt was identified was the sighting of an obviously gravid female followed shortly thereafter by a single sighting of the male alone on the territory.

Territory requirements

Most territories were established over pasture, each encompassing one or more of the 66 ponds and 16 natural empoundments within the study area. Of the 103 pairs followed during 1973-76, 87 (84%) established territories about ponds or empoundments, and 7 (7%) centred their activities along a section of the Mata River or its tributary. The territories of the rest (9%) contained no open water, but instead, fresh water seepages and swampy areas were substituted.

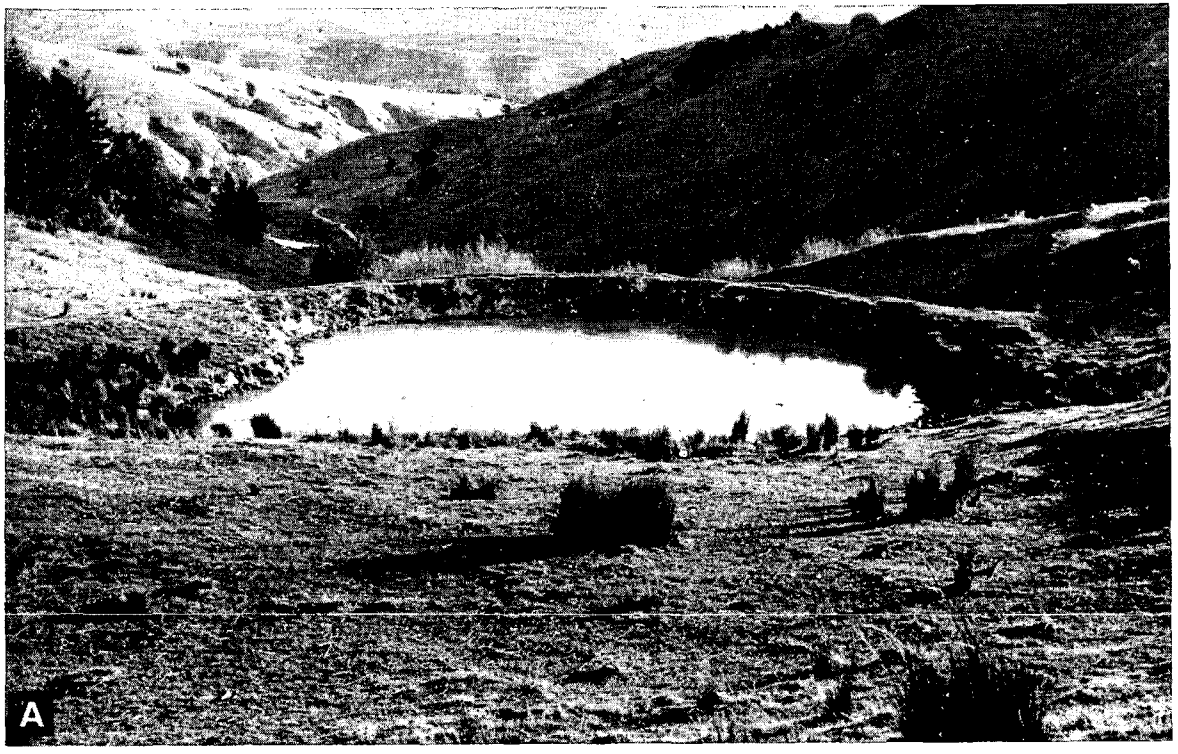
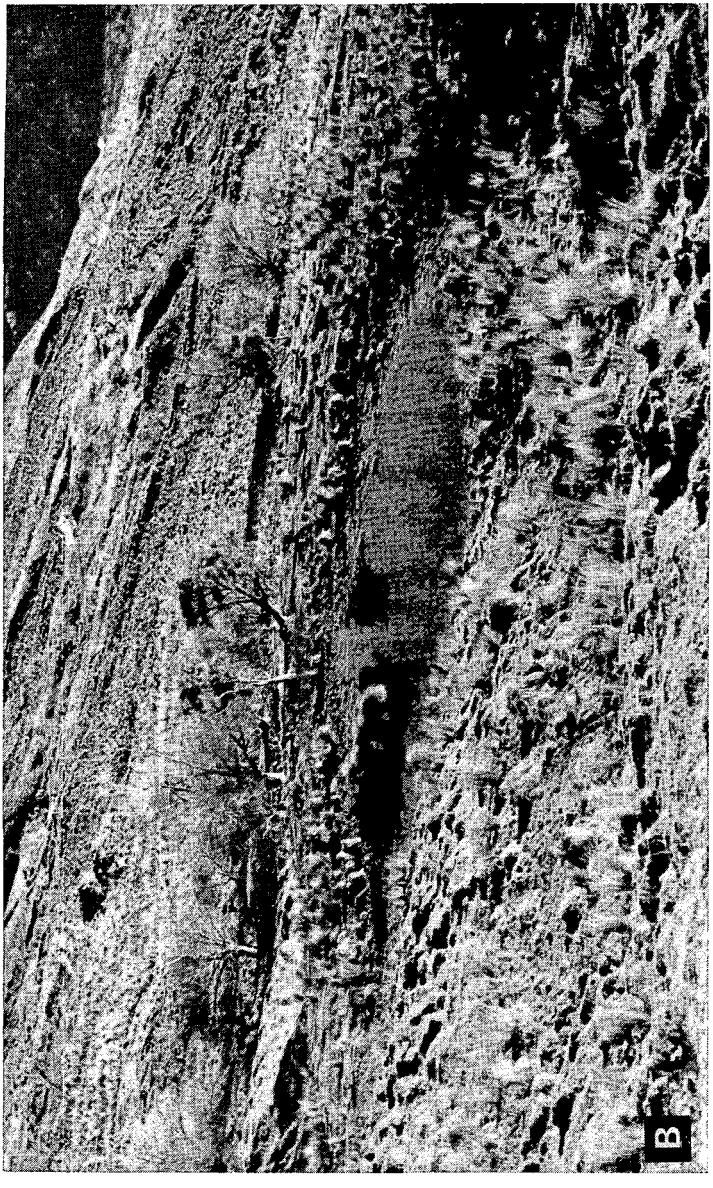


FIGURE 5 — Locations and characteristics of stock ponds and natural empoundments included by Paradise Shelducks in their territories. A — a stock pond on a hill or ridge top with a panoramic view. B — a natural empoundment on a large hillside. C — a stock pond on flat ground containing suitable escape cover for ducklings. D — a stock pond deep in a gully.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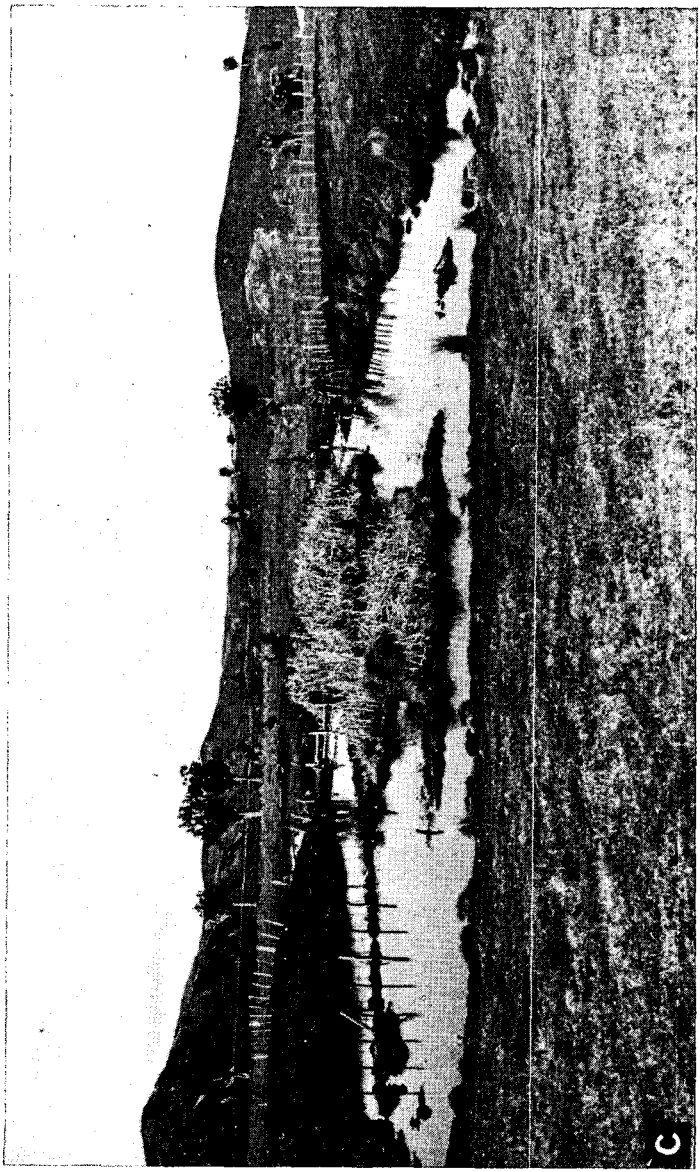
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Although most pairs established their territories about ponds, not all ponds appeared suitable; some were used each year, some never. The choice seemed primarily determined by the pond's surroundings. To examine this, ponds were classified into four categories according to their location — on hilltop or ridge-top (Fig. 5A), on hill face (Fig. 5B), on relatively flat land (Fig. 5C) and in a gully (Fig. 5D), and their frequency of inclusion in a territory over the four years of study was determined. The analysis (Table 3) shows a clear preference for ponds on hillsides and flats and an avoidance of ponds in gullies.

TABLE 3 — Frequency with which 66 stock-ponds in different locations were included in Paradise Shelduck territories during the four years 1973-1976.

Frequency of use	Stock-pond location			
	Gully	Hillside	Hilltop	Flat
In 3 or 4 years	4	21	2	14
In 1 or 2 years	6	1	2	2
Never	10	2	0	2
Total ponds in each location	20	24	4	18

The preferred ponds had one major feature in common — a panoramic view from at or near the dam face (Fig. 5A). Five other characteristics of ponds — size, depth, extent of marginal vegetation, zooplankton content, and water clarity were also examined but there were no significant differences between those ponds used regularly and those used occasionally or never.

Of the nine territories established about swampy areas, two were in a broad gully, four on hillsides and three on flats.

Most pairs included only one pond within their territory; of 87 territories, 56 (64%) included one pond, 17 (20%) included two and 14 (16%) three or more. Where two or more ponds were occupied, they were usually only a few hundred metres apart and often all ponds could be seen from the pair's main roosting point. In five territories, the ponds were spaced well apart and birds spent much time commuting between them. Three of these five pairs were non-breeders; the two which attempted breeding reduced their occupied area once the female commenced incubation but, after the ducklings emerged, re-used all the ponds they had originally occupied.

Territorial pairs fed mainly in swampy soaks and gullies, eating the roots and shoots of the semi-submerged grasses. The extreme irregularity of the countryside — the flatter land having numerous shallow gullies and creeks, the steep expansive hillsides having numerous slumps and soaks — provided everywhere an abundance of these choice

feeding areas and their distribution is probably one of the factors determining territory size.

Constancy of territory site

The records of 36 identifiable birds (21 female, 15 male) which occupied territories in two or more successive years showed that changes in territory site rarely occurred. All 21 females and 13 of 15 males established their territories at the same site in successive years.

Of the two defaulting males, one as a juvenile occupied and defended its natal area with its sibling. The following year however, I did not see its sibling and the male paired and bred with an established breeding female on a nearby territory. The other male lost his mate in June and re-mated with a two-year-old. Although the re-pairing occurred on the male's original territory this area was abandoned and the pair established a new territory about the female's natal pond, removing a pair which had newly established themselves there.

Apart from these examples, the loss of a mate during the breeding season did not cause breeding or non-breeding birds to abandon a territory. One male and one female from two non-breeding territorial pairs were shot in October. Both the survivors found new mates and remained on their territories. In another three pairs which had started breeding, one member either died or was experimentally removed. All three survivors (two females, one male) quickly obtained new mates, remained on their territories and commenced breeding a second time.

Location of territory in relation to natal site

Eighteen females whose natal sites were known established territories either as breeders or non-breeders within the study area. All but one did so at or close to the pond on which she had been raised.

Three males whose natal sites were known established territories within the study area. One male, referred to in the previous section, occupied its natal pond in one year and another nearby the next. The territories of the other two breeding males were well removed from their natal areas.

Timing of territory occupation

Intensive observations of breeding pairs commenced on 25 July in 1973, 1974 and 1975. By that date most pairs had established their territory (24 of 25 pairs in 1973, 17 of 21 pairs in 1974, and 26 of 32 pairs in 1975). None subsequently changed their territory site and none of the territorial birds changed mates.

Visits were made to the study area in late March and mid-May 1974, mid-April and mid-June 1975 but in 1976, although intensive observations throughout the breeding season were not attempted, territorial pairs were identified during visits in late June, early September and early November.

In late March 1974, only two of the pairs which occupied territories during the subsequent breeding season were found back on their territory while another male, without its mate, was defending the pond he had occupied the previous season. By May 1974, 10 (48%) of the 21 breeding territories were occupied. The birds involved were probably territorial pairs of the previous year; three of four banded individuals which bred in both 1973 and 1974, were occupying territories then.

In April 1975, six pairs which subsequently attempted breeding were then occupying territories; this group included three of the seven banded individuals which bred in both 1974 and 1975. By mid-June 1975, 19 (63%) of the 32 territories were occupied. All of the identifiable individuals from the previous year were re-established on their territories at that time.

In June 1976, 18 (72%) of 25 pairs recorded on territories in September were observed defending their chosen pond or water body.

These observations suggest that the breeding area is reoccupied gradually with previously territorial pairs returning first, those attempting to breed for the first time establishing themselves later, and a few juvenile pairs setting up territories after the breeding season has commenced. This is true only of permanently occupied territories: during both May and June I saw pairs defending ponds which later during the breeding season remained unoccupied. For example, in June 1975, 25 pairs had established territories but only 19 of these remained during the breeding season. Of the 12 birds which abandoned their territories five were banded, four being two-year olds, the other was of unknown age. Similarly, in June 1976, 26 pairs were occupying territories, seven on areas which were not used during the breeding season although six ponds subsequently used were at that time unoccupied. Four of these 26 pairs had by September established their territory elsewhere within the study area, and another four pairs left the area: ten of these 16 birds were banded, six of which were two-year olds, (one as a juvenile had occupied a territory the previous year), three were of unknown age and one was a juvenile.

Thus, most of the identifiable birds involved in the temporary establishment of territories were two-year-olds.

Amongst these " prospecting " territory seekers some pair associations were obviously temporary. For example, of the 26 pairs encountered in June 1976, changes of mates occurred in three pairs, all involving a two-year old. Four mate changes occurred amongst pairs encountered in both June and the breeding season of 1975 and three pairings changed between May and August 1974.

These observations on temporary territories and pairings suggest that amongst pairs which have not previously attempted breeding or established territory there may be considerable competition for both space and mates. A dominance hierarchy may develop amongst these

young birds with some pairs establishing territories on highly suitable areas (and maintaining their pair bond), other less successful pairs occupying less suitable areas (from which they attempt to occupy better sites and amongst which pair-bonds may not be permanent), while in a third category, pairs may fail to establish themselves at all and so remain in the flock for a second year.

Defence of territory

Territories were defended mainly by boundary flights and physical attacks. Boundary flights in which two pairs of birds flew close alongside each other in wide circuits over a territory appeared to be the principal method of territory defence during the period of territory re-establishment and before the onset of laying. During these flights, the defending pair flew on the inside or territory side of the other, steadily widening the circuits until the intruders were outside the defended area, at which point the defenders would wheel away and return to the territory. Both pairs would call vociferously, the females uttering their Inciting call and the males responding with a disyllabic call identical to that associated with the High and Erect posture on the ground. Occasionally the defending pair attempted to strike or peck at the others in flight.

I also observed these flights in response to a single intruder. Since the response was similar to both males and females, I interpreted these flights as territorial defence. However, Riggert (1977) suggested that similar flights involving single females in the Australian Mountain Duck *(T. tadornoides)* were courtship flights. He made no comment about flights involving single males.

Immediately before egg-laying, during egg-laying and early incubation, and during the care of the ducklings, the drake was particularly aggressive and immediately pursued or attacked any intruding individual, pair or flock. However he became more tolerant of single intruders as incubation proceeded. Solitary juvenile females were often seen standing or resting for extensive periods within a territory while the defending male rested on the pondside awaiting the reappearance of his incubating mate. But as soon as the incubating female returned to feed, intruders were immediately driven off.

Chases and physical attacks were not always necessary to drive intruders away. The adoption of the Threat posture by the male (Fig. 4C) or the Inciting posture (Fig. 4B) or Inciting call by the female was often sufficient to put intruders to flight and prevent others from landing in the territory.

BREEDING

Males

AGE OF FIRST BREEDING

Five banded males established territories as two-year olds, four of which attempted to breed. The fifth male paired with a female of the same age and did not attempt breeding until its third year.

Seventeen banded one-year-old males were identified during the breeding seasons, only three of which occupied territories. Two of them made no breeding attempt, their mates being juveniles also. The third territorial male was, according to the criteria given earlier, a member of a breeding pair. His mate, of unknown age, developed the greatly distended abdomen typical of a female about to lay, and subsequently the male was twice observed alone on the territory. Six days then elapsed without a further sighting of the male alone. I then attempted to shoot the male but succeeded only in breaking its wing and it was a further five days before it was recovered and killed. Some testicular regression may have occurred in the meantime. Histological examination of the testes (by Dr M. L. Gorman, Aberdeen University) showed that interstitial (testosterone-secreting) tissue was well developed and Leydig cells were numerous and large but that no spermatozoa were present. Although this one-year-old male was probably sexually active in its behaviour (as a result of well-developed testosterone tissue), it was not fertile.

Females

Nineteen two-year-old females were observed throughout a breeding season. Three remained in the flock, the other 16 occupied territories, 10 of which attempted to breed.

All females of the above sample which survived into their third year attempted to breed.

Forty-one banded one-year-old females were seen two or more times during a breeding season, eight of which established a territory for a brief period. None were found breeding.

Thus, while most two-year-olds occupied territories, about half of the females delayed their first breeding attempt until their third year, whereas most males may have bred as two-year-olds.

NESTS

Nest-site prospecting

Some pairs began searching for nest sites up to two months prior to laying, and during August it was their main early morning activity. Prospecting seldom occurred in late afternoon.

Only the female investigated likely nest sites. Throughout all prospecting activity the male remained alert and on guard nearby. When examining trees for suitable holes, the female would fly on to branches before sidling along to investigate holes in the main trunk. To reach more inaccessible holes the female would attempt to hover briefly in front of the opening before trying to settle on the lip. Tall dead trees were particularly favoured and occasionally the male would also settle in the tree alongside the female.

Prospecting occurred mostly amongst logs and stumps on the ground (Fig. 6). Two females, for example, spent over four hours continuously prospecting all logs on a hill face and several others were

seen investigating logs for over two hours. Every likely hole in or under each log was explored, some by merely poking the head inside, others by the female entering completely. Some holes were investigated several times; the female first exploring the hole, moving off to look at another log nearby and then returning to investigate further; this activity being repeated several times.

The behaviour of one pair about its nest site was followed from their initial investigation to egg laying. The nest was in a tree hole, about 300 m from the main resting and feeding area of the territory. At dawn each morning, the pair would circle above the nest site calling loudly, eventually settling on pasture about 50-80 m away. There the birds remained feeding and resting for 3-4 hrs before flying off. Several times during the rest of each day, they returned and landed nearby. On each visit the female called vociferously but I did not see her visit the nest site. This pattern of behaviour was repeated day after day until egg-laying commenced and presumably served to keep other pairs and stray flock females from investigating the nest site.

Nest sites

Forty-seven nests were located: 29 (62%) were inside hollow logs on the ground (the nest being either in the log or beneath the log), 4 (9%) in holes or burrows in the ground (mostly the tunnel left following the decay of a tree root), 3 (6%) in holes at the base of cabbage trees *(Cordyline australis)*, and 11 (23%) in holes above ground level in standing live or dead trees (Fig. 7A).

Nine of the 11 nests in tree holes were in willows *(Salix fragilis)* (Fig. 7B), one in a "blue gum" (*Eucalyptus* sp.), the other in a dead rata *(Metrosideros robusta)*. Ten were within 3 m of the ground, the other about 20 m high.

Most of the 47 nests found were close to the pond or water area in the territory; 14 (30%) were within 100 m, 12 (26%) were 100-300 m away, 11 (23%) 300-500 m distant, 6 (13%) 500-1000 m away, and 4 (8%) over 1 km from the pond.

Seven nest sites were used in consecutive years by the same female. All were those in which all eggs had successfully hatched in the previous year. However, not all old sites were re-used. The sites of four nests in which all eggs had hatched and 10 in which only some had hatched seemed to have remained unaltered over two years but the females did not use them again. The re-use of a nest site seems primarily dependent upon a total hatch in the previous year.

Nest bowl

All nests were placed as far from the entrance hole as the female could scramble. Those on the ground or on the floor of a hollow log were simple concavities containing a few fragments of bark, decayed wood or grass (all probably accidentally added) and some breast feathers. Large amounts of down were usually found at each nest

FIGURE 6 — The numerous stumps and logs on hillsides were investigated by Paradise Shelduck pairs when searching for nest sites.

but were not used to insulate the eggs from the ground. When the female was off the nest, the down was heaped over the top of the eggs (Fig. 8) but when incubating the female arranged it around the rim of the nest bowl (Fig. 9).

EGGS

Colour

All freshly laid eggs were pure white. However, once incubation commenced, they quickly became discoloured to a dirty brown-yellow.

Dimensions

All 223 eggs measured were ovoid and only slightly tapered. They ranged in length 61.7-72.3 mm (mean 67.2, SD 2.1) and in width 44.5-52.1 mm (mean 48.6, SD 1.4). One small 'albumen only' egg was found but not measured.

The eggs of two females nesting for the first time were measured; a two-year-old laid 10 eggs which measured 66.3 ± 2.2 x 47.8 ± 0.6 mm and a three-year-old laid 7 eggs which measured 66.6 ± 2.5 x 48.1 ± 0.7 mm.

Weight and composition

A complete clutch of 10 eggs was weighed in the laboratory; mean weight 84.5 ± 5.2 g, range 72.0-90.7 g.

These eggs were hardboiled and the yolk, albumen and shell with its membrane separated and weighed. Each constituent was then dried in an oven at 50 °C until no further weight loss occurred, and the percentage dry weight composition determined (Table 4).

TABLE 4 — Mean percentage composition of 10 Paradise Shelduck eggs.

Constituent	Wet weight %	Wet weight SD	Dry weight %	Dry weight SD
Yolk	40.0	0.9	56.0	1.2
Albumen	47.7	0.9	15.5	1.0
Shell + membrane	12.3	0.4	28.5	0.7

CLUTCH SIZE

The sizes of 36 clutches each believed to have been laid by a single female, are shown in Table 5. Data for all years 1973-76 have been combined.

Three clutches to which more than one female may have contributed were found. An unpaired two-year-old female was twice seen to enter the nest of another two-year-old. This nest contained 14 eggs, seven of which hatched, one contained a dead embryo and six were infertile. I believe that both females laid in this nest. For a first-time layer, 14 eggs is an exceptional clutch and was greater than the female subsequently laid (12 and 10).

FIGURE 7 — Nest sites of Paradise Shelducks. A — inside a hollowed stump, the entrance being from the top; B — in a hole in the trunk of a willow tree.

FIGURE 8 — The nest of a Paradise Shelduck inside the stump shown in Fig. 7A. Plucked breast feathers (more usually down) are heaped on top of the eggs while the female is away from the nest.

TABLE 5 — Size of Paradise Shelduck clutches, 1973-1976.

No. of eggs	5	6	7	8	9	10	11	12	13	14	15
No. of clutches	1	2	1	8	7	10	1	5	0	0	1
Total clutches	36			Mean 9.4					SD 2.0		

The history of another dual clutch is more precisely known. One female, on laying her sixth egg, broke one and subsequently abandoned her nest. Two days later she was observed entering another female's nest nearby and five days later this nest was also abandoned. Of the 13 eggs in the second nest, nine showed signs of early embryo development, the other four no development. When length v. width of these eggs were plotted graphically, there were two distinct groups of eggs, 10 and 3. (A similarly clear separation occurred between the eggs of the second clutches of the two females involved).

In a third nest, a clutch of nine eggs was approximately two-thirds incubated when an unpaired female added two infertile eggs. This clutch was not abandoned.

Included in Table 5 are three repeat clutches. Both females involved in the 13-egg dual clutch laid again; that which broke its egg laid nine, the other 10. Another female whose initial clutch size was unknown laid a second clutch of 10.

Three females nesting for the first time as three-year-olds laid clutches of seven, eight and 10; four nesting as two-year-olds laid clutches of six, eight, eight and 10. (Mean for all 7.9 ± 1.2). One of these three-year-olds increased her clutch from seven to eight, another from eight to 11 and a two-year-old from eight to 12 in the succeeding year. The two-year-old involved in the combined clutch of 14 laid 12 eggs as a three-year-old and 10 eggs the following year.

INCUBATION

Only the female incubated (Fig. 9). The male's sole duty at or near the nest was to accompany the female on her return. He seldom landed, however, but instead circled overhead while the female landed and approached the nest.

Incubation period

The full incubation period is known only for two nests. Ducklings emerged from these 32 and 33 days after the laying of the last egg of the clutch. In four others, ducklings emerged 29-31 days after I found the already incubated nest. The average incubation period for 11 nests of captive birds was 30 days (T. A. Voss, pers. comm.). Other authors have reported the incubation period as 30 days (Delacour 1954, Soper 1963), 34 days (Oliver 1955) and 35 days (Williams 1963). The incubation period of the closely related Australian Mountain Duck is 30-32 days (Riggert 1977) and 30-31 days for the European Shelduck, *T. tadorna* (Hori 1964).

FIGURE 9 — A female Paradise Shelduck on her nest inside a hollow log. Down is heaped to the front and side of the bird.

Incubation spells

Most incubating females left their nest twice daily, at dawn and in late afternoon, but a few, especially early in the incubation period, also appeared at midday. As hatching approached, most females left their nests only once daily.

The first feeding period usually commenced within an hour of dawn and seven females spent an average of 65 min (range 30-150 min) off the nest then. Late afternoon periods off the nest averaged 50 min (range 25-75 min) for nine females.

Individual females tended to leave their nests at about the same time each day, being especially regular during the last 10 days of incubation. For example, one female appeared within 15 minutes of midday on six consecutive days. When the number of daily feeding spells was reduced, females usually appeared only at midday, feeding then for up to 2 hours.

Thus, females on average incubated their eggs for 21-22 hours each day.

Behaviour on territory

From the nest the female flew direct to the pond or water area within the territory alongside which the male was usually waiting. When well away from the nest and close to the pond, the female

uttered a shrill monosyllabic contact call similar to that used by individuals to locate flocks. Immediately on hearing the call, the male flew towards and joined her and together they landed at the pond. There followed a brief greeting display, the female with head held low and pointing towards the male uttering a growling note similar to the Inciting call; the male adopting the High-and-Erect posture and repeating rapidly a disyllabic honk. The female then quickly drank or bathed and then began feeding. Her feeding style was unmistakable — she fed avidly, often running from one feeding site to another, spending on average 93% of her time feeding while on the territory.

While the female was present, the male remained constantly alert. Occasionally he joined her to feed, but this was exceptional and I observed it only after females had been present for more than 90 min. Males waiting alone on their territories spent most of their time resting; ten males observed for a total of 96 hours spent 65% of the time resting, 25% feeding, 5% bathing and preening, 3% walking or flying and 2% in defence of the territory.

HATCHING

Only those clutches laid by a single female and from which at least one duckling hatched are considered in this section.

Most eggs were fertile (Table 6). However, 13% of the fertile eggs failed to hatch, the failure being significantly greater ($X^2 = 8.95$, $0.01 > p > 0.001$) in 1974 than in 1975 for unknown reasons. Most failures occurred at or near hatching; 18 full-term embryos in unhatched or pipped eggs were found in nine (31%) of the 29 clutches upon which Table 6 is based. All eggs hatched in only nine (31%) of the clutches.

TABLE 6 — Fertility and hatching success of Paradise Shelduck eggs.

	1973	1974	1975	1976	Total
No. of eggs	25	68	116	73	282
No. (%) of eggs fertile	23(92)	65(96)	109(94)	70(96)	267(95)
No. (%) of fertile eggs hatched	19(83)	48(74)	99(91)	67(96)	233(87)
Unhatched eggs					
Full-term embryo (pipped or almost so)	3	11	2	2	18
Early embryo death	1	0	2	0	3
Rotten	0	6	6	1	13

This high loss of fully developed embryos suggests that some incubation occurred prior to the completion of the clutch and that hatching was not always synchronous. Only one of the full-term embryos was trampled to death. The rest were simply abandoned before they had hatched, and the extent of this loss was similar in nests that were well illuminated and those which were in total darkness.

RENESTING

In 1973, none of nine pairs whose nesting attempt failed attempted to renest. In 1974, two of six unsuccessful pairs renested and both successfully hatched their second clutch. In 1975, the nesting attempt of nine pairs failed. Three renested, two successfully. The female of another pair disappeared during incubation. Her mate remained on the territory, re-paired almost immediately and bred successfully.

Renesting occurred only when the clutch was lost early in the nesting cycle. I found the first nests of four of six renesters; one was abandoned during laying, three during the first 10 days of incubation. Ten of the above 16 pairs which did not renest failed during incubation; three almost at hatching, five when their embryos were more than half developed, and two after about 10 days. I am unsure of the time of failure of the other six pairs.

The interval between failure and renesting was 14-16 days in two cases (obtained by observing the laying female entering the new nest), while in three cases the interval, based on sightings of the male alone on the territory (a rather imprecise method) was 4-5 weeks.

DUCKLINGS

Classification

For ease of identification and as a means of assessing rates of growth and survival patterns, ducklings were classified according to their stage of plumage development (Table 7). Plumage stages are related to age, and although there was some variation between broods, all ducklings within a brood grew at a similar rate.

My classification system is similar to that widely used for dabbling ducks (Mosby 1963), although some of Mosby's classes were ignored or changed because the transition from one to another was too gradual. The system is the same I used for the European Shelduck (Williams 1974).

The plumage classes are referred to in the text as C.I, C.II, C.III, C.IV and C.V.

Nursery areas

From the nest, the female led her ducklings to a suitable rearing area nearby. The male seldom walked with the young, remaining instead in the air or alert on a lookout nearby.

TABLE 7 — Classification of shelducklings used in this study and the mean number and range of days spent by broods in each plumage class. The number of broods on which growth rates were assessed is given in parentheses after the range. The fledging period is recorded under Class V.

Plumage class	Mosby (1963) equivalent	Description	Number of days in plumage class	
			Mean	Range
I	Ia + Ib	Downy, newly hatched, patterns bright and distinct. Neck and tail not obvious, body rounded.	7	6 - 8 (10)
II	Ic	Down colour fading and patterns becoming progressively less distinct. No contour feathers. Head and neck become obvious, body shape long and oval.	19	15 -21 (8)
III	IIa + IIb	First feathers appear on flank and later on shoulders. Other contour feathers and secondaries develop. Face remains downy.	21	16 -26 (12)
IV	IIc + IIIa	Face loses down cover. Remaining down on nape and rump gradually disappears. Predominantly feathered.	16	13 -21 (10)
V		Fledged young	61	55 -65 (10)

Usually the nursery area was the pond or other water body within the territory. Of 44 pairs which appeared with broods and whose territories were centred about ponds, 43 (98%) reared their young there. The territories of another four successful pairs contained no open water; two reared their young in the swampy areas of their territory, the others took their young to the nearby river or creek. Of six pairs whose territories were along a river or creek, three reared their young there, and three raised them on unoccupied ponds nearby.

The characteristics of ponds which made them suitable as nursery areas were those which initially determined their choice as territorial ponds, namely their exposed position and the panoramic view from them. Some marginal or emergent vegetation, mainly small clumps of *Juncus* sp., occurred in only 62% of the ponds used and did not seem a major requirement. Broods reared in territories containing more than one stock pond often moved from one pond to another and did not obviously favour that with most marginal vegetation. Aquatic invertebrates in the ponds in which C.I and early C.II ducklings fed were not sampled during summer, but their abundance may have influenced the choice of pond.

Those parts of the Mata River in which ducklings were reared were the wider, more slowly flowing sections. There, the gently sloping banks and shingle flats provided easy access to and from the water and it was from amongst the river-side pools or swampy margins that ducklings obtained their food.

Some ducklings were raised in the narrow creeks which cut across some of the pastoral flats; others were reared on hillsides where no open water occurred. The latter spent almost all their time feeding and hiding amongst vegetation which grew in the numerous hillside seepages.

Each brood was reared separately from others on its own nursery area. However, a single example of brood amalgamation was observed when 19 ducklings, derived from at least three broods (there were three distinct size classes) were reared on the same pond by one set of adults (Fig. 10). This behaviour has not been reported previously for Paradise Shelduck although it occurs in other species of shelduck (Williams 1974). It is possible that broods amalgamate more frequently when reared near each other on rivers.

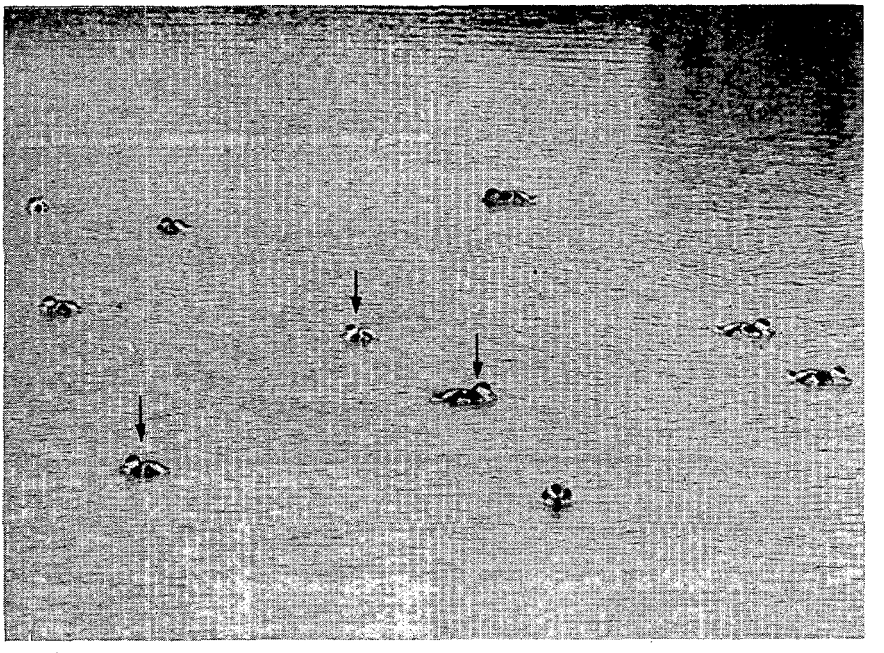

FIGURE 10 — Part of a creche of 19 containing ducklings of at least three different ages (arrowed).

I did not record two or more families using the same pond or nursery area simultaneously. There were however two occasions when by December early broods had fledged and left their nursery pond and another pair and their newly hatched brood occupied the same pond. Such overlap in use is probably the source of the erroneous belief that Paradise Shelducks are double-brooded (Henry 1907, Oliver 1955, Falla *et al*, 1966).

Parental behaviour

The female constantly stayed close to the ducklings throughout their development; the male spent his time standing alert on suitable lookout points, often 100-200 m away.

Females were observed brooding their young C.I ducklings several times each day but I did not observe this after ducklings were eight days old. Thereafter, when resting, the ducklings simply huddled together on the pondside.

There was almost constant vocal communication between the female and ducklings, particularly during C.I and C.II. The duckling's call was a continuous rapid twitter, the female's a soft cluck. This kept the ducklings in a fairly tight group and close to the female at all times. However, by C.III (about 25 days) the continuous calling ceased and ducklings tended to range widely.

I did not observe the parents' response to mammalian predators but when with ducklings, both adults invariably responded to me by performing a broken-wing display. The adults would run in a very crouched posture, raising and lowering their half-opened wings in the manner of flightless moulting birds paddling on water. They would sometimes half flutter and then run again, all the time leading me away from their brood. If I followed one of them, the other would eventually return to the ducklings.

Australasian Harriers *(Circus approximans)* were very common throughout the study area. They were seen frequently to swoop down over the feeding or resting broods but never to take a duckling. When this aerial harassment persisted, one or both of the adults flew at and struck the harrier. The adults' usual response to a harrier, however, was to utter an alarm call to which the ducklings responded by assembling in a tight group in the centre of the pond.

Duckling escape behaviour

Escape from any form of harassment was simply by diving. Older ducklings on ponds escaped from danger by hiding amongst whatever marginal vegetation was present or beneath small overhangs of the eroded pond bank (Fig. 11A, B). However, if disturbed from their hiding place, they too would dive.

Ducklings reared on rivers and creeks either dived in the centre of the river, if it was large enough, or would hide wherever possible on the river edge. Those reared on hillsides away from open water hid in tall vegetation or under logs, but if caught in the open without cover, would simply ' freeze,' remaining absolutely still.

Food

The 13 ducklings collected to determine their food (Table 8) came from three broods: five C.I ducklings while feeding on the surface of a pond, five C.III ducklings while feeding by diving to the bottom of a pond, and three C.IV ducklings while feeding on pasture alongside a pond.

FIGURE 11 — Escape cover for ducklings. A — amongst grass and **Juncus** clumps on land. B — under vegetation overhanging the pond margin.

TABLE 8 — Food of Paradise Shelducklings

		Maximum number in one duckling	No. of ducklings in which present
CLASS I DUCKLINGS (Sample 5)			
Insecta			
O. Hemiptera			
Notonectidae	Anisops assimilis-imago	3	2
Corixidae	Sigara arguta-imago	15	3
O. Odonata			
S.O. Zygoptera	unident Damselfly-nymph	2	2
O. Diptera			
Culicidae	Culex sp?-larvae/pupae	7	1
Chironomidae	Chironomus zelandicus-larvae	1	1
Tipulidae	unident imago	1	1
Plant Material			
Dicotyledones			
Callitrichacene	Callitriche stagnalis-apical rosettes	5	1
	fruits	'hundreds'	5
CLASS III DUCKLINGS (Sample 5)			
Insecta			
O. Hemiptera			
Corixidae	Sigara arguta-imago	2	2
O. Odonata			
S.O. Zygoptera	unident Damselfly-nymph	2	3
O. Diptera			
Culicidae	Culex sp?-larvae/pupae	8	3
Chironomidae	Chironomus zelandicus-larvae	1786	5
Crustacea			
Ostracoda	2 unident. genera	'hundreds'	5
Annelida			
Hirudinea	unident. genus	1	1
Plant Material			
'Aquatic detritus'			5
CLASS IV DUCKLINGS (Sample 3)			
Plant Material			
Dicotyledones			
Leguminosae	Trifolium sp.-leaves		3
Monocotyledones			
Graminae	Poa pratensis - seed heads		3
	Festuca rubra - tillers		1
	Glyceria fluitans - tillers		2
Compositae	Taraxacum officinale - leaves		3

The youngest ducklings had eaten a number of free-swimming aquatic insects; one had caught 15 water boatmen *(Sigara arguta)* and four had also eaten back-swimmers *(Anisops assimilis)*. Other insects taken included damselfly nymphs, mosquito larvae and pupae, chironomid larvae and a tipulid imago. One duckling had eaten the apical rosettes of the aquatic plant *Callitriche stagnalis* and all ducklings had eaten many of its small seeds.

Before I shot the C.III ducklings I observed them for about 15 minutes diving to the bottom of a pond dredging the pond floor. All had consumed numerous chironomid larvae, the most in one bird being 1786. With these larvae were several hundreds of two genera (unidentified) of Ostrocods and all birds contained decaying fragments of plant material — aquatic detritus. Small numbers of free-swimming aquatic insects were found in three ducklings and one had eaten a small leech.

The near-fledged C.IV ducklings had eaten only plant material. The leaves of clover *(Trifolium repens)* and dandelion *(Taraxacum officinale)* and the seedheads of the grass *Poa pratensis* were found in all, and two had also nibbled at tillers of *Festuca rubra* and *Glyceria fluitans.*

These data do not completely describe feeding habits. C.I ducklings reared on ponds were seen to feed only there but obviously those reared entirely on soaks or swamps must have had a different diet. Ducklings first left their ponds to feed on pasture only when they had reached C.II and thereafter plant material probably formed the bulk of their diet.

Timing of brood emergence

The dates on which broods were first seen in 1973-75 are summarised in Figure 12.

The peak of duckling emergence occurred in the last week of September and first week of October and the overall distribution of emergence dates was similar in all years. The earliest brood encountered as day-old ducklings was on 12 September (1974) although a brood of nine first seen on 27 September (1974) had flank and scapular feathers and presumably had hatched during 3-10 September. The latest newly hatched brood was seen on 16 December (1973).

Most of the females nesting for the first time appeared with their broods after the peak of hatching. Of six two-year-olds, three hatched their eggs in the first week of November and one in each of the preceding three weeks. Of the four females nesting first as three-year-olds, two appeared with broods during 24 September-1 October, and two during 15-22 October. Five of the 12 clutches which hatched after 5 November were known to be re-nests.

Weight at hatching

Ten newly hatched and dry ducklings had an average weight of 49.0 g (SD 3.1, range 43.0-53.1 g), equivalent to 58% (SD 4.5%, range 50.0-63.2%) of the fresh egg weight.

Survival

(a) From nest to nursery area: Twenty-one nests were checked immediately after ducklings were first observed on their nursery area. In these nests 163 ducklings had hatched but only 145 (89%) reached

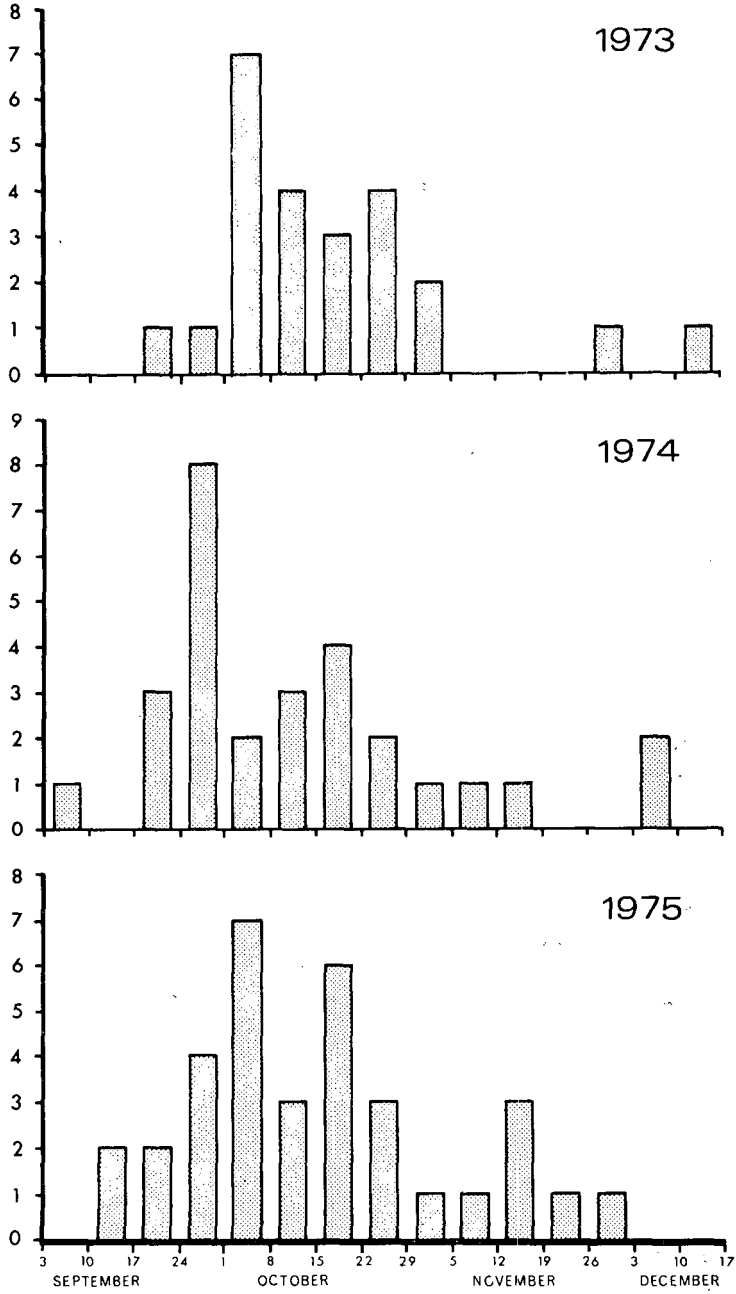

FIGURE 12 — The numbers of newly-hatched Paradise Shelduck broods encountered during various weeks in 1973, 1974 and 1975.

the nursery area. Losses occurred from seven (33%) of the broods, the greatest loss being five ducklings from one brood apparently the result of feral cat *(Felis catus)* predation en route. From two nests established in old tree stumps about 1 m below ground level, four of 13 ducklings failed to clamber out.

In general, parents were extremely successful at leading their ducklings long distances from nest to nursery area. Some of the more formidable journeys exceeded 1 km and involved descents from hillsides into deep gorges and then a climb on the other side; in two examples these climbs exceeded 200 m and both were accomplished without loss.

(b) After reaching nursery areas: For each newly hatched brood reaching a nursery area, the initial number of ducklings seen and the number alive at the end of C.I were recorded; these data for all broods were summed and percentage survival was determined. The number of ducklings alive at the end of successive plumage classes was similarly used to determine percentage survival during those classes (Table 9).

TABLE 9 — The survival of ducklings from the time of arrival at their nursery areas until fledging.

	1973	1974	1975	Total	% Survival in each class
No. of broods	15	18	21	54	
Initial No. of ducklings	93	125	147	365	
No. ducklings alive at end of —					
Class I	60	118	134	312	85.5
II	47	107	108	262	84.0
III	44	92	96	232	88.5
IV	40	89	93	222	95.7
% Fledging	43.0	71.2	63.3	60.8	

Over the three years 1973-75, approximately 61% of all ducklings reaching nursery areas fledged and, with the exception of C.I and C.II in 1973, survival during all plumage classes in all years exceeded 80%.

Most C.I ducklings died during cold, wet and windy weather. One entire brood of eight C.I ducklings perished during three days of strong cold winds and rain and the low survival of C.I and C.II ducklings in 1973 was caused by the two weeks of poor weather in late September-early October of that year.

In both 1974 and 1975, the percentage survival of C.I ducklings was higher than for C.II, whereas in dabbling ducks and the European Shelduck (Williams 1974) most deaths occur during C.I. This is related to a change in feeding habits; C.I ducklings feed within the pond, C.II ducklings on pasture. Although during C.II, ducklings are probably more tolerant to cold weather than during C.I, greater predation by cats occurs when ducklings feed away from the pond. All dead C.III and C.IV ducklings found had been killed by cats.

Of the 54 broods followed throughout their development, all ducklings in 10 (18.5%) died, three during C.I, six during C.II and one during C.III.

Sex ratio at fledging

The sex ratio at hatching is unknown but I assume that equal numbers of males and females hatched. However, in those broods in which all of the almost fully fledged ducklings were caught and banded in the study area both before and during this study (Table 10), there were 55% males, a significant departure from parity ($X^2 = 6.24$, $0.02 > p > 0.01$). Although more males were caught in all years, the sex ratio of ducklings departed significantly from parity in 1973 only. These findings contrast with data from the Southland district where, during 1970-1973, 1400 ducklings were banded, 720 (51.4%) of which were males ($X^2 = 0.57$, $0.50 > p > 0.30$).

TABLE 10 — *The percentage of males in Paradise Shelduck broods on* Huiarua Station 1971-1975.

Year	No. of Broods	Total ducklings	% Male
1971	15	98	52.0
1972	18	110	53.6
1973	32	141	61.0
1974	31	160	51.2
1975	34	168	55.4
Total	130	677	54.7

Post-fledging dispersal

The break-up of a brood usually occurred when the adults left their territory to undergo their annual wing moult. Frequently the young accompanied their parents to the moulting site where they joined the large flocks of other juveniles, yearlings and adults. Those which did not accompany their parents remained near their natal pond, making daily flights over the surrounding area, eventually joining with other groups of juveniles nearby. Eventually these groups found their way to one of the nearby moulting sites and became part of the large flocks there.

Within these large flocks and also in those flocks which remained near the moulting sites after most of the adults had departed, siblings tended to keep together. For example, 50% or more of the sightings of 15 ducklings seen four or more times in February-April were in the same flocks or small groups as one or more of their siblings.

To determine the areas to which they dispersed, 688 ducklings were banded on or near Huiarua Station between 1970 and 1975 and another 819 at sites near Gisborne. The locations at which some were shot or found dead are summarised in Table 11 and shown in Fig. 13 and 14.

TABLE 11 — The number of Paradise Shelducks banded as ducklings near Huiarua Station and near Gisborne, 1969-75, shot or recovered dead at various distances from their banding site.

DISTANCE (km)	0-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-100	101+	Total
HUIARUA DUCKLINGS												
MALES												
Number	3	4	5	8	5	9	2	2	0	1	3	42
Cumulative %	7.1	16.7	28.6	47.6	59.5	81.0	85.7	90.5		92.9	100	
FEMALES												
Number	5	3	1	8	0	3	2	1	2	0	3	28
Cumulative %	17.9	28.6	32.1	60.7		71.4	78.6	82.1	89.3		100	
GISBORNE DUCKLINGS												
MALES												
Number	18	17	19	4	8	0	3	0	0	1	13	83
Cumulative %	21.7	42.2	65.1	69.9	79.5		83.1			84.3	100	
FEMALES												
Number	32	28	11	2	1	1	4	0	0	1	2	82
Cumulative %	39.0	73.2	86.6	89.0	90.2	91.5	96.3			97.6	100	

When adults in the moulting flocks dispersed back to their breeding areas, many juveniles presumably followed for within 5-6 months of fledging, some were widely scattered and more than 100 km (60 miles) from their natal area; all six Huiarua-banded ducklings and 11 of 15 Gisborne-banded ducklings recovered more than 100 km from their banding site were shot in their first six months of life. Some of the dispersing Huiarua ducklings found their way south to join the juvenile flocks which remained near moulting sites at Lake Repongaere and Parehaka; here six of eight and seven of nine males recovered 31-40 km and 51-60 km respectively away from Huiarua were shot in the May following fledging.

The recoveries of ducklings banded at Huiarua Station are few and show no differences in the movements of males and females (male

and female distributions in Table 11 are not significantly different, $X^2 = 7.6$, 4 d.f., $0.2 > p > 0.1$). A difference in dispersal is shown, however, by the more numerous recoveries of ducklings near Gisborne (Table 11), ($X^2 = 22.5$, 6 d.f., $p = 0.001$); they show that females remained closer to their natal areas than males.

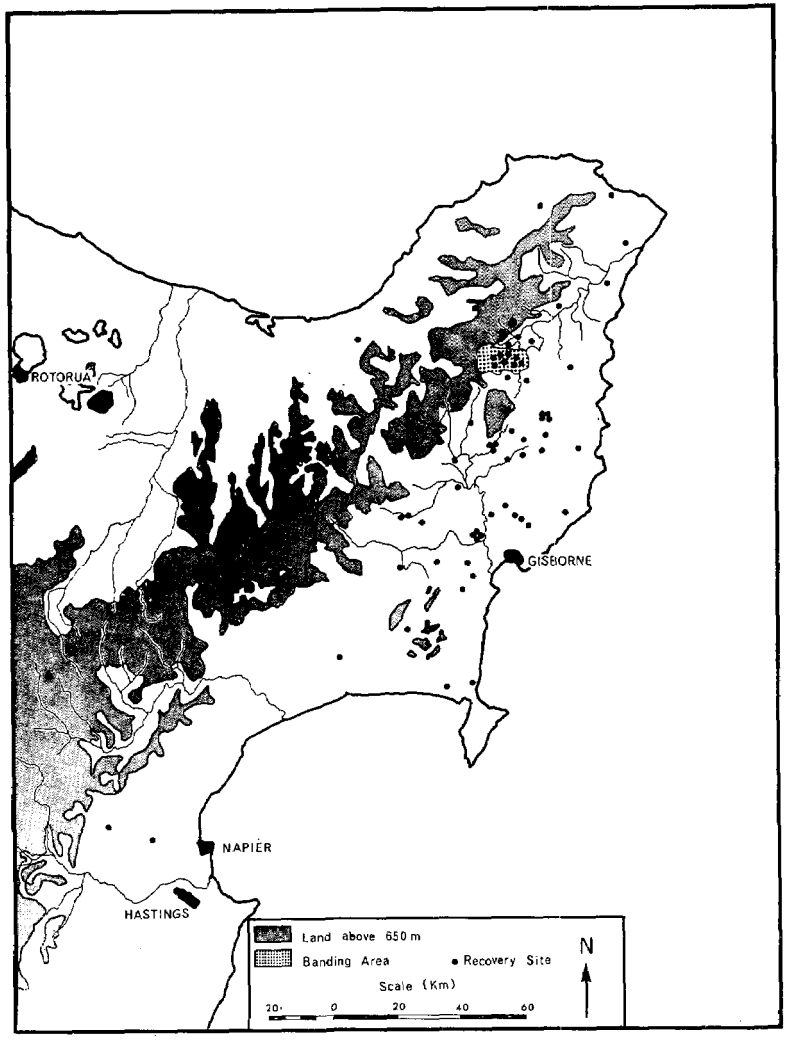

FIGURE 13 — The locations of recovery of Paradise Shelducks banded as ducklings on or near Huiarua Station, 1970-1975.

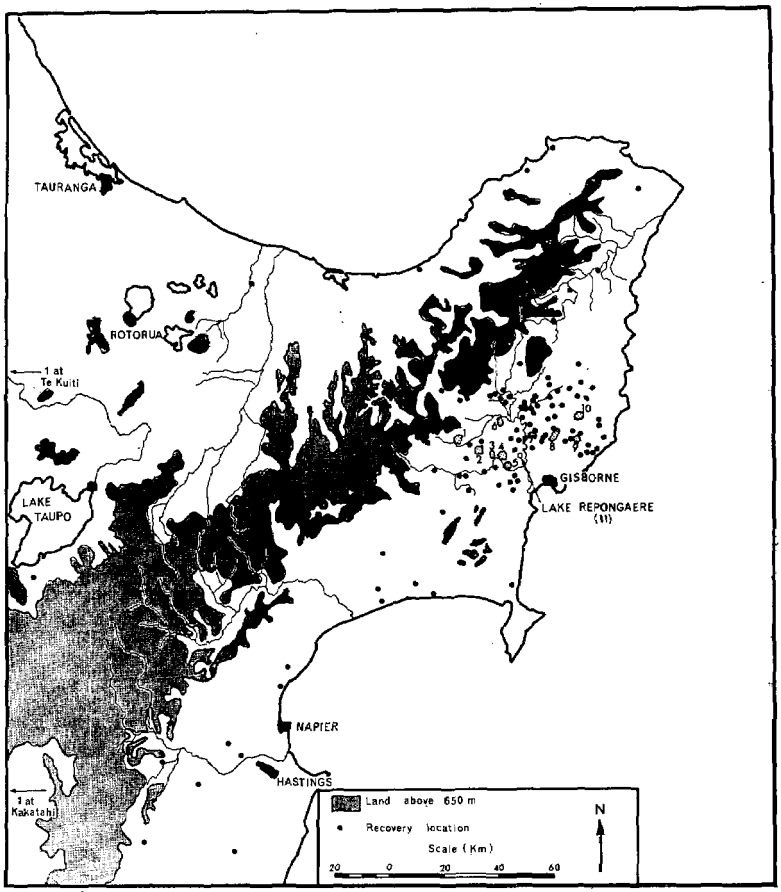

FIGURE 14 — The locations of recovery of Paradise Shelducks banded as ducklings at various sites near Gisborne 1969-1974. The banding sites were on the following farm stations: 1 — Rere, 2 — Hiwinui, 3 — Sunworth, 4 — Broadhurst, 5 — Smithfield, 6 — Holdsworth, 7 — Ngakaroa, 8 — Waimata Valley, 9 — Glenroy, 10 — Panikau.

POPULATION DYNAMICS

PRODUCTIVITY

Status of territorial pairs

Not all the intensively observed territorial pairs attempted to breed; some included juveniles not physiologically capable of breeding, others included two-year-olds, only some of which nested. Using the criteria described earlier to determine whether a pair attempted breeding, I concluded that 13% of the territorial pairs did not breed (Table 12).

TABLE 12 — The breeding status of territorial pairs of Paradise Shelducks on Huiarua Station 1973-1975.

	1973	1974	1975	All years
Total pairs	25	21	32	78
No. (%) appearing with ducklings	12(48)	15(72)	19(59)	46(59)
No. (%) whose nesting failed	9(36)	4(19)	9(28)	22(28)
No. (%) not attempting to breed	4(16)	2(19)	4(13)	10(13)

Because I observed pairs only once each day or two I may not have detected the breeding attempt of any pair which failed during egg-laying. I cannot therefore be certain that all "non-breeders" did not make some unnoticed breeding attempt. In 1973, for example, one non-breeding female was recorded as "medium gravid," indicating that some enlargement of the oviduct had occurred, but her mate was not seen alone on the territory; in contrast, the three other non-breeding females did not show any abdominal enlargement. Of the two non-breeding pairs in 1974, one included a two-year-old female which I saw two or three times each day, often enough to be sure she did not attempt breeding; the second pair was less frequently seen. In 1975, two non-breeding females were juveniles, the third a two-year-old (and the only one of five two-year-old females which in this year did not attempt breeding), while a fourth was caught during the moult the previous year and was therefore at least two years old. All four pairs were intensively and frequently observed.

Because I may have missed the breeding attempt of four pairs in 1973 and one pair in 1974, I have assumed in the subsequent discussion on productivity that in 1973 the percentage of breeding pairs which successfully appeared with ducklings was 48% (all 25 pairs nested) to 57% (only 21 pairs nested), in 1974 75% (20 pairs nested) to 79% (19 pairs nested), in 1975 68% (28 pairs nested), and over the three years 63% to 68%.

Duckling production

Of the 54 broods followed throughout their development, ducklings fledged from 44 (81.5%); four (27%) of 15 broods disappeared in 1973, two (11%) of 18 in 1974 and four (19%) of 21 in 1975. These 54 broods were the progeny of all but two of the 46 successful breeding pairs referred to in Table 12 plus another 10 pairs whose territories were outside the main study area but who reared their ducklings on creeks, swamps or empoundments within it.

Over the three years, an average of 4.1 ducklings were reared by each of the 54 pairs which initially appeared with ducklings (Table

13) — an average of 5.0 (SD 2.8, range 1-13) ducklings for each of the 44 pairs which raised at least one.

Not all of the pairs which attempted breeding hatched their eggs; over the three years, 63-68% appeared with ducklings. Thus the average number of ducklings fledged per territorial pair which attempted to breed was between 2.6 and 2.8 (Table 13).

TABLE 13 — Mean production of ducklings per pair of territorial Paradise Shelducks which attempted to breed on Huiarua Station 1973-1975.

	1973	1974	1975	All years
No. of broods	15	18	21	54
No. of ducklings fledging	40	89	93	222
Mean No. of ducklings per brood	2.7	4.9	4.4	4.1
% Breeding pairs hatching ducklings	48-57	75-79	68	63-68
Mean No. of ducklings per breeding pair	1.3-1.5	3.7-3.9	3.0	2.6-2.8

To determine if similar production occurred outside the study area I observed broods reared on a series of ponds alongside the Mata, Tuakau and Waitahaia Roads (Fig. 1). Some broods were not seen until some ducklings had died and the total disappearance of others was probably because they changed their nursery area. Thus, I could determine only the number of ducklings which fledged in each brood (Table 14).

Although the average brood size inside and outside the main study area differed in all years by slightly more than one duckling per

TABLE 14 — Mean size at fledging of Paradise Shelduck broods within and outside the Huiarua Station study area, 1973-75.

Year	In study area		Outside study area		Both areas	
	No. of broods	Mean size	No. of broods	Mean size	No. of broods	Mean size
1973	11	3.6	21	4.8	32	4.4
1974	16	5.6	17	4.2	33	4.9
1975	17	5.5	17	4.4	34	4.9
Total	44	5.0 ± 2.8	55	4.6 ± 2.2	99	4.7 ± 2.5

brood, these differences were not statistically significant (1973 $t = 1.64$, $0.2 > p > 0.1$; 1974 $t = 1.02$, $0.3 > p > 0.2$; 1975 $t = 0.73$, $0.5 > p > 0.4$) nor were the overall figures between years (1973-74 $t = 1.24$, $0.3 > p > 0.2$). Thus, production in the study area was similar to that from a wider area.

SURVIVAL

Estimates of adult survival were determined in two ways; from the disappearance of marked territorial birds and from an analysis of bands returned by hunters. For juveniles, survival estimates were obtained from hunting returns and from sightings of marked birds in the field. A full discussion of survival data will be published separately and only the results are summarised here.

Territorial adults

Because the established territorial birds did not change the location of their territories, the disappearance of banded birds from their territories was used to determine the annual survival of adults (Table 15). These data are derived only from those territorial birds which attempted breeding, thus excluding all juveniles and yearlings which established territories, for whom a different survival rate may apply.

Survival of males was higher than females although this difference was not statistically significant ($X^2 = 1.89$, $0.20 > p > 0.10$).

Causes of death are not known. Only one of the 21 adults which disappeared was reported to the Wildlife Service Banding Office as having been shot and one female disappeared while nesting. All others simply failed to reappear after their annual moult.

Moulting adults

The annual survival of birds caught and banded during their wing moult at sites throughout the Gisborne-East Coast district during 1961 to 1969 was estimated to be about 64% (Williams 1972). In 1969 the hunter's daily limit was reduced from 10 to three and was maintained at three until 1977. The returns of bands from moulting birds banded from 1969 to 1975 and shot during 1969 and 1976

TABLE 15 — Percentage annual survival of male (M) and female (F) Paradise Shelducks on Huiarua Station, 1973-76.

Year	No. identifiable		No. present next year		% Survival		
	M.	F.	M.	F.	M.	F.	M & F
1973	1	7	1	3	100	43	50
1974	6	8	5	6	83	75	79
1975	15	23	10	14	67	61	63
1976	8	7	6	3	75	43	60
Total	30	45	22	26	74	58	64

TABLE 16 — The number of moulting Paradise Shelducks (adults) and ducklings (young) banded throughout the Gisborne-East Coast district between 1969 and 1975, and the numbers of each reported shot in each year 1969 to 1976.

Adults

Year banded	No. banded	1969	1970	1971	1972	1973	1974	1975	1976	Total
1969	750	65	22	11	4	7	3	3	0	115
1970	750		55	16	8	5	6	2	2	94
1971	747			37	28	8	2	7	3	85
1972	692				53	36	12	8	7	116
1973	750					53	21	4	1	79
1974	842						46	17	8	71
1975	956							16	4	20
TOTAL	5487	65	77	64	93	109	90	57	25	580

Young

Year banded	No. banded	1969	1970	1971	1972	1973	1974	1975	1976	Total
1969	137	15	5	7	0	1	1	0	0	29
1970	187		17	14	4	3	1	0	0	39
1971	233			20	18	9	2	1	1	51
1972	218				17	7	5	1	0	30
1973	180					14	14	2	2	32
1974	383						28	14	3	45
1975	169							6	3	9
TOTAL	1507	15	22	41	39	34	51	24	9	235

(Table 16) were analysed by computer using the highly advanced Fortran IV program 'BROWNIE' (Brownie *et al.* 1978). The analysis was by courtesy of the Office of Migratory Bird Management, U.S. Fish and Wildlife Service. The percentage mean annual survival of moulting adults was determined as 70.3 ± 6.4%, the annual survival varying between 57.2% and 82.9%.

Juveniles

From 1969 to 1975, 1507 ducklings were caught and banded immediately prior to fledging and by the end of September 1976, 235 had been reported shot (Table 16). This total comprised 70 of 688 banded during 1970-1975 on or about Huiarua Station and 165 of

819 banded during 1969-1974 elsewhere in the Gisborne-East Coast district. The combining of the two samples, necessitated by the smallness of the Huiarua returns, may introduce some bias because significantly fewer of the Huiarua ducklings were reported shot (of those banded 1970-74, 11.5% of 519 from Huiarua, 19.9% of 682 elsewhere; ($X^2 = 15.2$, $p < 0.001$) which may indicate different survival rates in the two areas.

Analyses of these data were confusing: program 'BROWNIE' determined the percentage mean annual survival to exceed 100%, a nonsense result which indicates the assumptions implicit in the statistical models were not satisfied. Analysis using the now out-dated and statistically inferior time-specific method (Farner 1955, Reid 1966) determined that an average of 53% of the ducklings which survived their first 5-6 months of life remained alive during the subsequent year and that over the next four years average annual survival was poorer at approximately 45%. Analysis of these band returns of 123 males and 112 females indicated that males survived better than females. The survival of males was determined as 56% in the first year and an average of 53% (range 44-65%) over the next four years, for females the survival was 51% and 41% (range 24-54%) respectively. These results conflict with estimates of adult survival presented above and elsewhere (Williams 1972).

I analysed the sightings of ducklings banded and seen within the study area to determine how many were present during the breeding season in their first year of life. Because males tended to disperse away from their natal area, only records of females were examined. In 1974, 75 were banded and in the 1975 breeding season (August-October) 34 (45%) were identified. A further three (4%) were alive for they were later seen in 1976. On the unlikely assumption that all survivors were observed or accounted for, a minimum of 49% of females survived their first 8-10 months of life. Data for other years were not considered because less effort had been made to read juvenile band numbers.

Using only females introduces some bias because fewer of the Huiarua females were shot (8.7% compared with 11.4% of males) and their survival may therefore be different from that of males.

This confused situation cannot be resolved here. In subsequent discussion I will assume that 50% of both sexes survive their first year and 55% their second year.

SURVIVAL AND PRODUCTIVITY

A principal aim of this study was to determine the breeding output of the shelduck population and to relate this to known losses. The various components in the life equation have now been calculated and it remains only to relate these to one another.

Between 30% and 36% of the breeding adults died each year. To replace themselves each breeding pair must produce, each year,

sufficient ducklings to enable between 0.60-0.72 ducklings to attempt breeding. Is this being achieved by the Huiarua population ?

Consider 100 breeding pairs (Table 17), an annual production of 2.6-2.8 ducklings per pair at fledging, and assume that equal numbers of males and females are produced. Applying the 50% and 55% survival rates of the first and second years, between 35.7 and 38.5 ducklings of each sex would remain alive at the end of the second year. Not all of these birds would attempt to breed at that age, however; earlier I recorded that only four (80%) of five males and 10 (53%) of 19 females did so. The non-breeders must wait a further year (30-36% will die in the interim) before they enter the breeding population. Overall (Table 17), 33-36 males and 27-31 females become breeders, sufficient to maintain the population.

The precision of this type of analysis is especially dependent on statistically reliable estimates of male and female mortality during the first two years of life. I have been unable to obtain these during this study.

POPULATION FLUCTUATIONS WITHIN THE STUDY AREA

Flock size

Twice monthly during the peak of the breeding season (August, September and October), I counted all the non-territorial birds. Flocks at all the ten flock sites (Fig. 1) were counted and I also searched areas adjacent to territorial pairs where, from time to time I had

TABLE 17 — Production per 100 breeding pairs of Paradise Shelduck.

	Male ducklings	Female ducklings
Number of ducklings fledged	130-140	130-140
First year survival (%)	50%	50%
Number alive at end of first year	65-70	65-70
Second year survival (%)	55%	55%
Number alive at end of second year	35.7-38.5	35.7-38.5
% Breeding as 2-year-olds	80%	53%
Number of ducklings first breeding at 2	28.6-30.8	18.9-20.4
Number of non-breeding 2-year-olds	7.1-7.7	16.8-18.1
Third year survival (%)	64-70%	64-70%
Number of ducklings first breeding at 3	4.5-5.4	10.7-12.7
Total number of ducklings entering breeding population	33.1-36.2	27.5-30.8

encountered small groups of juveniles. Censuses were standardised in that I always followed the same route between flock sites, conducted the census over the same period of the day, spent about the same length of time at each site and made five counts of the birds present. In analysis I have used the highest count because when viewing some sites, I was several hundreds of metres away from the birds and often some were obscured.

Two counts were not completed: on 20 September 1973 when low cloud obscured three flock sites and on 20 August 1974 when I was away from the study area. Data are summarised in Table 18.

In early August each year 80-100 birds were present, but by the end of September or early October, the number had doubled. This increase occurred initially at flock sites 4, 5, 6 (Fig. 1) and later at sites 8, 9, 10, suggesting a gradual movement of birds up the Mata River valley from areas nearer the coast.

Most of the birds which reached the study area at this time were males, for there was a gradual decline in the percentage of females in the flocks as numbers increased (Table 18).. Many juvenile and yearling pairs which had temporarily been occupying territories also returned to the flocks in October. However, in all years, the numbers of flock birds decreased at the end of October and the resulting change in the sex ratio suggested a substantial emigration of males and a lesser emigration of females.

Density of territorial pairs

On Huiarua Station I tried to find every territorial pair present. Some were in difficult areas but they were observed at least fortnightly throughout August-October, and for inclusion in the following statistics a pair had to be seen at the same locality on at least three successive counts. Some pairs were undoubtedly juveniles — females could be

TABLE 18 — Number and sex ratio of Paradise Shelducks counted within the study area during censuses, 1973-1975 (* — count incomplete).

1973			1974			1975		
Date	Number	% Female	Date	Number	% Female	Date	Number	% Female
10/8	94	76.6	2/8	86	53.5	7/8	80	67.5
20/8	100	71.0	==Not counted==			20/8	125	67.2
7/9	137	68.6	10/9	109	72.5	11/9	152	63.2
20/9	53*	60.4	28/9	145	62.8	26/9	178	53.9
17/10	171	53.8	7/10	112	60.7	6/10	205	50.2
31/10	152	50.7	31/10	91	69.2	3/11	120	73.3

identified by their plumage but males only if banded — and it was difficult to be sure that the same juvenile pair was always present at the same locality unless one or both birds were banded. However, if a juvenile pair was seen at the same locality on three successive counts (and actively defended the area) it is included in the statistics, but the number of juveniles occupying territories may have been greater.

In 1973, 25 pairs occupied territories. Three pairs included a juvenile female and another a (banded) juvenile male (his female being of breeding age). Most birds encountered this year were not individually identifiable but I covered the area more frequently than in later years.

In 1974, 22 pairs occupied territories. The territory of one pair in 1973 was divided and occupied by two pairs while another pair enlarged their territory over an area which the previous year had supported two. All three territories occupied by juveniles in 1973 remained unoccupied, and five other 1973 territories were not used. Four new ones were established, one by a juvenile pair, the others by apparently adult pairs.

The number of territories occupied in 1975 increased to 27, two of them held by juvenile pairs. Two new territories were established about newly-created ponds and three in localities not occupied in the previous two years. Three areas occupied in 1974 were not used in 1975 while another three used in 1973 but not in 1974 were reoccupied.

In 1976, 25 territories were established, three by juvenile pairs. One 1975 territory was split into two and another which had previously housed two pairs was occupied by a single pair. Three territories of the previous year remained unoccupied but one adult pair established their territory around a pond not previously used.

Thus, in the four years, territories were established at 37 localities on Huiarua Station, only 15 of which were occupied in all years.

Recruitment of locally reared young into the breeding population

Few of the ducklings banded in the study area were subsequently seen breeding there. Data presented in Table 19 indicate that three (1.9%) males and eight (6.1%) females reared in the study area bred there as two-year-olds and a further four (4.8%) females as three-year-olds. In addition, a one-year-old male was considered a member of a breeding territorial pair in 1973.

Clearly this level of recruitment was too low to maintain the breeding population. Substantial immigration must have occurred. Although ducklings were banded elsewhere within the Mata River catchment and many were later observed in the non-breeding flocks, only two males bred within the study area, implying that immigrants came from further afield. Three males and four females caught prior to 1973 at moulting sites near Gisborne bred in the upper Mata River valley which may indicate that some potential recruits reach the area

TABLE 19 — Recruitment of Huiarua-reared male (M) and female (F) ducklings into the Huiarua breeding population.

Year ducklings banded	No. banded		— Recruited as — 2nd-year breeder		3rd-year breeder	
	M.	F.	M.	F.	M.	F.
1971	41	30	1	3	–	1
1972	22	17	–	–	–	3
1973	46	36	1	4	–	–
1974	49	49	1	1	No data	

during the post-moulting dispersal. To determine the origin of immigrants to the Huiarua breeding population would require an extensive banding programme outside the upper Mata River valley.

Population regulation

It was beyond the scope of this limited study to investigate how (or if) the breeding population was regulated, whether the density of territorial pairs was related to the breeding output of preceding years and whether the annual production of young was in any way related to the number of potential breeders. However, the following hypotheses may assist future studies on shelduck population dynamics:

1. Although local production appeared sufficient to replace losses from the breeding population, few of the locally-reared ducklings were recruited, and most new breeders were immigrants. Recruitment of an immigrant into the breeding population probably requires the prior step of recruitment into the resident non-breeding population, and the most likely time for this to occur would be during September and October when juvenile pairs first occupied territories to which they returned as breeders the following year. The large increase of males in the non-breeding flocks during September and October may therefore be directly related to this juvenile territorial behaviour and the number which become permanent residents may depend on the number of territories being contested by juvenile pairs.

2. Changes in the density of territorial pairs did not seem to reflect positively the breeding success two years previously (Table 20). Low breeding success in 1973 was followed in 1974 by a relatively small flock, and yet in the next year, the number of territorial pairs on Huiarua Station was the highest encountered during the study. Conversely, high duckling production in 1974 was followed by a larger non-breeding flock, and yet in 1976 the number of territorial pairs declined. I have no evidence to show that the number of territory sites was limiting and that this limit varied annually. On the contrary, the frequency of territory reoccupation was low; only 15 of 37 territory sites were used in all four years of study, implying that other factors accounted for the relationship between the number of non-breeders and territorial pairs.

I suggest that the proportion of two-year-old shelducks which attempt to breed varies annually and that this variability is related to duckling production in each of the previous two years. When the non-breeding population is high, reflecting high productivity in the previous year, competition amongst juvenile pairs attempting to establish a preliminary attachment to a territory site to which they may return as two-year-olds to breed, may be so intense that all but a few are unable to defend the site successfully. Without that preliminary attachment in the first year, breeding may not be attempted in the second — instead, the breeding attempt is delayed a further year. Thus, two years after a high duckling production, one year after a large flock size, the number of territorial pairs may remain static or even decline. Conversely, when the non-breeding flock is small, competition for preliminary territory sites is less intense and more pairs may successfully enter the breeding population as two-year-olds. Hence, two years after a poor breeding season (e.g. 1975) the number of territorial pairs may increase.

TABLE 20 — The annual productivity and the number of flock birds and territorial pairs of Paradise Shelducks on Huiarua Station 1973-1976.

Year	1973	1974	1975	1976
Ducklings per pair	1.3-1.5	3.5-3.9	3.0	Not recorded
Maximum number of flock birds	171	145	205	Not recorded
No. of territorial pairs	25	22	27	25

3. I found no evidence that the number of nests which failed or the number of ducklings reared was limited or regulated. Interference at the nest by other breeders or non-breeders is a potential regulatory mechanism but I found evidence of only three cases, and in all, productivity was not significantly affected. Almost all ducklings were reared in family units away from contact with other broods, and I found only one example of creche formation. Creche formation is a potential density-dependent regulator (Williams 1974) but seems insignificant in hill-country habitat, although it may assume more importance in river habitats where broods make frequent contact with each other. The numbers of successful nests and the numbers of ducklings raised were therefore determined by 'accidental' rather than 'regulatory' factors.

In summary, I suggest that if the Paradise Shelduck population on Huiarua Station is regulated or limited in any way, the operating factors affect the rate of recruitment into the breeding population rather than the productivity of those pairs which attempt to breed.

CONCLUDING REMARKS

Paradise Shelducks are mainly found in two very different habitats; (i) hill-country farmland of which the Gisborne-East Coast district is typical but which also occurs in parts of North Auckland, King Country, inland Taranaki, coastal Wairarapa and the Taihape-National Park district; and (ii) the tussock grasslands of the South Island, land mainly above 400 m along the eastern foothills of the Southern Alps, stretching from inland Marlborough to northern Southland.

The biology of Paradise Shelducks as described in this paper is probably similar throughout the North Island hill-country habitat. The Gisborne-East Coast district shares with most other North Island areas where the bird is common the 'big' landscape of large hillsides, deeply dissected terrain where even the smallest streams have cut deep into the soft underlying strata (mostly papa), numerous stock ponds scattered throughout, abundant naturally-formed ephemeral ponds which have resulted from widespread erosion, copious littering of decaying logs and tree stumps, small depleted remnants of the original forest cover, and fertile riverside flats where the exotic grasses provide rich feeding areas for the flocks.

The South Island habitat is so different as to suggest that there the bird may behave differently. Stock ponds are not a regular feature of this habitat; most territories seem to be established about areas of running water and many broods are reared on the open shingle riverbeds. Suitable nest sites may be difficult to find and multiple nesting may be common (records of broods of 15-20 ducklings suggest this or extensive brood amalgamation). Flocks roam widely in the large river valleys and moulting sites may draw birds from a much greater area than is the case in the North Island (unpubl. data). The ecology of the Paradise Shelduck in New Zealand cannot be completely understood without a study, similar to that reported in this paper, being conducted somewhere in the eastern foothills of the Southern Alps.

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MURRAY WILLIAMS, *Wildlife Service, Department of Internal Affairs, Private Bag, Wellington.*