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THE BEHAVIOURAL ECOLOGY
OF THE POPULATION OF BLACK SWAN
(*Cygnus atratus* Latham)
ON A MANAWATU DUNE LAKE

A thesis presented in fulfilment
of the requirements for the degree
of Doctor of Philosophy
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ABSTRACT

The behavioural ecology of a population of Black Swan (*Cygnus atratus* Latham) on the Manawatu dune lake, Pukepuke Lagoon, is examined. This population is of interest as breeding is by territorial swans, whose behaviour has not been completely studied previously.

A non-breeding flock comprises approximately 75% of the population, at time of nesting. The behaviour patterns and time-activity budgets of this flock are examined, and its relationships with the breeding swans are also studied.

Aggressive behaviour and the mechanisms of territory selection and defence are described. Territory sizes vary considerably, but this is not shown to have any effect on breeding success; rather, the strength of brood defence appears to influence cygnet mortality.

Courtship, pair-bond maintenance, and copulatory displays are listed. All show distinct daily and annual rhythms. Black Swans do not pair for life but do remain together for at least one season. Bond strength and duration are related to the degree of investment necessary to breed successfully in a territorial situation.

The physical and behavioural development of wild and captive cygnets are recorded and compared, providing data on growth rates, ontogeny of behaviour patterns, and the development of social relationships.

Parental care, and the relationships between families and other swans, are examined. Clear sex roles are apparent, with the male being most prominent in defence of the brood. The survival value of family behaviour in a territorial context is examined.

The main points arising from the preceding sections are interrelated, and suggestions and hypotheses presented for future investigation.

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ABBREVIATIONS AND SYMBOLS USED IN THE TEXT

g	grams
kg	kilograms
m	metres
ha	hectares
h.	hours
d.	days
sp	species
df	degrees of freedom
p	probability
sd	standard deviation
\bar{x}	mean
α	accepted level of significance
χ^2	Chi-squared
log.	logarithm
<	less than
\leq	less than or equal to
>	greater than
\geq	greater than or equal to
Σ	the sum of
σ	male
ϕ	female
σ^2	pair

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Chapter 1

INTRODUCTION AND METHODS

1.1 BLACK SWANS

1.1.1 Introduction to New Zealand.

The Black Swan (*Cygnus atratus* Latham) was introduced into New Zealand from its native Australia in the 1860s, originally for the control of waterweeds but later as an ornamental and game species. In the South Island the Nelson and Canterbury Acclimatisation Societies released a few birds in 1864, while the earliest North Island liberations were by Sir George Grey on Kawau Island in 1864, and the Auckland Acclimatisation Society, on Kaipara Harbour, in 1867 (Lickers 1977; Miers & Williams 1969). From these and subsequent liberations the population grew rapidly and was soon widespread, probably because of the wide availability of suitable habitat and the lack of predators and competitors (Ogilvie 1972). They are now regarded as pests in some districts, due to their use of pasture land (Williams 1979); earlier in their history they were mistakenly viewed as voracious predators on fish (Pascoe 1957).

1.1.2 General habitat and habits.

C. atratus, like all other swans excepting the Mute (*C. olor*) and Whistling (*C. columbianus*) Swans (Owen & Kear 1972) is wholly vegetarian. Though grazing mainly on aquatic vegetation it also makes use of pasture land, especially when this is flooded (Briggs 1979; Frith et al. 1969; Williams & Imber 1970). This habit may cause considerable damage to pastures and has led to calls for reduction of the population in some areas (e.g. Lake

Ellesmere N.Z.: Williams 1979).

The Black Swan is found over a large part of Australia (Lavery 1965; Ogilvie 1972), but numbers are greatest in the wetter coastal and southern regions (Braithwaite 1970; Guiler 1966; Hemsley 1973). Here they concentrate on coastal lakes and estuaries during the dry season, before dispersing to utilise the large temporary water areas created by the rains. The transitory nature of much of their habitat means that breeding is not strictly seasonal (Frith 1959), but occurs whenever suitable conditions are available. In New Zealand the swans are found on all suitable water areas - lakes, estuaries, lagoons, and ponds - with major concentrations on Lakes Wairarapa and Whangape in the North Island and Lake Ellesmere in the South Island (Lickers 1977; Ogilvie 1972; Williams 1980). The breeding season is more restricted than in Australia, although its timing depends in part on water levels at nesting sites (Miers & Williams 1969).

The Black Swan is often regarded as a colonial-nesting species, a habit which sets it apart from its relatives, although the Mute Swan occasionally nests in colonies (Kear 1972; M. Williams pers. comm.). Relatively recent studies (e.g. Braithwaite 1970) have shown that *C. atratus* exhibits both territorial and colonial breeding habits. The dichotomy appears to be based on the availability of nesting cover and more particularly of food for the young brood, since downy cygnets cannot dive or feed off the bottom (Ch. 5) and require large shallow areas for feeding.

The breeding biology of colonial-nesting Black Swans has been extensively studied. Large numbers of swans (up to several thousand) breed in colonies on large shallow water areas, which may be present for only part of the year and which have little nesting cover but good food resources in the form of extensive shallow-water weed beds (e.g. Braithwaite 1977; Guiler

1966; Hemsley 1973; Lickers 1977; Miers & Williams 1969; Williams 1979, 1980; J. Cheyne pers. comm.). The ecological and behavioural characteristics of this group are presented in Table 1.1.

In contrast, territorial breeding has been largely unexamined, apart from examination of breeding success (Williams 1980), and some work on behaviour (e.g. Braithwaite 1981b; Tingay 1974), which still leave large gaps in the data available. Table 1.2 presents what was known when I commenced my own research. In general, territorial pairs live on smaller, permanent water areas, with good shelter and nest cover but less potential feeding area for cygnets. Pukepuke Lagoon (section 1.2) is one such area.

1.2 THE STUDY SITE: PUKEPUKE LAGOON

1.2.1 Habitat

Pukepuke Lagoon (175°15' E, 40°10' S) is a dune lake on the Manawatu coast, west of Palmerston North. It is a Wildlife Management Reserve administered by the Wildlife Service (Department of Internal Affairs), which maintains a permanent field station there. The reserve comprises 15ha (37 acres) of open water set in 87ha (213 acres) of mixed raupo (*Typha orientalis*), flax (*Phormium tenax*), niggerhead (*Carex secta*) and cabbage tree (*Cordyline australis*) swamp. The shallow open lagoon has a maximum depth of 1.5m and is completely surrounded by extensive raupo and flax stands (Plate 1.1; Caithness 1969; Caithness & Pengelly 1973; Williams & Imber 1970). The area provides shelter and food (Potts 1977) for a large number of waterfowl species and supports a variable, but often substantial (Fig. 1.1) Black Swan population.

1.2.2 Swan population

The number of swans attempting to breed over the 1978-1979 study period varied. In 1978 four territorial

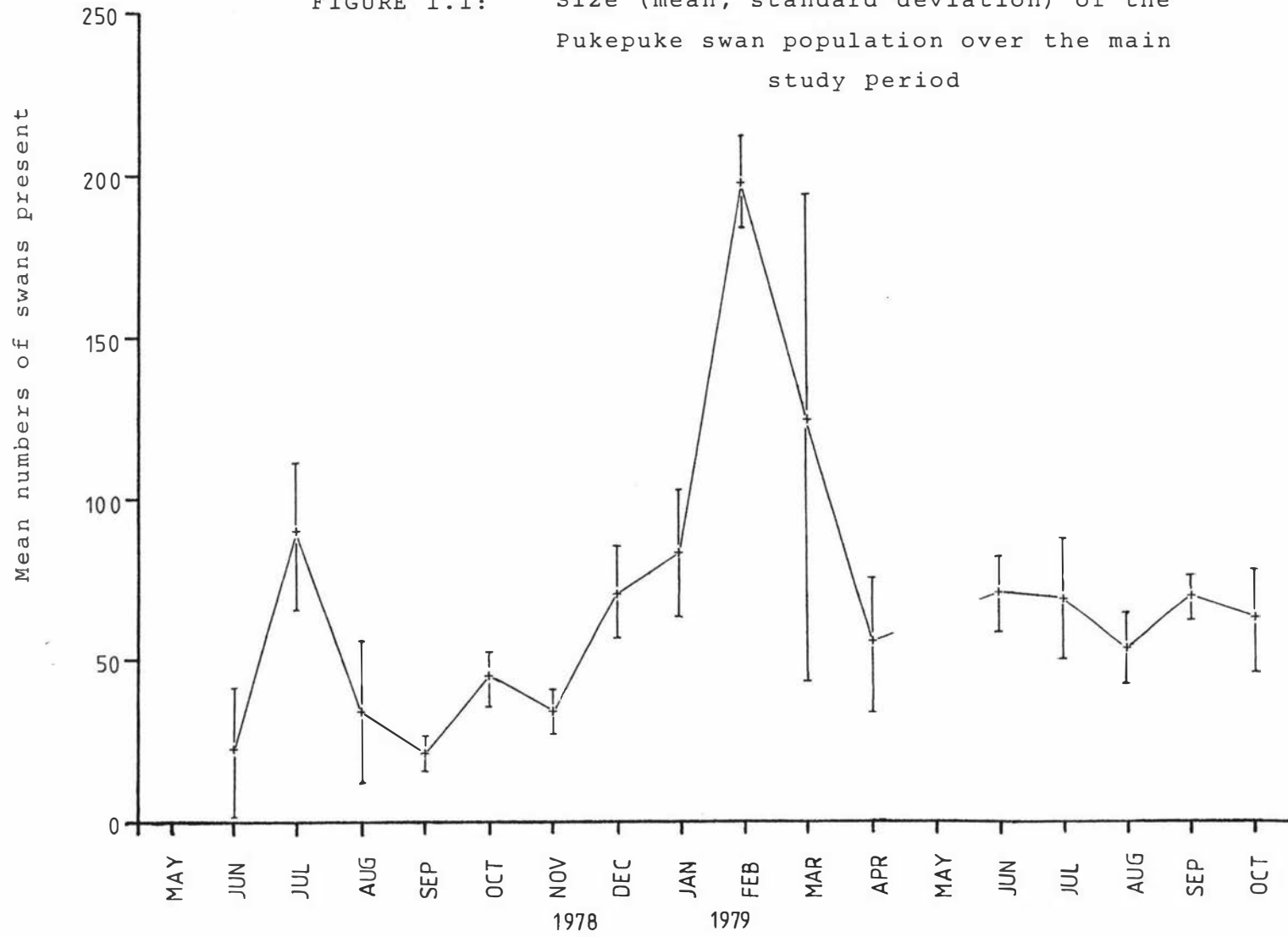
TABLE 1.1 ECOLOGICAL AND BEHAVIOURAL CHARACTERISTICS
OF COLONIAL BREEDING IN BLACK SWANS.

- (1) Breed on large open water areas, where
- (2) Feeding areas for cygnets are large and widespread.
- (3) Water levels fluctuate, different feeding areas exposed.
- (4) Breeding may occur at most times of the year.
- (5) Australian data suggest breeding associations other than monogamous pairs.
- (6) Territory size varies but is usually a pecking distance around the nest, and
- (7) Brood defence may be weak or absent.
- (8) Broods not segregated and may coalesce into creches.

TABLE 1.2 ECOLOGICAL AND BEHAVIOURAL CHARACTERISTICS
OF TERRITORIAL BREEDING IN BLACK SWANS

- (1) Breed on relatively small water areas, having
- (2) Small, discrete feeding areas suitable for cygnets.
- (3) Water levels stable throughout the year.
- (4) Breeding seasonal.
- (5) Breeders are monogamous pairs, who
- (6) Defend a large area about the nest site, and
- (7) Show very strong defence of an area around their broods, generally within the original territory.
- (8) Broods kept strictly apart until 100+ days old.

FIGURE 1.1: Size (mean, standard deviation) of the Pukepuke swan population over the main study period



pairs nested on the main lagoon - later reduced to 2 nests - and 2 broods were produced. In 1979 at least 11 pairs attempted to nest, producing 11 broods, not all of which survived (Ch. 6). Usually 4 - 8 pairs nest each year (A.Garrick pers. comm.). The breeding population represented about 25% of the total number of swans present at the time of nesting.

The size of the non-breeding flock varies from 10 to 200+, reaching a peak in late summer. Flock size is smallest when territorial birds are nesting, and aggression by territory holders may contribute to this (K.Potts pers. comm.).

1.3 STUDY TOPICS

Although the ecology of the Black Swan has been widely studied in both New Zealand (Lickers 1977; Miers & Williams 1969; Williams 1977,1979,1980; Williams & Imber 1970) and Australia (Braithwaite 1970,1977,1981a; Braithwaite & Frith 1969a,1969b; Frith 1959,1967; Frith et al. 1969; Guiler 1966; Hemsley 1973; Lavery 1965; Norman 1971), its behaviour has not been studied in any detail: some data are available on breeding and aggression (Braithwaite 1981b; Poulson 1948; Soper 1960; Tingay 1974). The small proportion of the population that nests territorially has been largely ignored. My research concentrated on the behavioural ecology of the Pukepuke Lagoon population, having 3 main aims:

- (1) to provide a catalogue of all observable behaviour patterns used by the Black Swan population of Pukepuke Lagoon;
- (2) to describe the yearly activity cycle of territorial and flock birds on the lagoon;
- (3) to examine in detail the birds' sexual, aggressive, and family-related behaviour, and the physical and behavioural development of cygnets.

The study population can be divided into 2 parts: the relatively large, transient, non-breeding flock and

the small, resident breeding population (Section 1.2.2). The second part, of major interest to me, may be further subdivided on the basis of the breeding cycle, producing the list of topics which follow in the order in which they are presented in this thesis:

(a) Non-breeding flock (Ch. 2): description of behaviour patterns seen in flock activities; time-activity budgets over a year; relationships between the flock and the breeding population.

(b) Selection and maintenance of territories (Ch. 3): description of relevant behaviour patterns; analysis of behaviour sequences and contexts; sex roles in selection and defence; basis of choice (present and future resources).

(c) Mate selection, pair-bonding, and breeding activity (Ch. 4): description of relevant behaviour patterns; analysis of sequences and contexts; sex roles in breeding activity; daily and seasonal patterning of breeding behaviour.

(d) Physical and behavioural development of cygnets (Ch. 5): physical changes; description of behaviour patterns; ontogeny of behaviour; social interactions.

(e) Brood care and family relationships (Ch. 6): description of relevant behaviour patterns; sex roles in care; duration of care, and eventual breakup of family; interactions with other swans.

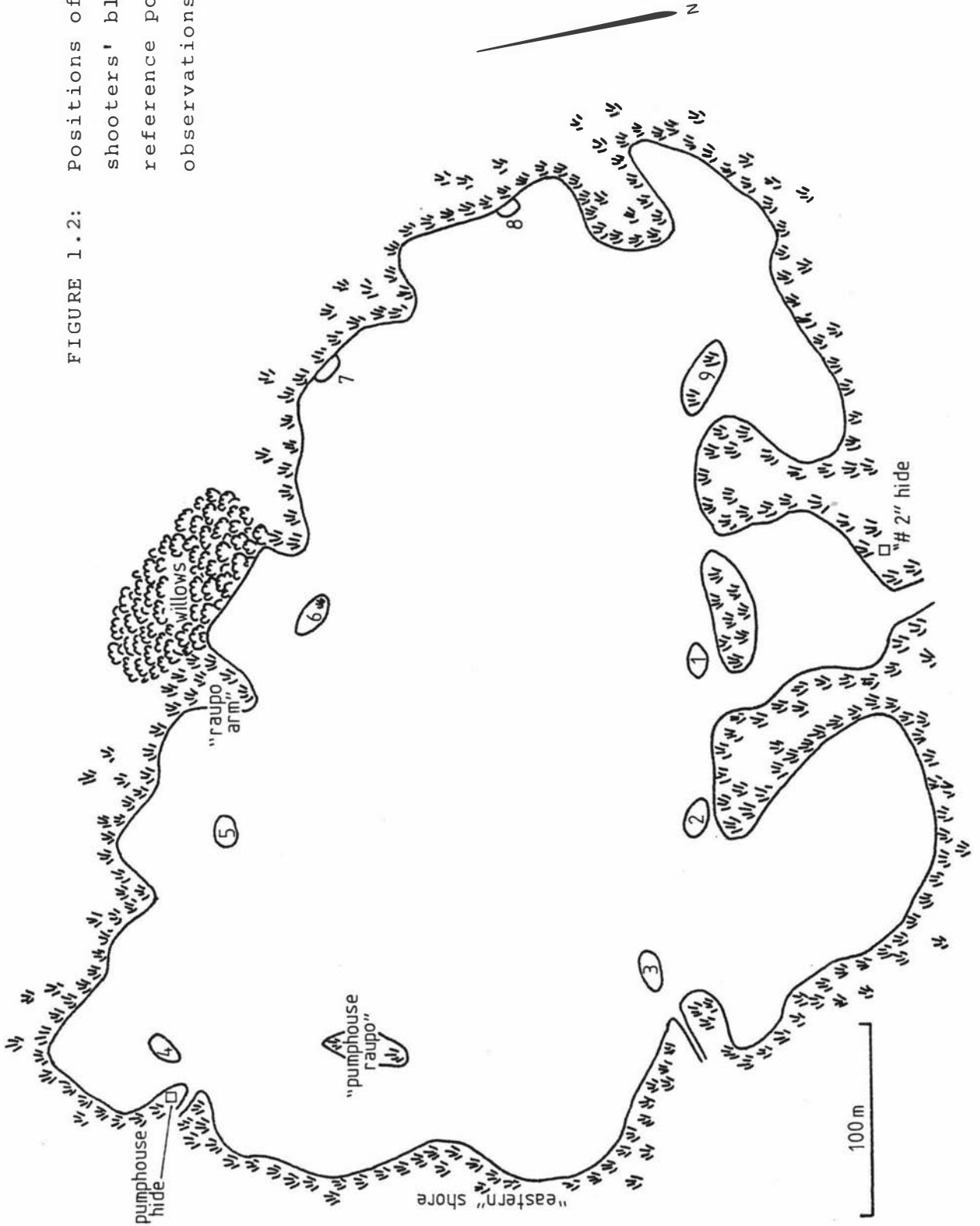
(f) Synthesis (Ch. 7): derivation of behaviour patterns; evolutionary relationships of the species, shown by cygnet and adult behaviour; discussion of territorial versus colonial nesting habits; functions of territoriality in Black Swans.

1.4 METHODS

1.4.1 Choice of hide

In 1978 the Wildlife Service had two permanent hides on the main lagoon, each providing a clear view of the main water area (Fig. 1.2).

FIGURE 1.2: Positions of hides and shooters' blinds used as reference points during observations



The pumphouse hide was the taller (approx. 7m high) and, facing W-N, provided an excellent view of what was often a lee shore - where swans congregated in rough weather - as well as overlooking the main flock areas at very close range. However, some disadvantages accompanied its use:

(1) its approaches were not completely sheltered from the swans unless a lengthy detour was made;

(2) it was the length of the lagoon distant ($\geq 100\text{m}$) from active territorial pairs;

(3) being high and unprotected it tended to shake in high winds, making use of a telescope difficult.

This hide was used only in the initial stage of my study.

"Number 2" hide (approx. 4m high), placed centrally on the northern side of the lagoon, proved much more suitable. Access, along plank walks through flax and raupo stands, was sheltered from view and disturbance was minimal. Its position provided good views of both flock areas and territories, although the shoreline immediately below was hidden. The hide was stable in high winds. This hide was used for the duration of the study.

1.4.2 Equipment

All hide observations were made using a Kowa monocular telescope (10 x 40). Zeiss binoculars (10 x 50) were used for supplementary observations at other Pukepuke ponds, Ahuriri Lagoon (Napier), and Western Springs (Auckland).

Observations were at first recorded using small (15-minute tapes) battery Phillips tape recorders, and augmented with sketches of positions and actions. The recorders proved unsatisfactory and I changed to entering all data by hand, using standard abbreviations for all behaviour patterns. With practice, clear notes could be made with only brief glances at the paper, so maintaining almost constant observation of the swans (Schnierla 1950).

All field observations were transcribed into clear copy on the same or subsequent day.

Photographs were taken at Western Springs in Auckland, where the swan population was used to humans and easily approached. I used an Asahi Pentax SP1000, with 55mm and 200mm lenses and colour slide, colour print and black-and-white film. Line drawings in the text are based on these photographs and on freehand sketches.

1.4.3 Data collection

My first 3 visits to Pukepuke Lagoon were spent familiarising myself with the area and the swans. I observed the daily activity patterns of the swans, noted the water and shoreline areas they used, and described and sketched their behaviour.

Subsequently each visit to the lagoon lasted 2-3 days, one spent in travelling and preparation and 2 in the field. I spent alternate hours in the hide, working over 2 consecutive days so that a whole day, from pre-dawn to post-sunset twilight, was covered. Working in this way allowed for rest periods, as my concentration weakened after longer periods of telescope work. This method made the basic assumption that weather conditions would remain the same, or similar, over each 2-day period.

In summer the full day extended from 0400 to 2000h., and in midwinter from 0700 to 1700h. At the extreme ends of each day visibility was often poor due to reflected light, heavy cloud, or mist. However, some idea of gross movements and interactions could be obtained at these times, although accurate counts and descriptions were not possible.

I combined collection of data sequences from individual birds with recording positions and activities of all swans visible, as the seasonal activity patterns of the whole population were of interest (Section 1.3; Ch. 2). I made 2 total-counts in each hour, beginning 30 minutes apart. For analysis of time-activity budgets I used 6 activity classes: Relaxed-Upright (undisturbed), Feeding, Preening (and bathing), Dozing, Aggression, and Other. Preening and Dozing were later combined as "Loafing" in some analyses. "Aggression" included both territorial displays and disputes among flock birds. "Other" comprised all other recorded activities, which occurred at very low levels: higher intensities of alertness, flying about the lake, mating and breeding activities. Distances from reference points, usually shooters' blinds ("mai-mais"; Fig. 1.2), were estimated in metres, based on the waterline length of an adult swan (approx. 0.6m).

Initially, between counts I recorded 5-minute sequences (in blocks of 30 seconds) of activity from swans chosen at random, starting alternately from right and left of my field of view and working round the lagoon, using a table of random numbers to select individuals. I anticipated that this relatively unbiased selection method would provide data on patterns, frequency and sequencing of various types of behaviour. However, it proved unsatisfactory:

(1) I gained many feeding and loafing sequences but little data on social interactions;

(2) the method had a strong bias in favour of flock birds (making up most of the population), omitting the territorial swans which, as a group, were of most interest to me.

To obtain information on social interactions, particularly those involving the territorial breeders,

I changed my methods. I continued with the twice-hourly flock counts, but between these scanned the whole lagoon continuously, noting positions and actions of groups and individuals, especially pairs and families. The scan stopped at the first bird(s) to display any of a number of chosen behaviour patterns (Table 1.3). This is essentially the Focal-Animal Sampling technique described by Altmann (1974). Using sequences of behaviour as foci for observation, "a sample period begins when an interaction begins. During the sample, all behaviours under study are recorded, in order of occurrence. The sample continues until the interaction sequence terminates or is interrupted, and the next sample begins with the onset of another sequence of interactions" (Altmann 1974:248). This approach provided a mass of data on social behaviour, although it focused on territorial swans and those interacting with them. A number of other parameters were also included with each data record (Table 1.4).

Swans were placed in several age- and social-group categories.

- (1) Age:
 - (a) adult: body plumage black; some estimate of age possible, using the amount of black in the flight feathers (Braithwaite 1981a). 1+ years.
 - (b) juvenile: body plumage brownish; usually associated with no particular adults. Less than 1 year (bird-of-the-year).
 - (c) cygnet: downy or with variable feathering; travelling in family group with parents. 0 - 4 months.
- (2) Social grouping:
 - (a) flock: variable number of swans in loose group; no obvious social relationships.
 - (b) pair: 2 swans travelling in close company for extended periods, maintaining average

TABLE 1.3 BEHAVIOURAL PATTERNS SELECTED
FOR EXAMINATION

- (1) Range of alert postures, from dozing to preflight.
- (2) Feeding behaviour.
- (3) Preening.
- (4) Aggressive behaviour, of both flock and territorial birds.
- (5) Sexual behaviour: selection and attraction of mate, pair-bonding, copulatory activity.
- (6) Behaviour of young.
- (7) Brood care: defence (see 4), carrying, brooding (if observable), development of family / social bonds.

Behaviour sets 1 - 3 described and used in time-activity budget analysis.

Behaviour sets 4 - 7 described and used in time-activity budget analysis; emphasis on sequences of behaviour, frequency, σ^7 - Q roles etc.

TABLE 1.4 PARAMETERS NOTED WITH EACH
 BEHAVIOURAL DATA RECORD MADE

Time

Identity of (interacting) individual(s), where known

Sex of actor / reactor, where known

Position on lagoon

Sequence of behaviour, where aggression / breeding /
 family - related

Or note of its occurrence

Others present, and their reactions

Preceding event(s), if known

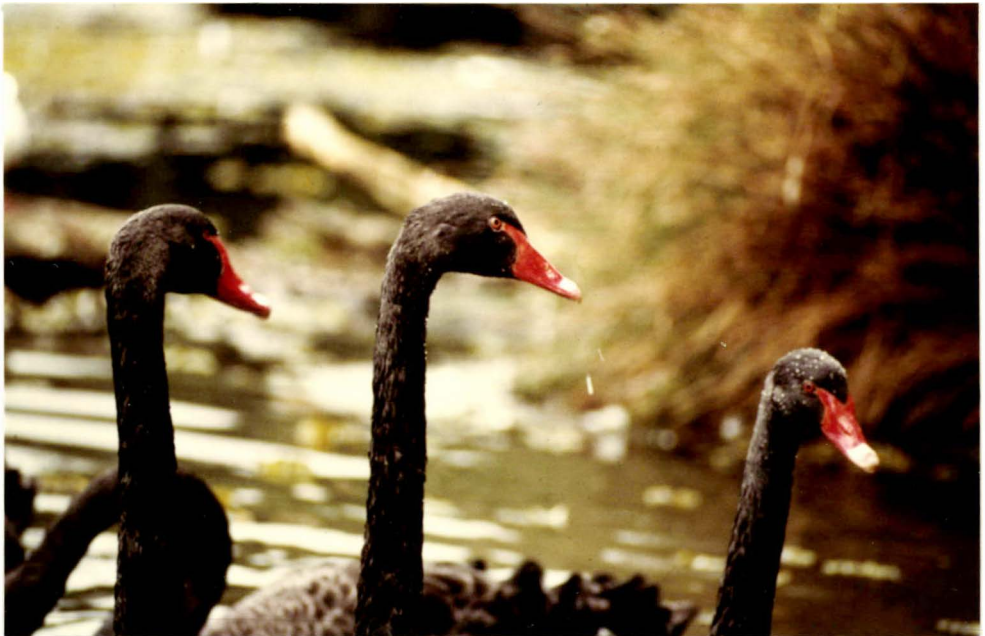
Subsequent event(s), if known

Weather conditions noted at the beginning of each
 hour's observation

NOTE: sexes distinguished as follows: ♂ larger, neck more erect, voice
 deeper, head broader; takes superior position in copulation

PLATE 1.1: A view of Pukepuke Lagoon, from the path
to "Number 2" hide

PLATE 1.2: Black Swan faces are very much alike to
the human eye



separation of 1 - 2m; shared greeting ceremonies (Ch. 4; Butterfield 1970).

(c) family: pair and associated cygnets or juveniles.

(d) siblings: juveniles travelling in a group; low individual distance; shared Greeting ceremonies ("brood remnants": Prevett & MacInnes 1980).

(3) Sex: could only be determined in known pairs, using size, postural and vocal differences as well as aggressive and sexual behaviour*. Unless obvious cues were presented, I did not classify flock birds by sex.

1.4.4 Difficulties encountered in field work.

1.4.4a Identification of swans.

A major problem lay in the identification of individuals: only a few (6 - 10) of the Pukepuke swans could be reliably identified. Black Swans possess no obvious facial characteristics useful in recognition (Plate 1.2). Some of the study population wore coloured neck collars, denoting a capture site elsewhere in New Zealand, but these were usually transients. Capture of Pukepuke swans, for marking, was not attempted on a large scale (see below): 2 adults and one juvenile were caught. There could be no guarantee that any birds caught were resident and so useful in a study of breeding behaviour on the lagoon. The few birds marked on other Manawatu lakes did not enter the study area: 18 juveniles and adults were banded and collared on Lake Horowhenua (Levin) in December 1978, but none appeared on Pukepuke Lagoon during my study.

Several capture methods were discussed, or had been tried by Wildlife Service personnel, but they

* ref. Table 1.4

were considered to involve an unacceptable level of disturbance to the swan population:

(1) The Pukepuke swans were wary and could not be approached closely enough to capture by hand or with a noose or crook unless sitting on the nest. Nests were hard to pinpoint and there was the possibility that disruption of incubation would lead to nest desertion. One adult was caught while incubating; the effect of this on breeding success could not be ascertained, as the clutch was removed at the same time as part of another project. One moulting adult and one juvenile were also captured.

(2) attempts to run swans down in a boat only led to their escape in the surrounding raupo.

(3) unlike the dabbling ducks they did not seem amenable to grain baiting and trapping; a surprising result, since they take grain readily in captivity (Ch. 5).

(4) the use of a cannon net over loafing areas was deemed expensive, time-consuming, and disturbing and hazardous to the swans (T.Caithness, M.Williams pers. comm.).

Thus identification of individuals was based on plumage, size, postural and behavioural characteristics, on specific collars where present (in 1978 these were A₇V, white collars "stripe" and "3-dot"; in 1979: QGC₂); and to some extent on the areas they frequented. Lack of reliable identification for most swans introduced bias into my results, since the effects of individual differences in behaviour could not be accounted for (Section 1.5.2). Using a captive brood in the study of cygnet development (Ch. 5) removed this source of error as far as cygnet studies were concerned.

1.4.4b Effect of distance from subjects.

Hide "number 2" was approximately 20m from the

water's edge. Much greater distances usually separated observer and subject: 40 - 60m for the area behind mai-mai (MM) 9, about 80m for MM6, and 100m+ for the area from MM3 to MM4 (Fig. 1.2). Thus it was impossible to obtain data on soft vocalisations and on subtle postural variations. This gap was partially filled by information gathered on visits to Western Springs, and by study of a captive brood of cygnets.

1.5 DISCUSSION: EFFECTIVENESS OF FIELD OBSERVATION METHODS.

1.5.1 The value of observational studies.

Ethology has been defined as "the study of function, biological significance, causation, and evolution of species-typical behaviour" (Dilger 1962: 83). The first step in an ethological study such as mine must be a detailed description of all behaviour patterns used by the animal in question; more detailed analyses may then follow. Difficulties arise immediately, in determining the focus of research and in ensuring that no behaviour patterns are omitted from the catalogue. The latter problem may be resolved in part by complementing field work with observations of captive animals (Ch. 5).

My study centred on describing all the observable behaviour of the Pukepuke Black Swan population, and on the analysis of specific sets of behaviour patterns. Decisions and constraints on sample methods (1.5.2) have inevitably added some degree of bias to my results. However, as Altmann (1974) points out, direct observation provides a necessary link between experimental studies and the "real world". The results it gives usually have "low internal validity", i.e. they do not adequately eliminate alternative explanations for

any data obtained, such as the effects of collecting methods or of observer bias. They may, however, be readily used to generalise to other samples. The choice of sampling method is an excellent basis for improving the internal validity of data by removing or reducing such biases. Observer-level sampling decisions provide the major controls in observational work (Schnierla 1950).

1.5.2 Sampling methods and sources of error.

A major source of error lay in my inability to recognise more than a few individuals (Section 1.4.4a). Slater (1978) states that this reduces the confidence of quantitative data, since individual differences in behaviour may affect results. The end result, as stated earlier, is low consistency between samples, but it is easy to generalise from the results. This difficulty was overcome to some extent by collecting much data in the form of sequences i.e. by using Sequence Sampling, a modified form of Focal-Animal Sampling (Altmann 1974). A large sample size may also help to remove bias (Dilger 1962).

Proper scheduling of sample sessions is also important. Making observations at varied times throughout the day and year gives the best chance of seeing the population's complete behavioural repertoire. However, to obtain quantitative data regular and standard-length sessions are required (Slater 1978). This removes observer bias toward preferred sampling times, and improves consistency since it allows for the effect of circadian rhythms on behaviour patterns. Slater (1978) adds that, if some behaviour patterns are known to be rare or unusual, the observer should be free to record their occurrence at any time.

I used a combination of rigid scheduling (for time in hide, timing of flock counts) and Ad Lib. (Sequence) sampling within the set hide periods (for

general behavioural data). Choice of individuals was "irregular", "with the individual [being] chosen on the basis of some behavioural criterion" (Altmann 1974; Table 1.3). Such behaviour-determined selection does result in dependence between samples and between participants, but permits accumulation of data about relatively infrequent acts (Slater 1978) and so, given my research questions, is the best sample method. My initial decision, to reduce bias by choosing individuals completely at random, without reference to their social behaviour (Altmann 1974), led to a deficit in data for those behaviour patterns of most interest to me.

One other major source of inconsistency existed, namely that "Any time that more is visible than can be recorded, sampling decisions remain and, in the absence of systematic sampling, the observer's preferences will come into play" (Altmann 1974: 239). This source of error exists wherever data are obtained from sequences in which actions occur faster than they can be recorded. For copulatory data this is true for rapid repetitions of dipping movements, and given the manner of their analysis (Ch. 4) is unlikely to be important. In agonistic sequences some bias is avoided if a sampling decision is adhered to throughout: I recorded the actions of a focal individual (actor), and where possible the reactor; if more than one was present I followed the first observed reactor.

Sampling for specific acts, or sequences of acts, as they occur, provides a form of Focal-Animal Sampling on an Ad Libitum basis (Altmann 1974; Section 1.4.3). This method is quite acceptable, although biased in that sequences may not be sampled in proportion to their

frequency of occurrence. It is also necessary to identify the beginning and end of sequences, and to avoid dependence of data if possible: if the next available sequence is sampled, data may not be independent. In the case of copulations, sequences are so far separated in time that dependence is most unlikely, nor is there any evidence for social facilitation. This is not necessarily true of aggressive interactions.

"The primary advantage of this form of sampling is that it enables the observer to obtain large samples of social behaviour and to sample sequences that may persist regardless of the continued participation of any one individual. The primary disadvantages stem from problems in selecting sequences and identifying their beginning and end" (Altmann 1974: 251). However, given the difficulties associated with other sampling methods, Sequence Sampling proved most acceptable for my use.

Chapter 2

FLOCK ACTIVITY

2.1 INTRODUCTION

Many different bird species are known to enter flocks for at least a part of their yearly cycle, for breeding, migration, or wintering. In addition, the non-breeders in a given population may remain in a flock while others nest and breed, as do some of the Black Swan flock on Pukepuke Lagoon.

Joining an overwintering or non-breeding flock may have several advantages. However, there is some uncertainty about the pressures affecting the formation, structure and ultimate size of flocks. Murton (1971), Zahavi (1971) and Ward & Zahavi (1973) agree that, in general, communal roosting in birds serves to improve the feeding prospects of an individual, since it may follow the flock to feed each morning. Safety from, or a reduced risk of, predation is viewed as a secondary factor. Murton (1971) notes that individuals of many species fly to join feeding flocks (see also Inglis & Isaacson 1978), thus reducing their own searching time. "Social facilitation effectively ensures that vital information is obtained by the individual and this would seem to provide a complete explanation of flock feeding" (Murton 1971: 535). Conversely Lazarus (1972) states that predation is a major factor influencing the formation of both roosting and feeding flocks. "Predation presents a somewhat unitary selection pressure on feeding dispersion, favouring increased gregariousness" (Lazarus 1972: 557), while the demands of feeding may either support or oppose aggregation. Flocking is most likely

to be the result of several selection pressures in combination.

Flocks may demonstrate daily and seasonal changes in composition, structure and activity. Such changes may in turn be linked to major events in the social or physical environment (e.g. Anderson et al. 1969; Inglis & Isaacson 1978; King 1974; Minton 1971). Thus composition is altered by an influx of juveniles and / or families after breeding, and by the exit of breeders earlier in the season. Structure may be influenced by group size, individual relationships within the flock, or the nature of the food supply, while activity may alter with energetic requirements, the activities of others (social facilitation), or the weather.

Structure and composition studies use demographic techniques (e.g. Hewson 1964; Minton 1971; Sladen 1973; Williams 1977), while the use of energy budgets is an excellent method of demonstrating the costs and benefits of various activities to the individual or group. However, it is not always possible to determine the energy value of all parts of the budget. Instead, time-activity budgets provide a rough estimate of the importance and costs of various activities, and may be used to gain "some comparative insights" on the nature of time and energy allocations within and between species (King 1974). "Conspicuous generalisations include the relatively small time spent in flight during the breeding season; ... [and] in intra- and interspecific aggressive encounters; and the great variability among species in the amount of time spent foraging and resting" (King 1974: 48). Time allocations and strategies, particularly for feeding, are affected by temperature; photoperiod; body size and reproductive condition; quality, quantity and dispersion of food; and social factors.

On Pukepuke Lagoon a flock, of varying size, is present throughout the year. The majority of its members

(70 - 90% in Aug.-Oct. 1978; 70 - 76% in Aug.-Oct. 1979) do not breed on the lagoon. This part of the population contributes relatively little to the aggressive and breeding activity examined in later chapters (3,4,6). However, it can provide data on daily and annual activity cycles followed by the population. Since birds were unmarked (Ch. 1), reliable data on these cycles could not be obtained from the small number of breeding pairs present.

This chapter examines the behaviour patterns exhibited by flock birds; the size and composition of the flock and changes in these over the year; patterns of area utilisation; and daily and seasonal changes of activity.

2.2 METHODS

Data used in examination of daily and annual rhythms were collected during twice-hourly flock counts, as outlined in Ch.1 (1.4.3). In addition, I made the following manipulations of data.

2.2.1 Changes in group size

Data in flock counts were recorded as group size, activities of members, and position. For each month, these records were used to give the total number of swan groups in each of the several size classes. Group size increased by 2's up to 10 (i.e. 1-2, 3-4....); and thereafter in 10's, up to 100+. The cutoff point for accurate counts should perhaps be the upper limit of family size (7-8), but there is no evidence that families remain intact in flocks (2.4.1).

Most groups on the open lagoon, and in some shoreline areas, could be accurately delineated and counted. However, particularly in the eastern loafing area, I could not always distinguish and enumerate separate groups. In such cases I only recorded the number present in a defined area, and described it as a "loose aggregation".

I could then produce histograms of group size. Groups of 11 - 100+ were combined to examine the frequency of occurrence of larger groups, since each larger category taken by itself generally occurred at a low frequency. (The larger aggregations could possibly be broken down with more accurate recording techniques.)

I derived the number of birds present each day from flock counts, and calculated monthly mean, range and standard deviation in flock size.

The areas used by groups were noted as counts were made. For each month I marked these areas on a map of the lagoon by drawing a series of circles centred on the areas concerned, having radii proportional to the group size recorded there. Visual examination of monthly maps permitted estimates of areas used frequently (>10 groups recorded) and the size of groups using them (small 1-10; large 11+; overlapping use by both group sizes). Comparison of the maps indicated any seasonal trends in area use.

2.2.2 Time-activity budgets

Estimates of time-activity budgets were based on the proportion of swans involved in each of several activity classes at the time of the half-hourly counts. Monthly totals were obtained by summation. The effects of changes in population size were not allowed for.

Although hourly data were available, I divided the day into three equal periods - morning, "middle-day" and evening - to compensate for photoperiod changes and to permit direct comparison between months having different daylengths. The proportion of the population engaged in each activity class was calculated for each period. I used 2x2 Chi² tables to compare activity in the 3 day periods within and between months and seasons.

Division of the year into seasons was based on photoperiod, so that winter (May - July) centred on the midwinter solstice of June 21 and summer (November - January) on the midsummer solstice. This division smoothes out monthly variations, but may also show up seasonal trends.

Calculations were made more approximate by the fact that swans are active at night, when I made no direct observations, and nocturnal activity patterns may (a) differ from and (b) directly affect daylight rhythms.

2.3 RESULTS

2.3.1 Description of behaviour patterns*

A. Alert

2.3.1a Relaxed-Upright (REU): body plumage is relaxed - neither depressed nor erected (Morris 1956) - and the neck is smooth and relaxed in a curve. The swan may be standing, walking, or swimming. (Fig. 2.1a)

2.3.1b Alert-Upright (ALU): seen when there is a slight disturbance or the bird is wary. Neck and head are held erect, although neck and body plumage is generally relaxed. An exception occurs in some conflict situations: a bird approaching humans will be in ALU but may have erect neck feathers. ALU with erect neck plumage serves as a threat in some contexts (Ch. 3). (Fig. 2.1b)

2.3.1c Anxiety-Upright (ANU): in strongly alarming situations, such as attack or the presence of a human and dog on the shore. Neck and body plumage are fully depressed so that the body outline is sleek and streamlined, and the neck is held stiffly erect or tilted slightly backwards. Movement is away from the alarming stimulus and may be followed by flight. ANU is ritualised as a pre-flight display (d below) and possibly as appeasement to threat. (Fig. 2.1c)

* basic behavioural categories seen in all swans: Table 1.3

The same depression of plumage, but combined with an "oblique-forward" neck, is seen in distressed cygnets (Ch. 5) or birds seized by an attacker after a chase or lunge.

2.3.1d Preflight display: ANU, together with a particular call and a head-jerking movement, is seen in preflight situations where a group (2 - 6) of swans is preparing to leave the lagoon. The displaying bird holds its head at an angle above the horizontal and jerks it up and down so that the neck is in an S-bend on the downward movement. The swan moves about actively on the water, generally facing into the wind - this would assist takeoff.

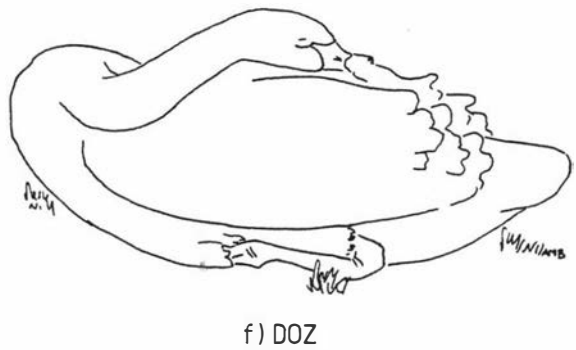
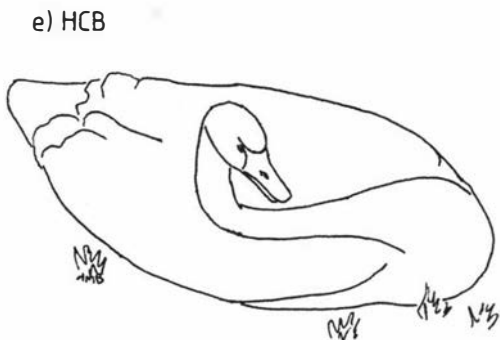
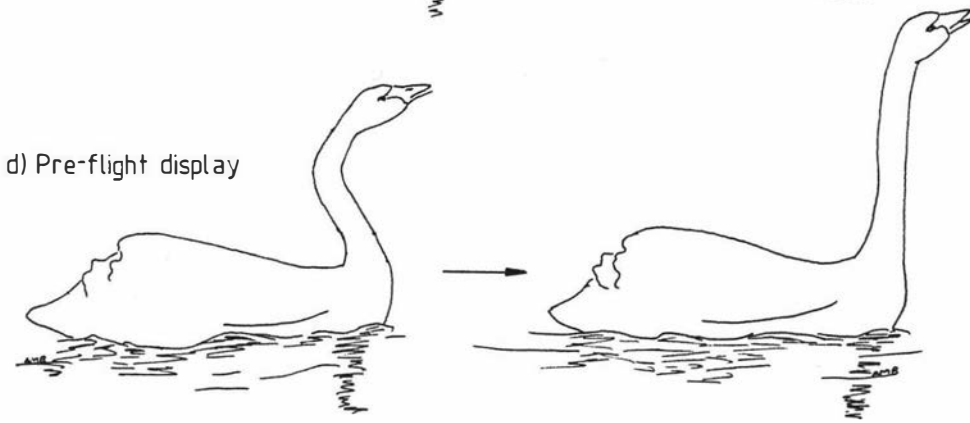
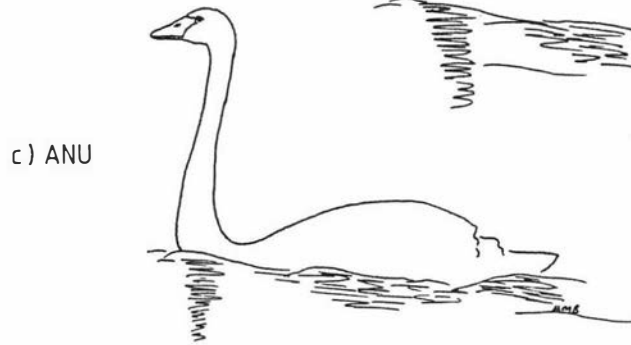
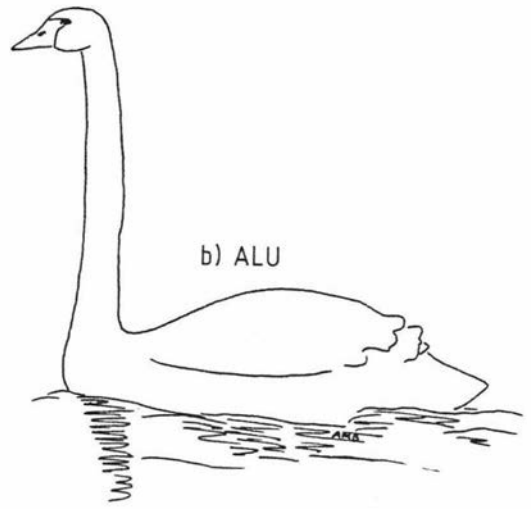
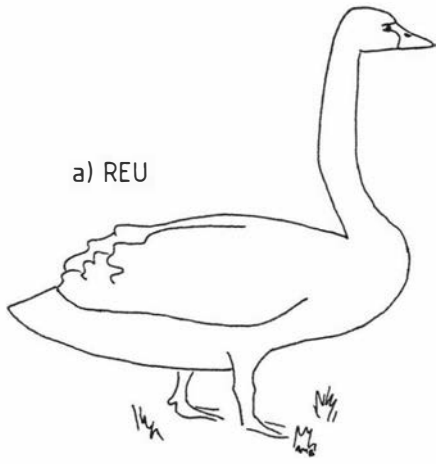
This display is frequently seen in late evening, when groups are preparing to fly out to other localities. It does not precede short flights to change position on the lagoon, nor flights avoiding an aggressor. (Fig. 2.1d)

2.3.1e Head-curved-back (HCB): seen rarely and seems characteristic of sick birds. I have observed it, alternating with bouts of convulsions, in swans found (by autopsy) to have suffered from lead-poisoning. The plumage is relaxed or fluffed, and the neck is laid very far back on neck and wings, with the head hardly raised. This is probably a consequence of extreme weakness or lack of muscular control. (Fig. 2.1e)

2.3.1f Dozing (DOZ): a dozing bird has its neck curved over its shoulders, bill tucked under the scapular feathers. A bird in this posture may still have an eye open and be alert to its surroundings. It may be on the water, or standing or sitting on land. Feather position depends on temperature (Morris 1956) but is usually relaxed, and one or both feet may be tucked up into the flank feathers. (Fig. 2.1f)

B. Feeding

Postures seen in feeding birds are related to the feeding site.



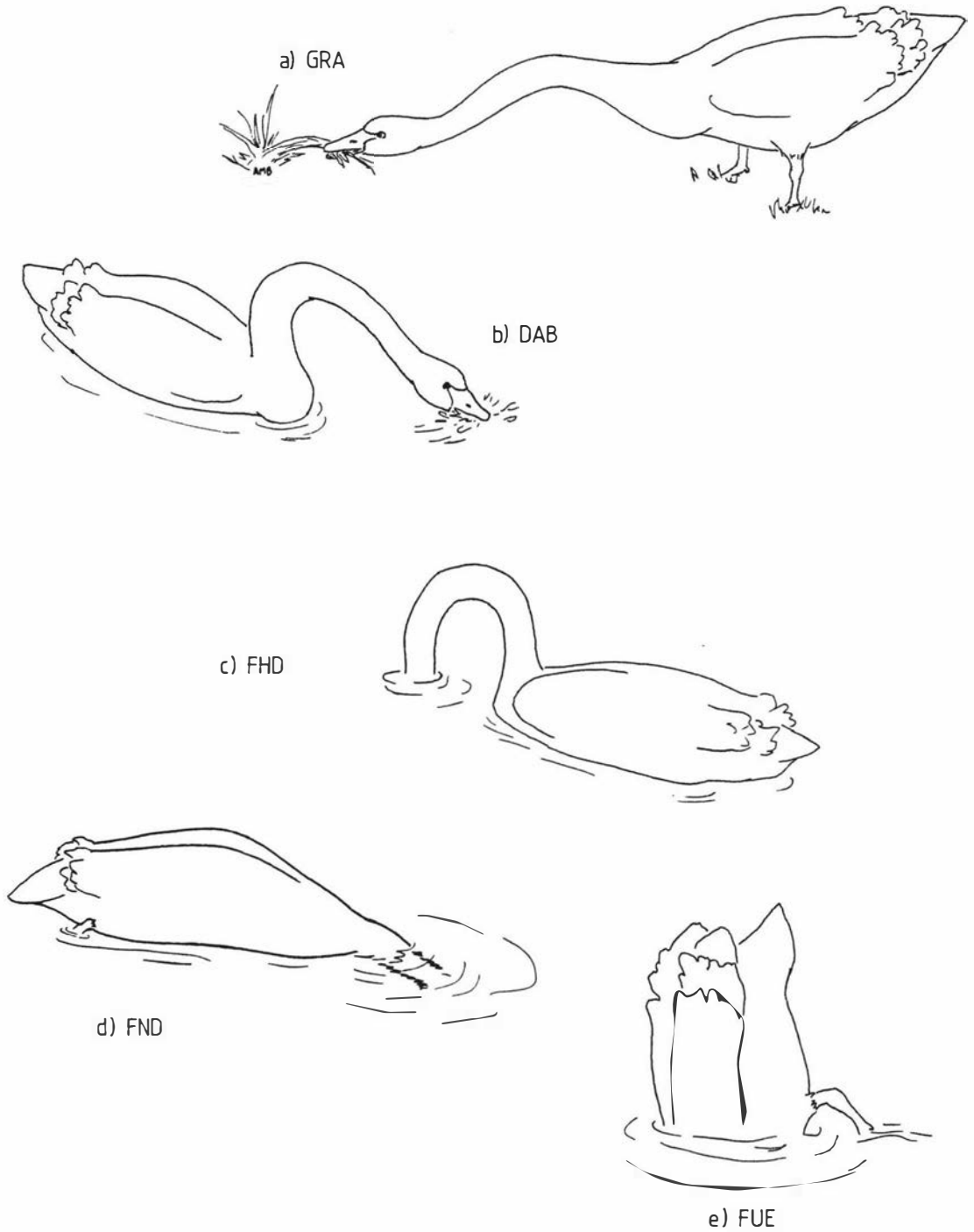


FIGURE 2.2: Feeding modes in Black Swans
 a) Grazing b) Dabbling
 c) Feeding-head-down d) Feeding-neck-down
 e) Feeding-upended

PLATE 2.1: Preening swan



2.3.1g Grazing (GRA): when at or on the shore, swans graze on emergent vegetation, willows, or pasture plants (Blomfield & Black 1963; Frith et al. 1969; pers. obs.). Leafy material is seized in the bill and torn off with a backwards and sideways jerk of the head. Black Swans normally graze pastures only when these are flooded. (Fig. 2.2a)

2.3.1h Dabbling (DAB): swans also feed by dabbling at the water surface, and so may compete with dabbling ducks for some food items. Water is drawn in at the front and ejected at the side of the bill, leaving food trapped on the bill lamellae. (Fig. 2.2b)

2.3.1i Feeding-head-down (FHD): occurs in very shallow water. Only the head is submerged to feed off the bottom, with the neck in an inverted "U" shape above. (Fig. 2.2c)

2.3.1j Feeding-neck-down (FND): in deeper water the neck is also lowered, but the body remains horizontal. Owen & Kear (1972) note that a FND swan may have its chin flat on the bottom, its neck in an S-bend. (Fig. 2.2d)

2.3.1k Feeding-upended (FUE): in water of approximately 1m depth, swans extend their reach by upending, maintaining this posture by paddling hard with their feet (Fig. 2.2e). It is assumed that submerged food is found by taste and touch (Owen & Kear 1972), but Black Swans appear to have adequate vision in fairly clear water. I observed a captive cygnet chasing and catching three tadpoles while swimming in a small tank, an action dependent on sight.

C. Preening and bathing

The comfort movements used by swans have been classified and described by McKinney (1965), who recognised seven categories of behaviour: shaking movements, stretching movements, cleaning movements, oiling preening, nibbling preening, washing, and bathing (Plate 2.1). My observations provide some additional data:

(1) McKinney (1965) did not observe incomplete and com-

plete somersaulting in swans, and was uncertain if they would occur. I saw both forms often, in captive and wild swans.

(2) Dashing-and-diving, a high-intensity bathing activity, was "not recorded, but probably occurs". I recorded it in both adults and cygnets, but more frequently in the latter, when it could possibly be described as "play" (Ch.5).

(3) McKinney had "never seen the movement of stretching both legs [at once] ", but I observed this in captive cygnets lying on the ground while preening. They were panting heavily in hot weather and the posture may have facilitated heat loss, through the stretched webs of their feet.

D. Aggression

Aggressive behaviour occurs at a low level in flock birds. In general disputes are over loafing or feeding areas and/or violations of individual distance. They involve low-intensity threat displays (Ch. 3) and are of short duration. Higher-intensity displays may be used where members of two pairs or families are involved.

E. Pairing and breeding activity

These activities are described in Ch. 4. Greeting and Triumph ceremonies occur in the flock, and are given by paired or family birds after a fight or other disturbance. Copulations and pair-bond maintenance behaviour are also seen in flock birds. Those engaged in these activities are probably testing partners (Ch. 4), or preparing for breeding while en route to their own nesting areas.

2.3.2 Composition, structure and size of the flock

2.3.2a Composition

The composition of the Pukepuke flock is unknown, but it is likely to include the following elements (see also 1.4.3):

- (1) Juveniles, with or without parents and/or siblings

i.e. brood remnants and/or family groups.

(2) Young adults, past their first year but too young to enter the breeding pool. (For (1) and (2) age determination is based on plumage characteristics.)

(3) Older birds, prevented from breeding by sickness, injury, or inability to hold a territory and attract a mate.

(4) Paired birds in transit to their own breeding grounds: some apparent pairs are always present in the flock.

The proportion of birds in each category varies with the seasons.

Some estimate of social relationships within the flock may be gained by examining the social distance maintained by its members. Pair or family members, moving together, maintain close contact of three or less body lengths although this is often expanded while feeding or during territorial or family defence. Non-paired birds travelling in company may be as far apart as 10 body lengths (6m) and rarely approach closer than 1 body length. When feeding on "popular" sites, preening, or dozing, they may approach to 1 body length or less (0.6m). In feeding, this distance may be increased again by threat from the approached individual(s). Loafing swans usually tolerate very close approach.

If spacing is compressed too much ("how much" depending on the individual), the bird intruded upon may react by (a) moving away; (b) low-intensity threat; (c) pecking, or an intention-movement to peck (Ch. 3). Higher threat intensities, or physical attack, are less frequent. Threatened birds usually move less than 5 body lengths away i.e. out of the immediate vicinity of the aggressor. If threatened by a territorial individual, however, avoidance is usually maintained until well clear of the territory.

2.3.2b Aggregation and entry

The flock as a whole is regarded as an anonymous group.

Stimuli for aggregation of flock birds are most probably the presence of preening and loafing sites (which are discrete) and food sources (over most of the lagoon), although the presence of swans in appropriate postures may be equally important (Section 2.4). During the breeding season, the activities of territorial swans may affect clumping patterns (2.3.2d).

Predation on adults is unlikely to be an aggregative stimulus for the non-breeding flock as predators on adult swans are few (Guiler 1966; Lavery 1965). However, sick birds may be attacked e.g. by mustelids (pers. obs.).

Flock birds may be joined at any time by swans from elsewhere on or outside the lagoon. In general entry appears to be open and immediate. An outsider usually approaches a loafing group in Relaxed or Alert-Upright (REU/ALU). The group may (a) show no overt reaction; (b) become briefly REU/ALU; or (c) there may be a brief threat from one or more members, then all resume feeding. Entry to a feeding group may involve a more pronounced threat.

2.3.2c Flock Size

(1) Overall size:

The Pukepuke flock is present throughout the year. Its size, excluding known breeding pairs during the breeding season, ranged from less than 10 to over 200 swans during my study, reaching a peak in late summer and early autumn (Fig. 2.3) when birds were travelling to and from moulting areas. Flock size was smallest when territorial birds were nesting, and aggression by territory holders may contribute to this reduction (K. Potts pers. comm.). However, although a greater number of pairs nested in 1979 the drop in flock size was not as marked in this year.

The large numerical variation observed in March 1979 was due to a rapid decrease in flock numbers during that

month. This may have been due to an exodus of potential breeders, moving to other nesting areas, or to a quantitative or qualitative change in food supply (A. Garrick pers. comm.).

(2) Subgroups within the flock:

On the lagoon the flock disperses as single birds or pairs, in groups of 3-4, and in larger assemblages. Similar groupings are seen among birds arriving on or flying out from Pukepuke. These groupings may reflect social affiliations (Section 2.4). One subgroup - juveniles, or birds-of-the-year - is easily recognised by the characteristic brownish first plumage of its members. Its size changes as the brood-rearing season advances (Table 2.1).

Group sizes were recorded during flock counts (Section 2.2.1), a group being defined as 2 or more swans acting in company, with <10 body lengths separating individuals. The proportion of larger (11+) groups in the monthly totals showed some seasonal variation, peaking in the 1978 - 1979 summer and early autumn (Dec. - March) at over 50% of the groups recorded, a highly significant ($2 \times 2 \chi^2$ tests, d.f.=1, $\alpha=0.01$, $p<0.001$) result. The highest flock counts were recorded in Feb. - March 1979, at 200 individuals. Maximum aggregation size exceeded 100 in these two months, and reached 80 - 89 in December and January (Fig. 2.4).

Groups of 11+ reached their lowest frequency in Aug.-Sept. 1978, when they comprised 1.58- 1.75% of total groups. Numbers on the lagoon were also at their lowest, with maxima of 51 and 28. Maximum group size was in the range 30 - 39 and 11 - 19. A similar pattern did not occur in the 1979 breeding season, although the number of breeding pairs was higher. Instead, the proportion of large groups in the total remained fairly constant after the March fall-off in population size, nor did monthly population maxima decrease.

Similarly, the proportion of groups of size 1-2 peaked

TABLE 2.1 PROPORTION OF BIRDS-OF-THE-YEAR
 IN THE PUKEPUKE POPULATION

date	number of birds- of-the-year	total population	% birds-of- the-year
8-9/10/78 ^a	4	66	6.06
18-19/10/78 ^a	10	46	17.86
29-30/11/78 ^a	10	77	11.49
5-6/12/78 ^a	19	115	16.52
9-10/1/79 ^b	20	110	18.18
24-25/1/79 ^b	39	125	31.20
31/1-1/2/79 ^b	53	167	31.74

a: only resident families

b: influx of juveniles from other areas, moving around
 after fledging and family disintegration (Ch. 6)

NOTE: new juveniles older than residents, & already fledged

FIGURE 2.3: Size (mean, standard deviation) of the Pukepuke swan population over the main study period

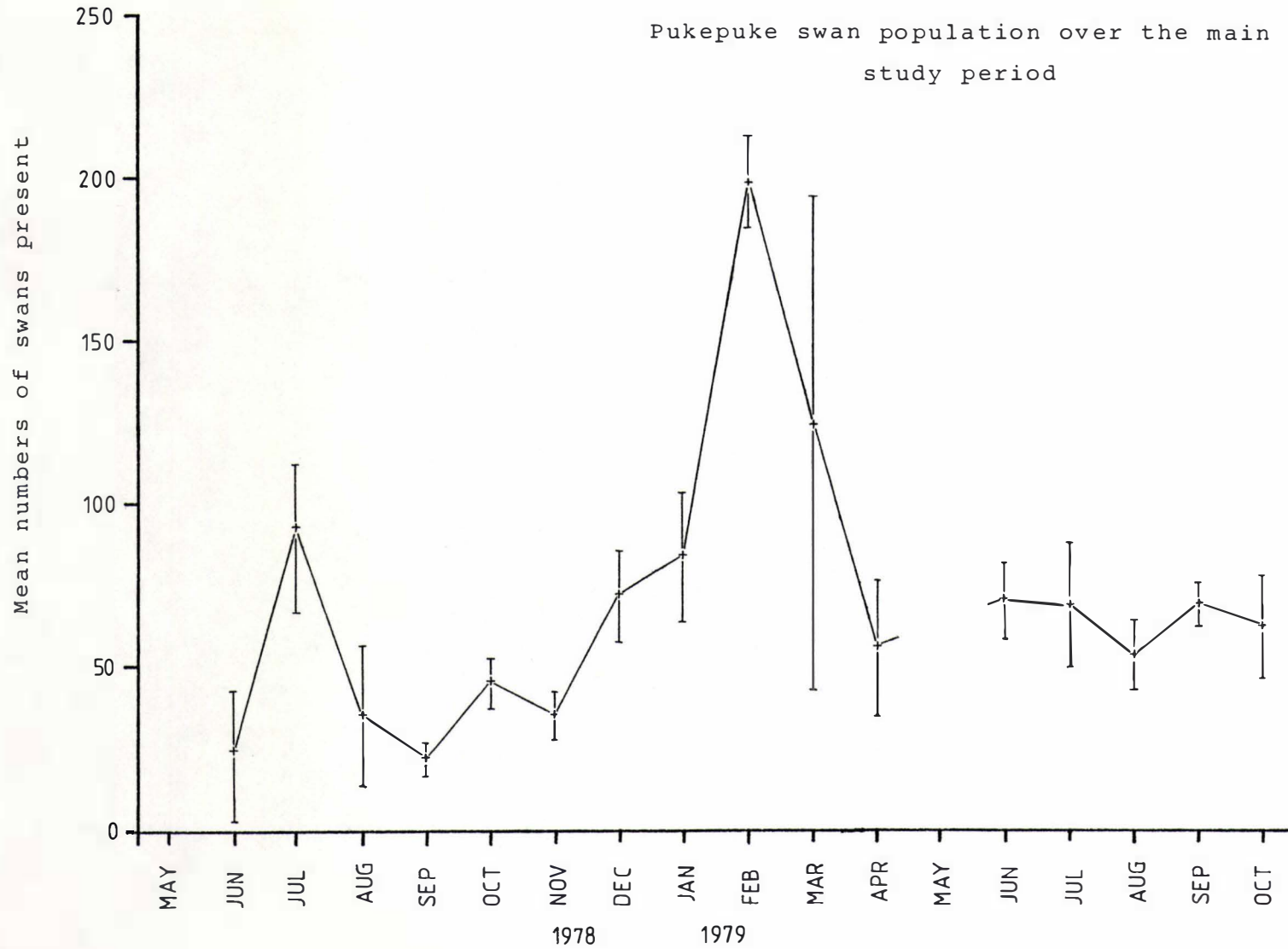
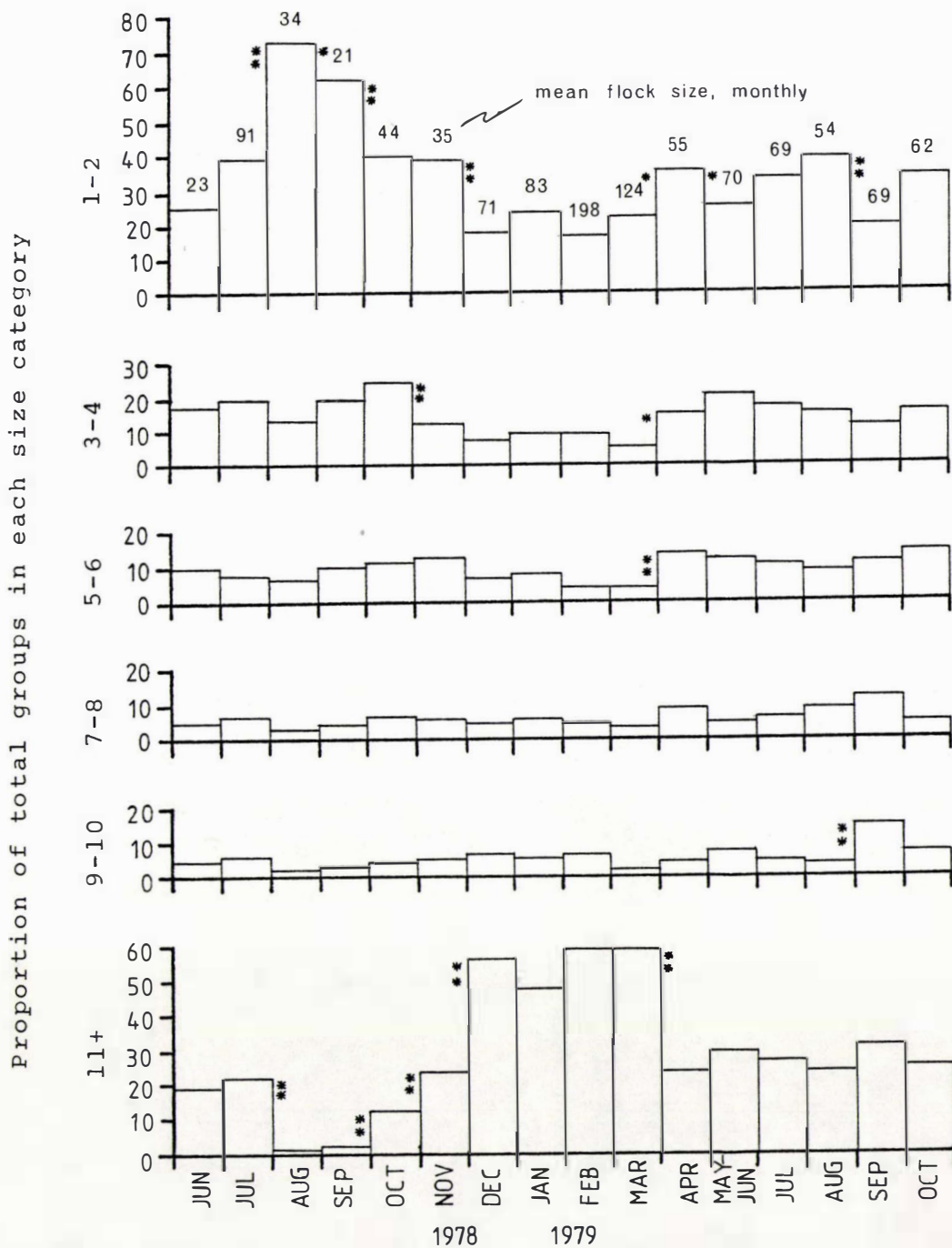


FIGURE 2.4: Proportion of total groups occurring in each size category, June 1978 - October 1979

* $p < 0.01$ ** $p < 0.001$



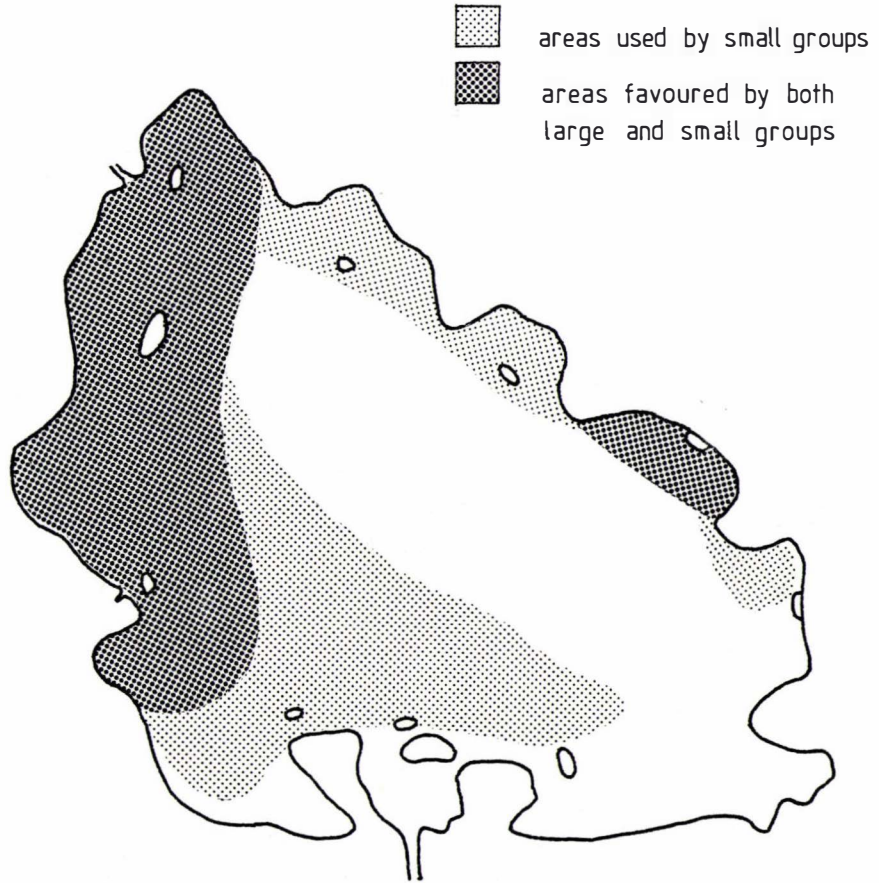


FIGURE 2.5: Area utilisation: areas favoured by large and small groups of swans

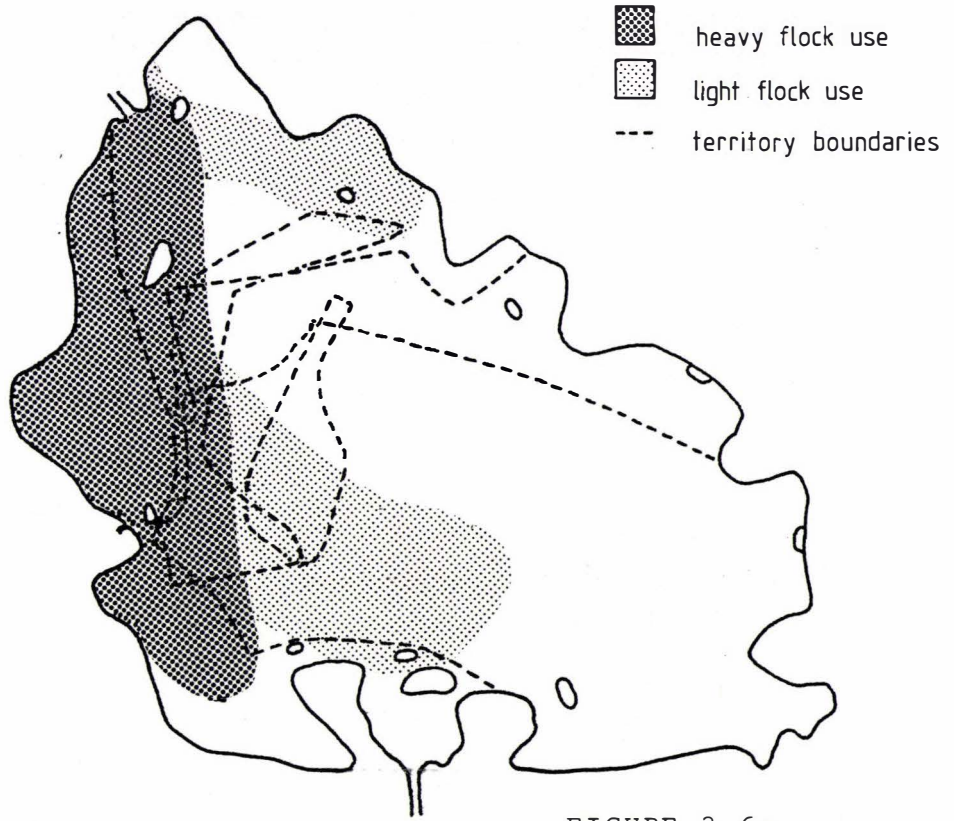


FIGURE 2.6a

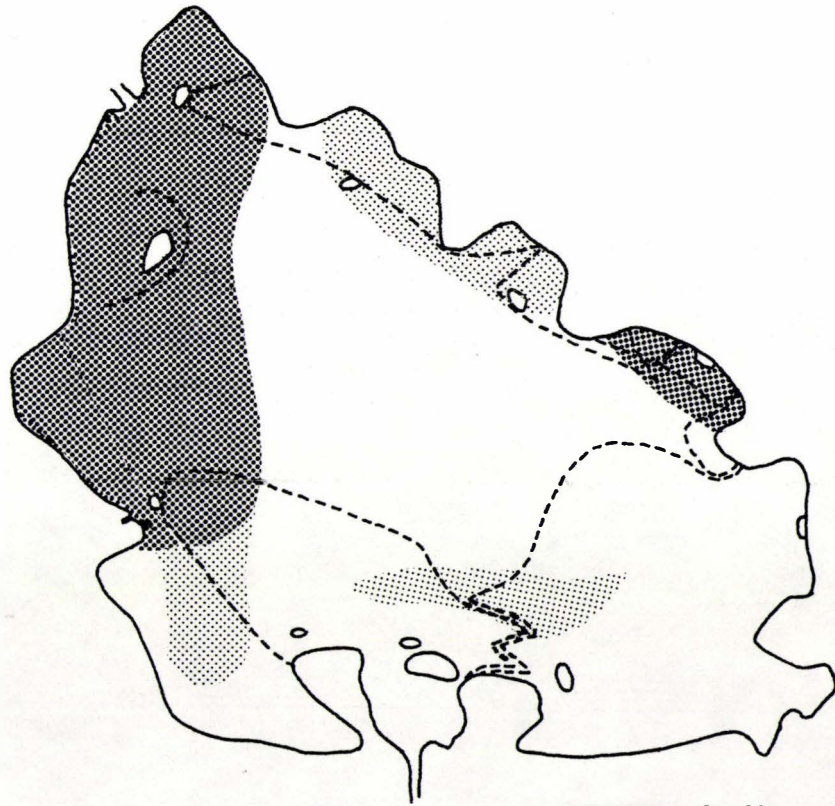


FIGURE 2.6b

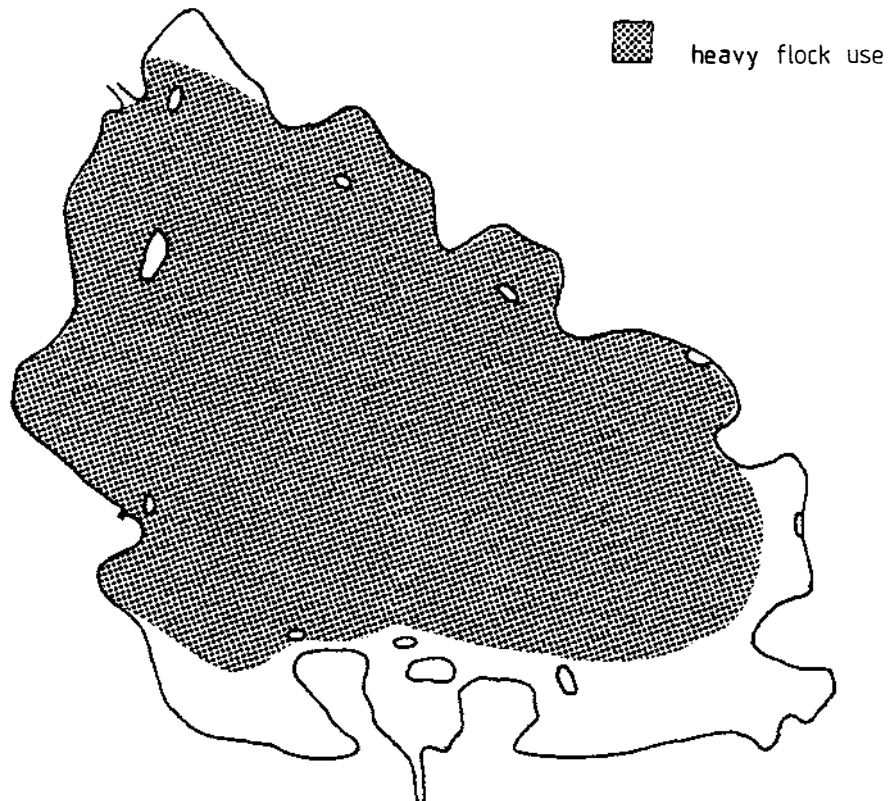


FIGURE 2.7: Flock use of the lagoon when territorial activity is at a minimum

NOTE: heavy flock use = 10 or more large (11+) groups recorded at each visit

in Aug.-Sept. 1978, a highly significant increase ($p < 0.001$), and decreased over the summer. The peak was not repeated in the 1979 breeding season. However, the number of single or paired birds was approximately the same in July (fertilisation-nesting) and August of both years.

The number of recognised pairs on the lagoon (both territorial and flock) never exceeded 15. Known territorial pairs were excluded from analysis. However, since two swans in company at one count generally could not be followed further and their social status accurately determined, the number of actually paired birds on the lagoon may have considerably exceeded the known total at some times of the year.

2.3.2d Area utilisation by the flock

(1) Area use:

Areas frequently in use were determined from flock counts (Section 2.2.1). Area utilisation by large and small groups, and by the flock as a whole, varied markedly, but showed more consistency between breeding seasons than did measures of group size (2.3.2c2).

Areas utilised by the flock could be divided into those used by small (≤ 10) and large (11+) aggregations. To a large extent small and large groups overlapped in their use of particular areas. This was especially true of the highly favoured eastern shore of the lagoon (Fig. 2.5). However, some areas were occupied only by small groups. These were peripheral to the large group/joint use areas e.g. on open water of the east side; along some edges.

(2) Seasonal trends:

In Aug.-Oct. 1978 flock use of the lagoon was largely restricted to the eastern half of the lagoon. Over the same period for 1979 a similar pattern occurred, with an extension along the southern shore. This extension was unexpected since a number of breeding pairs nested there (Fig. 2.6 a&b). The northwest corner and the western side, held by a particularly belligerent pair, were

noticeably unused during both breeding seasons, but were used over the summer and up until nesting in late July (Fig. 2.7).

Over the summer, as the families broke up (Ch. 6), flock numbers increased, and water levels fell to expose mudflats and new feeding areas, the flock area spread until in Jan.-March 1979 the whole open water area was occupied. Use of the central water area fell off in April - June although all edges were still utilised.

(3) Purpose of use:

Swans in all activity classes (2.3.1 a-e) occurred in all areas of the lagoon. However, the eastern shore, with shallow water, mudbanks, and open shoreline, was popular for loafing as well as feeding. To a lesser extent, the same was true of the central southern shore. Feeding was the prime activity in other areas.

2.3.3 Daily and seasonal time-activity budgets

Flock counts, with data on flock numbers and activities, permit the calculation of approximate seasonal and daily time budgets i.e. the proportion of swans engaged in various activities (Table 2.2) may be calculated.

2.3.3a Daily time-activity budgets

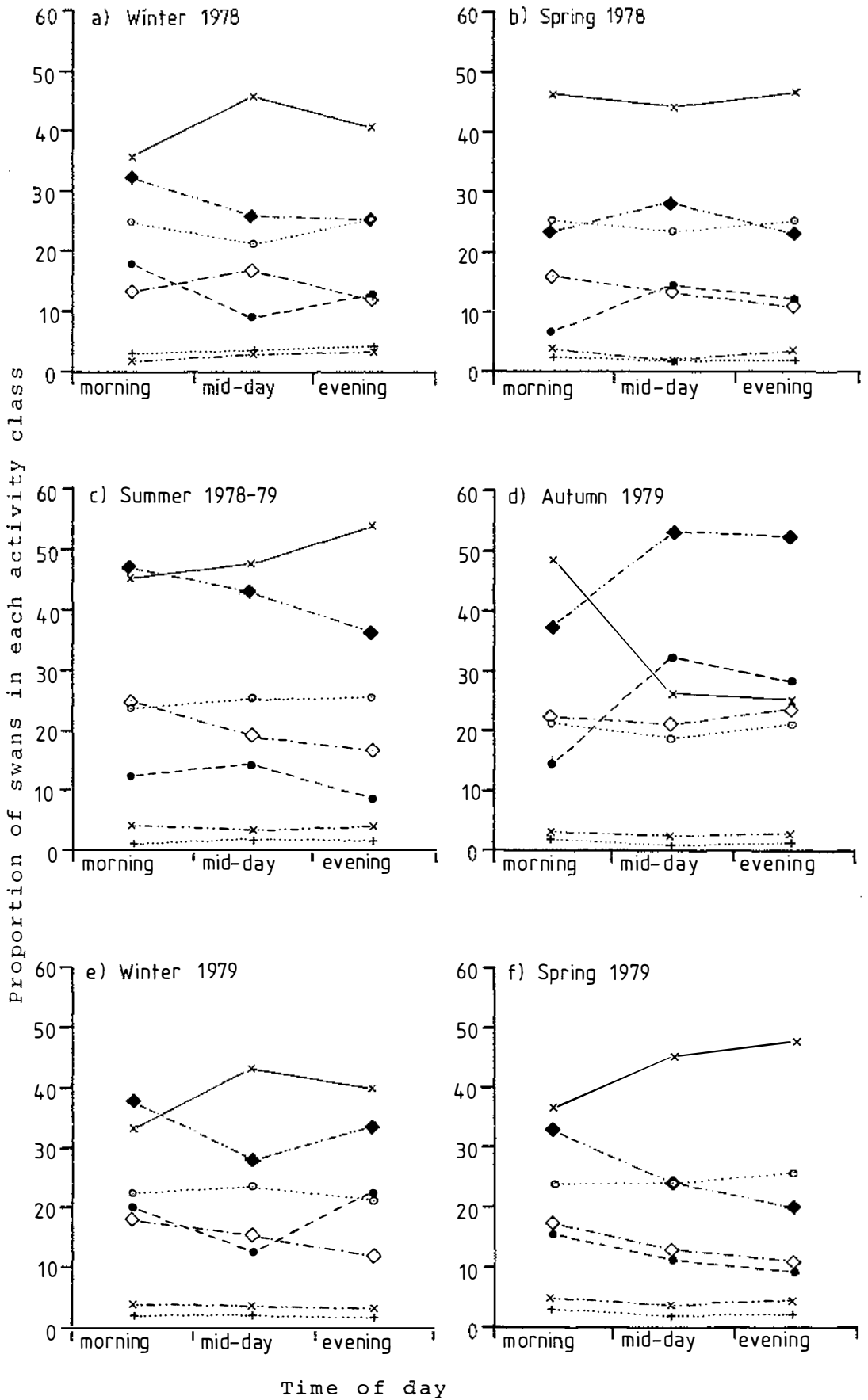
To compensate for photoperiod changes within and between seasons (2.2.2), data on daily patterns were combined into three day periods: morning, "middle-day", and evening. Data are presented in Fig. 2.8. No clear trends are apparent. There is little evidence for a bimodal cycle of activity (Section 2.4.2) with the possible exception of winter (both years), where a tendency to bimodal loafing (preening + dozing) patterns and a single feeding peak are seen.

In summary:

- (1) The proportion of alert (REU) birds remains fairly

TABLE 2.2 ACTIVITY CLASSES USED IN
 TIME-ACTIVITY BUDGET ANALYSIS

1. Relaxed-Upright (REU): alert to surroundings but not disturbed or alarmed.
2. Feeding (FEED): all categories (Section 2.3.1b; Fig.2.2) of feeding behaviour.
3. Preening (PREEN): all preening birds.
4. Dozing (DOZE): all swans actually or apparently asleep.
5. Aggression (AGGN): any aggressive behaviour; includes both flock and territorial swans.
6. Other behaviour (OTHER): all other behaviour patterns, normally occurring at very low frequencies: copulation, pair-bond maintenance, higher intensities of alertness, flying to change position.



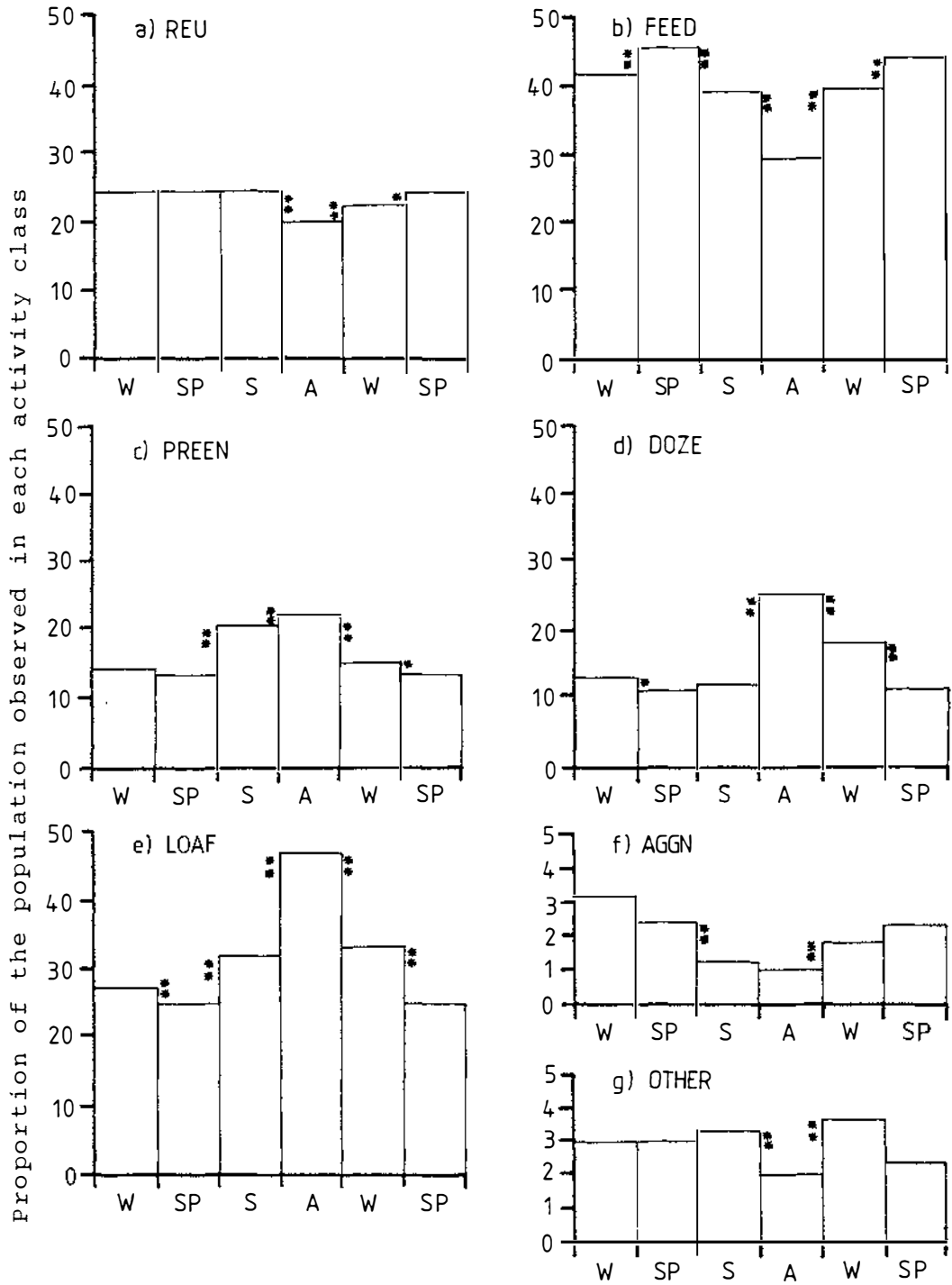


FIGURE 2.9: Seasonal time-activity budgets for seven activity classes: proportion of swans in each activity class, vs. seasons

a) Relaxed-Upright b) Feeding c) Preening
d) Dozing e) Loafing f) Aggression
g) Other activities

W: winter SP: spring S: summer A: autumn
* p < 0.01 ** p < 0.001

constant throughout.

(2) FEED shows a definite midday peak in winter 1978, less so in 1979. Feeding in spring 1978 is at a uniformly high level but there is a morning low in 1978. Summer feeding rises to an evening peak and autumn falls from a morning high.

(3) LOAF follows the reverse pattern to (2), as is expected since feeding and loafing are complementary activities.

2.3.3b Seasonal time-activity budgets

Data for seasonal participation in several activity classes (Table 2.2) are presented in Fig. 2.9, and seasonal trends are summarised below. The data were compared using a series of $2 \times 2 \times 2$ tables (d.f.=1, $\alpha = 0.01$), matching one activity in one season (e.g. FEED in winter 1978) against all other activities and seasons.

(1) General alertness (REU) is significantly low in autumn ($p < 0.001$) and winter 1979 ($p < 0.01$), otherwise fairly constant.

(2) FEED shows a very pronounced drop ($p < 0.001$) from a spring high (45% of individuals counted) to an autumn low (30%), rising significantly ($p < 0.001$) next spring.

(3) As for 2.3.3a LOAF complements the FEED pattern, for the same reason.

(4) Aggression is at its lowest ($p < 0.001$) in summer and autumn; this may parallel the drop in feeding activity.

(5) The proportion of swans in the category OTHER (chiefly flying and higher-intensity alert postures) is at its lowest in autumn.

These variations in activity patterns may be related to changes in the birds' energy requirements (Section 2.4.2).

2.4 DISCUSSION

2.4.1 Composition and aggregation of the Pukepuke flock

The Pukepuke flock is assumed to be of mixed age and sex composition (2.3.2a). Since there are other flocks in

the vicinity, frequent interchange between them and the Pukepuke population is likely, so that flock composition will not remain static. Changes in composition will reflect various stages of the breeding cycle (Anderson et al. 1969). Thus an increase in the number of juveniles (birds-of-the-year) followed the brood-rearing period of August-December (Table 2.1), and a greater number of apparently-paired individuals (Fig. 2.4) accompanied the onset of breeding.

Changes in social relationships within the flock are less apparent, due to the difficulty of recognising individuals (Section 1.4.4a). An examination of data on group size (Fig. 2.4) reveals a significantly higher ($p < 0.001$) proportion of groups of size 1-2 in the months June to November. It is possible that at least some of the swans in this class are paired birds en route to their breeding areas, since the New Zealand breeding season covers this period (Lickers 1977; Williams 1980), depending on local conditions. Minton (1971) notes some Mute Swan pairs, having previously bred successfully, may in some years remain in the flock over the breeding season; this category of birds may also be present in the Pukepuke flock. Certainly not all Black Swans that are capable of breeding do so in any one year: Williams (1980: 16) states that "Non-breeders seem to comprise the major proportion of the swans present on the principal breeding areas". Similarly the significantly higher ($p < 0.001$) proportion of groups of 11+ swans (i.e. loose aggregations) present in the period December - March probably includes numbers of separate and unrelated birds, as well as family members, moving to and from moulting and breeding grounds.

In general, on Pukepuke Lagoon high flock numbers appear mainly as loose aggregations, while lower numbers occur as small discrete groups. It is not known whether Black Swan families travel together once broods are fledged, as in other species (e.g. Hewson 1964: Whooper Swan *Cygnus cygnus*; Bateson et al. 1980; D.Scott 1980: Bewick's Swan *C. columbianus bewickii*). If family groups break up, as appears to happen

on Pukepuke (Ch. 6), then flocks after the breeding season should contain a large number of unbonded or unrelated swans, in large aggregations. Smaller groups, seen throughout the year, may well represent family or social entities (Elder & Elder 1949; Prevett & MacInnes 1980; Raveling 1969), as well as temporary associations of unrelated birds. Raveling (1969) notes that both related and unrelated yearling groups of Canada Geese (*Branta canadensis*) may show close association in roosting, feeding and flight. Closer examination of social distances within the Pukepuke flock, and of participation in Greeting ceremonies, might resolve this point.

Dispersion or aggregation within the flock or its subgroups may be maintained by factors other than social bonds. Vines (1980) found that intraflock spacing in Oystercatchers *Haematopus ostralegus* was directly affected by the active avoidance of individuals. Avoidance was due to feeding interference and related aggressive behaviour, rather than to violations of individual distance. The latter factor might, however, become important if the density of the group increases beyond a given point: Taylor et al. (1978) demonstrate that the density of a group affects the frequency and nature of interactions between its members, and so affects spacing within the group.

Aggression and feeding frequently coincide in other species. Raveling (1969) found that, although aggression in Canada Goose flocks occurred at varying frequency and intensity during most activities, it was closely associated with feeding. In his group fights were rare but threats and chases common. He also found that rank orders could develop in large stable groups. This last is unlikely to occur in transient groups. However, even in changing flocks, differences in posture will affect social relationships, by revealing the degree of confidence or aggression possessed by the individual. This probably affects the outcome of disputes in Pukepuke's flock.

Stimuli for the aggregation of swans on Pukepuke Lagoon are probably the presence of discrete loafing sites and of

a widespread and easily accessible food supply. Field of view may be important when birds settle to roost: on Pukepuke the usual loafing area on the eastern shore had only low vegetation and so gave a clear view in most directions. In addition, the presence of swans in certain postures may facilitate flocking in some situations and prevent it in others. Inglis & Isaacson (1978) have shown that feeding (HD: head-down) models of Dark-bellied Brent Geese *Branta bernicla bernicla* are attractive to other geese, while head-up (HU: alert) postures are aversive if combined with extreme head-up (EHU). It appears that geese monitor the proportion of highly alert or alarmed birds in a flock, and join groups where this proportion is low. These findings may also be applied to subgroups, and may determine where newcomers settle. Inglis & Isaacson propose two explanations for their results. The first is that alert postures, particularly EHU, may be related to predator detection, and in larger flocks individuals need spend less time in vigilance (see also Hoogland 1979). Secondly, a group with a low proportion of alert members may be on a good feeding area, and it would be advantageous to join them rather than a high-EHU group with a poor food supply. Since predation on adult swans is low (Guiler 1966; Lavery 1965), monitoring of feeding activity seems a likely function of relaxed alert postures in Black Swans.

It has been suggested that both feeding requirements and predation pressure influence flocking in many species. Individual members of a large flock have a reduced risk of predation (Hamilton 1971), due to (a) the effect of larger numbers on predator choice, and (b) the likelihood of a predator being identified by vigilant flock members. As a corollary individuals can spend more time feeding than if they were alone, since they need to spend less time scanning their surroundings for danger (Lazarus 1972). Lazarus notes that in White-fronted Geese *Anser albifrons* the time an individual spends alert decreases exponentially as flock size increases.

Feeding requirements have been regarded by many workers

(e.g. Murton 1971; Ward & Zahavi 1973; Zahavi 1971) as the main factor influencing the aggregation of both feeding and resting flocks. Ward & Zahavi (1973) see flocks as serving primarily to communicate information about the position and nature of food sources. The condition of birds returning to a communal roost would show whether or not they had fed well; a new member would have only to follow them the next day to obtain food itself. R. Evans (1982) derived a slightly different result from his work on Black-billed Gulls *Larus bulleri*. He found that both leaders and followers-on derived advantages from group feeding, and suggested that communal roosts, or "information centres", involved more than "parasitism" by some birds on information provided by others. Similarly O'Malley & Evans (1982: 1024) suggest that "flocks facilitate group foraging and permit effective use of local enhancement" in White Pelicans *Pelecanus erythrorhynchus*, instead of acting as "functional information centres".

Other authors suggest that membership of a flock may decrease the odds of being displaced by territorial individuals. Moore (1977) agrees that flocking may reduce predation and enhance feeding efficiency, but proposes that flock membership may also improve an individual's chances of encroaching on and benefiting from a territory's resources. Both inter- and intraspecific competition may be involved. Similarly Robertson et al. (1976) say that schooling in fish functions in defending members against territorial aggression, and increases the individual's chances of obtaining food in a territory.

Of the possible reasons for flock membership on Puke-puke, predation defence is unlikely since predation on adults is low. Predation does affect cygnets and eggs and, together with other environmental factors, may well influence nesting habits. On Pukepuke, with few nesting pairs, young may be best protected by nesting separately.

Flocking at Pukepuke is most likely to enhance feeding

efficiency, considering the amount of time adult swans must spend feeding. Watching for others already feeding may be much less costly than seeking food alone: although aquatic vegetation is widespread, preferred food species may well be patchily distributed. Feeding enhancement may explain the relatively constant proportion of time spent in vigilant postures throughout the day and year (Figs. 2.8 & 2.9) (see also Burton & Hudson 1978).

Flock membership may also reduce the risk of displacement by territorial swans, although its benefits would depend on the temperament of individual territory holders. Certainly, during the breeding season the Pukepuke flock makes heavy use of some areas occupied by breeders, but it is also actively excluded by other pairs (Figs. 2.6 a&b, 2.7). The use of some areas increases when territory holders are absent or inactive, implying that in these cases flock membership is little protection while the breeders are present.

2.4.2 Time-activity budgets and energy requirements

Data from flock counts were analysed to give daily and seasonal time-activity budgets for the Pukepuke swans. Such budgets are only roughly equivalent to energy budgets, since different activities have different energy requirements (King 1974). Energy budgets are affected by:

(a) physical factors, such as rainfall, snowfall, tides and photoperiod, and topography. The first four, especially photoperiod, affect food availability and time available for feeding e.g. the short days and low temperatures of winter may lead to nocturnal feeding, although in some anserines such feeding is the norm throughout the year.

(b) biological factors, including phenotypic (physiological, behavioural, and morphological) and biotic factors such as distribution of food, nest sites and cover, and the intensity of competition and predation (King 1974).

Seasonal variations in the energetic costs of life

may be reduced "(1) by behavioural adjustments ...; (2) by compensatory reduction in energy expenditure in some categories [of use] as the demands of others increase; and (3) by temporal separation of energy-demanding processes in the annual cycle" (King 1974: 53-54). Natural selection may act to minimise seasonal variation in energy expenditure. Circannual patterns of activity may be affected by circadian rhythms, which act, through the measurement of photoperiod changes, to trigger preparations for moult, reproduction or migration (Gwinner 1975). These three events in the bird's year are major energy consumers (King 1974; Owen & Kear 1972), although bad weather may also significantly affect energy expenditure and input.

The fulfilment of energy requirements, through feeding, will be of central importance; other activity patterns will depend, to some extent, on the rhythms of food-gathering. These are in turn affected by environmental temperatures; photoperiod; body size; the quality, distribution and amount of available food; and by breeding cycles and social characteristics (King 1974). Time-activity data give only a partial picture of the birds' activity, as Black Swans are very active, and feed extensively, at night.

Swans, like geese, have fairly inefficient digestive systems and it is important that they find a balance between "the ability to ingest large quantities of food and to select a relatively nutritious diet" (Burton & Hudson 1978: 111). Although day length does not limit food-gathering bouts by swans, disturbance, or changes in the food supply, may affect feeding routines. Feeding efficiency, in relation to available time and to food availability, becomes extremely important. Thus Burton & Hudson (1978) found that when rhizomes (a high-energy food source) were available, wintering Lesser Snow Geese *Anser caerulescens caerulescens* spent an unusually high proportion of time sleeping and relatively less in feeding.

Many bird species show a basic diphasic pattern of

daily activity (Aschoff 1966; Palmgren 1949). However, nocturnal behaviour is common in waterfowl (Bruggers & Jackson 1977; Burton & Hudson 1978; Owen 1972; Swanson & Sargeant 1972; Tamisier 1976) and it has been suggested (Swanson & Sargeant 1972) that the 24-hour rhythm in this group is made up of several shorter cycles which could obscure any generalised circadian rhythm. In addition, activity in some species may be independent of photoperiod. Burton & Hudson (1978) found that feeding by Lesser Snow Geese was related to the tide cycle and was quite independent of light intensity.

There is little evidence of bimodal circadian activity patterns in the Pukepuke flock. A polyphasic rhythm, involving nocturnal activity, is more likely. For feeding, the rise to an evening peak in summer and the fall from a morning high in autumn may represent the beginning and end respectively of nocturnal feeding activity. In some species changes over the day can also reflect changes in food availability e.g. through tidal patterns (Burton & Hudson 1978) or the activity patterns of invertebrate food species (Bruggers & Jackson 1977). Loafing follows the reverse pattern; this would be expected if preening, and dozing, follow intensive feeding. Such a linkage was found by Burton & Hudson (1978: related to feeding intensity and thus food availability) for *A.c.caerulescens*, and by Bruggers & Jackson (1977) in the Mandarin Duck *Aix galericulata*. If aggression in the flock is related to feeding interference (2.4.1), then on a daily basis this should parallel feeding rhythms, but this relationship was not apparent in the Pukepuke data.

Annually, increases in time spent feeding may reflect either changes in the quantity and/or quality of food, or changes in energy requirements, or a combination of these (King 1974). This distinction cannot be accurately resolved without data on the swans' energy needs and on the nutritive properties of food species available at different times of the year.

However, on Pukepuke the winter increase and spring

peak in the proportion of flock birds seen feeding may well reflect changing energy needs prior to breeding (since the flock contains many transient breeding pairs) and to moulting (late-spring - early-summer). Presumably a spring flush in plant growth would provide an ample food supply. Both Canada Geese (Raveling 1979) and Lesser Snow Geese (Ankney 1977) become hyperphagic before breeding. Similarly Braithwaite & Frith (1969b) noted an increase in the weight of a Black Swan population during spring and early summer, although Braithwaite (1977) found that Black Swans rarely showed actual hypertrophy of organs before breeding. Many species cannot lay until food supplies - and female weight (Reynolds 1972: *C.olor*) - reach a given level: Perrins (1970) found that "the date of laying in [at least] some species of birds may be determined by the date at which the female is able to find enough food to form eggs" (p.242). A correlation may also exist between laying date and the amount of food available for the young when they hatch (e.g. Inglis 1977: Pink-footed Goose *A.fabalis brachyrhynchus*).

There are several possible reasons for the summer and autumn decrease in feeding on Pukepuke:

- (a) it is possible that, for whatever reason, the swans feed more heavily at night;
- (b) food quality may be high e.g.much of the intake may consist of ripening seeds, or storage tissues;
- (c) energy requirements are lower.

Option (c) seems likely, as otherwise prolonged daylight feeding, as well as nocturnal activity, would be expected.

Like the daily pattern, seasonal loafing on Pukepuke shows a complementary rhythm to feeding. Decreased energy needs will leave more time available for such activity, and vice versa. Also, during moulting, an increase in preening may occur because of feather and skin irritation (c.f.Würdinger 1978: Bar-headed Goose *A. indicus*). DOZE is the major contributor to autumn loafing.

Aggression is highest in the flock during winter and spring. This may reflect increased competition for food due to higher energy requirements; it may also be due to the pressures of pair-formation and pair-bond maintenance in transient breeders. A major contribution will come from unrecognised territorial pairs, who show a much higher level of aggression than that recorded in the flock (Appendix I). Similarly, OTHER activities recorded during flock counts are low in autumn, perhaps because levels of aggression, and thus disturbance, are also low. The constant level of REU over the year will again reflect the need for continual attention to surrounding events.

The study of a flock, rather than of individuals, can thus provide answers to a number of questions:

what are the social subgroups in a population;

do families remain together for longer than a single breeding season;

what are the factors influencing aggregation of flocks and their subgroups;

how do members spend their time, over a day and over a year, and what factors underlie this division of time and activities?

Chapter 3

AGGRESSION AND TERRITORIALITY

3.1 INTRODUCTION

During the breeding season, establishment and maintenance of a territory is common among vertebrates (Manning 1972). The usual definition of a territory is "any defended area". Brown (1975) extends this to "a fixed area from which rivals are driven (excluded) by the active efforts ... of the owner ... commonly an adult male". By this definition territories are fixed, delineated with respect to geographical cues, not the position of the defending individual. Brown does not class individual distance, or the defence of moving objects (e.g. a mate or brood) as territorial defence. Hinde (1956) also emphasises the topographical fixity of most territories, but adds that "[some] mobile areas are defended by behaviour similar to that used in the defence of static ones, and must frequently be taken into account" in any consideration of territorial behaviour.

Hinde's (1956) statement makes it apparent that behavioural, as well as topographical, cues are used by the observer in defining a territory. Behavioural characteristics of territoriality are easily recognised. However, although environmental features may be categorised, the biological advantages underlying their inclusion in a territory are not always apparent.

The behaviour patterns involved in territory selection and maintenance may be divided into three parts (Hinde 1956):

"a) Restriction of some or all types of behaviour to a

more or less clearly defined area.

"b) Defence of that area.

"c) Self-advertisement within the area."

The functions of defence and self-advertisement may be subserved by the same behaviour. Hinde's list also points to the role that a territory may have in formation and maintenance of the pair bond: it provides a place where the male may advertise and the pair may meet. In addition, its defence reduces the likelihood of cuckoldry and, perhaps, philandering.

The significance of territory choice and defence has been widely discussed. Territories fall broadly into one of three categories: mating; nesting; and all-purpose (Brown 1975). They are often held to provide a food source for young and/or adults (see discussion in Hinde 1956). However, their value as an exclusive food source is not axiomatic:

"i) Many species nest in colonies, yet obtain adequate food;

"ii) Territories are [often] not defended against other species with apparently similar food requirements;

"iii) Many ... species collect food on neutral ground or neighbours' territories" (Hinde 1956).

Other important factors influencing territoriality may be the availability of nest and/or escape cover, protection from predation or disease, and freedom from disturbance while pairing. Verner (1977) adds that holding a territory may also produce benefits from interference competition: others are prevented from breeding, to the relative advantage of the breeder's genes. This argument leads to the suggestion that some individuals may defend more resources than they actually require. If this is the case, such territories should be at their maximum size early in the season, to prevent the establishment of other, competing pairs. However, if territories are held on the basis of food availability, their size should be maximised at the time of greatest food demand (Verner 1977). Verner's theory is not widely supported.

Black Swans are an interesting subject for the study of aggression and territory defence since they exhibit two breeding modes, territorial and colonial (Ch. 1), apparently in response to differences in habitat characteristics. The nature of these characteristics has not yet been determined: food supply for the young, nest cover, and anti-predator responses may all be important, and a comparative study of the two breeding types is required. This study of the aggressive behaviour and territorial characteristics of Pukepuke Lagoon breeders does provide some insights into the interaction of habitat and reproductive modes.

3.2 METHODS

Data were collected following the methods given in Chapter 1 (1.4.3). Both flock and territorial behaviour patterns were recorded. The following methods were used in further analysis.

3.2.1 Transition analysis

All sequences were broken down into diads and incorporated into a transition matrix (Table 3.2), as outlined in Appendix II (Lemon & Chatfield 1971; Radesäter 1974a), to search for linkages between pairs of acts. Relationships between behaviour patterns were also indicated by Single Link Cluster Analysis (3.2.2).

3.2.2 Single Link Cluster Analysis (SLCA) (Morgan et al. 1976)

In SLCA, based on the transition matrix of Table 3.2, each cell total is divided by marginal row totals to provide a measure of similarity between different behaviour patterns. The original matrix is a 19x19 table, with a blank upper-left - lower-right diagonal. It is symmetrised by summing corresponding off-diagonal terms. This gives the similarity between the pair of acts A and B i.e. "the propensity of A to follow B or B to follow A" (Morgan

et al. 1976) Thus a triangular table is constructed (x100 in all cells: Appendix III).

These data may be presented as a dendrogram or a "maximum spanning tree", either of which gives an indication of the groupings in which given behaviour patterns may lie.

3.2.3 Flock and territorial behaviour

The aggressive sequences were separated into territorial (T) and non-territorial (NT) and examined for differences in composition and length.

3.2.4 Territorial boundaries

To outline territorial boundaries, the positions of boundary-marking displays, threats, pursuits and fighting (3.3.1) were marked on monthly maps of the lagoon. Joining up the extreme points of the activity of known individuals showed the approximate extent of each territory (Pettingill 1970). Where male and female could be recognised I mapped their individual territories.

3.3 RESULTS

3.3.1 Behavioural description

Tingay (1974) recognised five main "types" of aggression in Black Swans: wing-lifting, pecking, fighting, parading, and vocalisations. This classification is misleading as vocalisations may be involved in each of the other 4 types, while wing-lifting occurs with pecking and parading. In the following descriptions Tingay's "wing-lifting" is separated into 3 display intensities, one of which is involved in "parading". I have not studied vocalisations in detail.

3.3.1a Alert-upright (ALU): see description in Ch. 2(2.3.1). Simply approaching an intruder in ALU, with neck feathers

slightly fluffed, appears to be effective as a threat in strongly territorial birds.

3.3.1b Low-intensity Threat (THR_{lo}): the neck is erect and slightly fluffed, the head may be "pendant" (Boase 1959), and the folded wings are raised vertically so that the white flight feathers (here only the primaries) are just visible. (Fig. 3.1a)

3.3.1c Medium-intensity Threat (THR_{me}): the neck is erect or slightly curved back, with head pendant and neck feathers fluffed. The wings are raised higher than in THR_{lo} so that a greater expanse of the primaries is exposed. (Fig. 3.1b)

3.3.1d High-intensity Threat (THR_{hi}): the neck, drawn back towards the shoulders (c.f. "busking" in *C. olor*: Boase 1959; Johnsgard 1965), is heavily fluffed and appears bloated. The wings are raised high to expose both primary and secondary flight feathers. (Fig. 3.1c)

Threats b - d are arbitrary divisions of a continuum of threatening display; the distinctions are based in part on observer decisions and part on accompanying and resulting behaviour patterns by the reactor. All intensities may be accompanied by movement towards the reactor; for THR_{hi} this is often a rapid charge, the swan moving forward by kicking both feet at once (c.f. *C. olor*: Delacour 1954; see also Daanje 1950). A bird in any of these postures may also hiss.

3.3.1e Parade (PAR): is a display performed by two territorial males along a shared boundary. The males, both in THR_{hi} , swim breast-to-breast along the boundary, turning in unison at the ends of their path. This is a lengthy display (up to 10 minutes pers. obs.; Tingay 1974), which may be interrupted by fighting or various comfort (? displacement) movements. The display ends with the swans separating and moving back into their territories. (Plate 3.1)

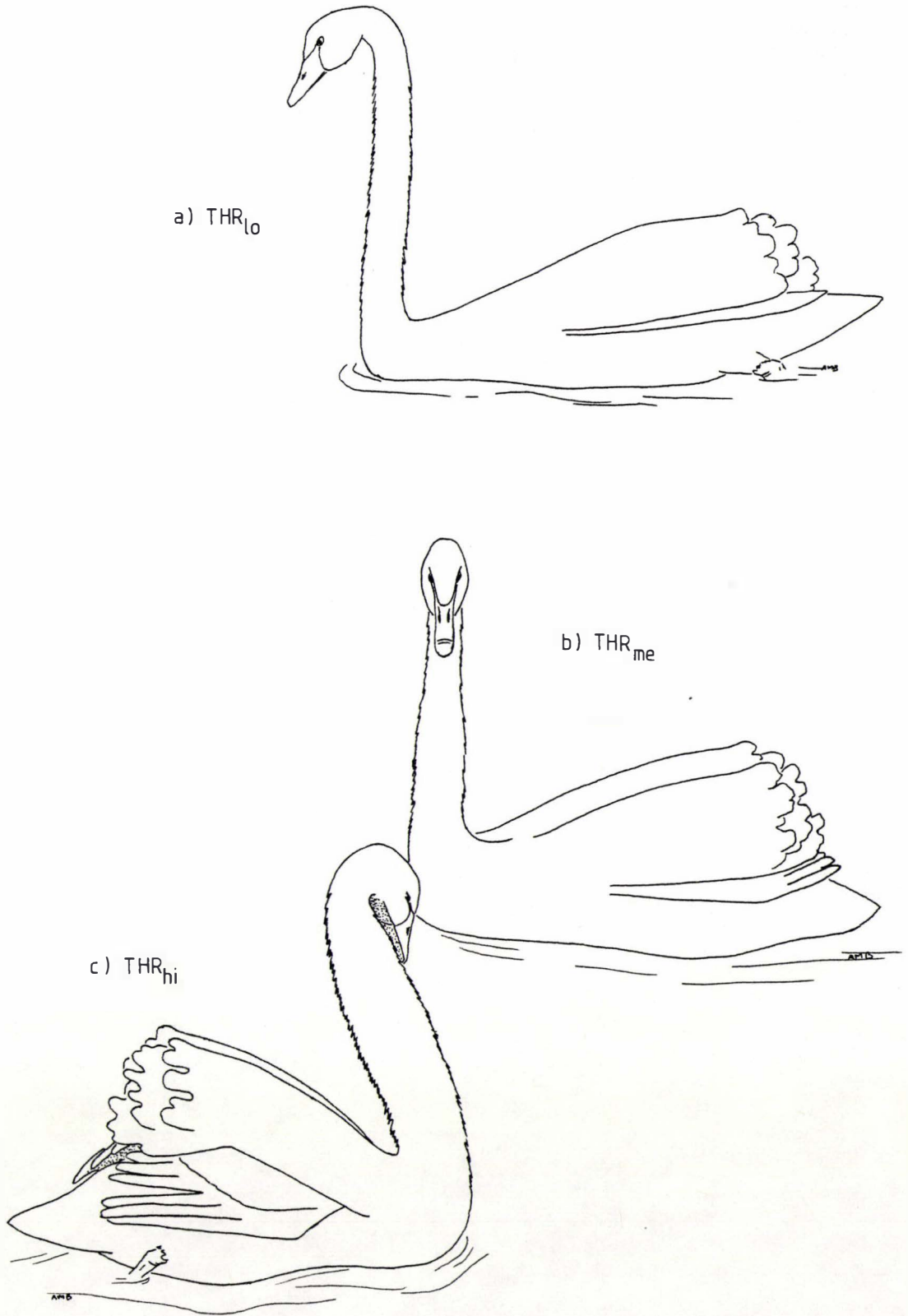


FIGURE 3.1: Variation in intensity of threat display
(a) low intensity (b) medium (c) high

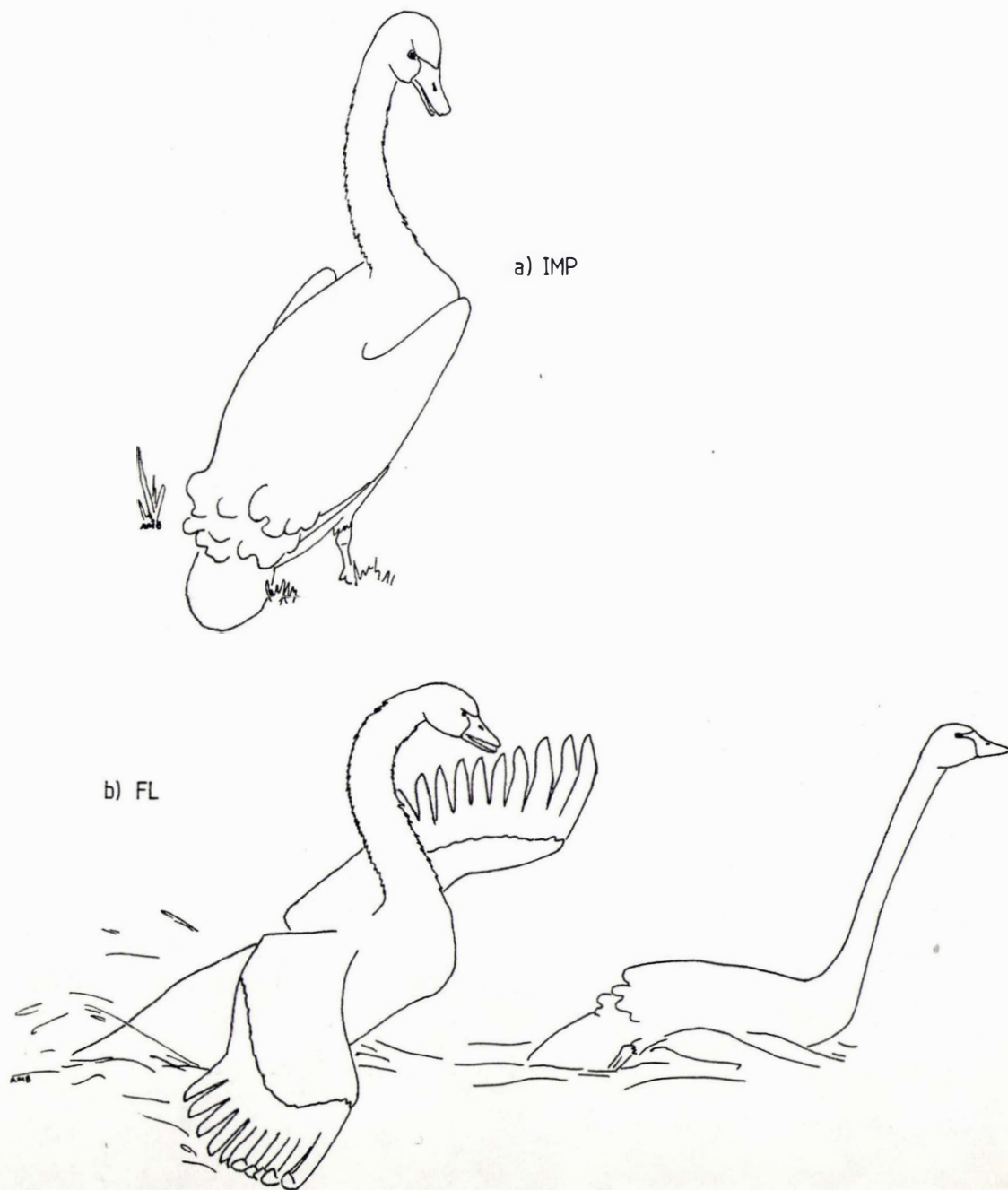
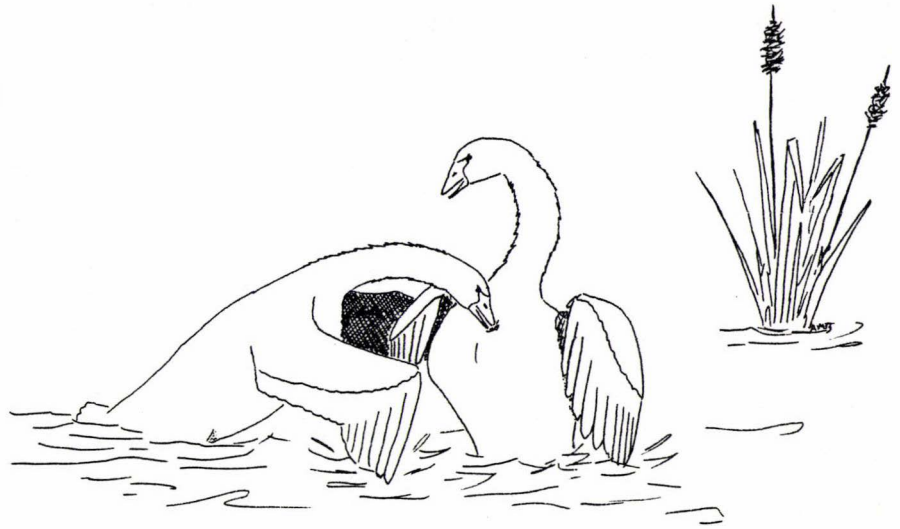


FIGURE 3.2: Threat and attack
(a) Intention-Movement-to-Peck
(b) Flapping-Lunge; victim in Anxiety-Upright

a) FBE



b) SWF

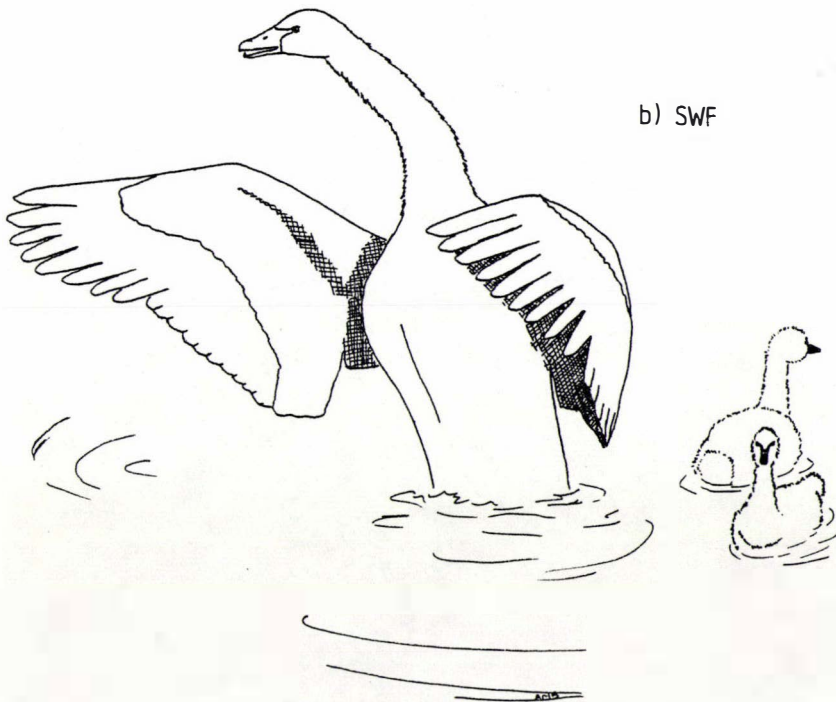
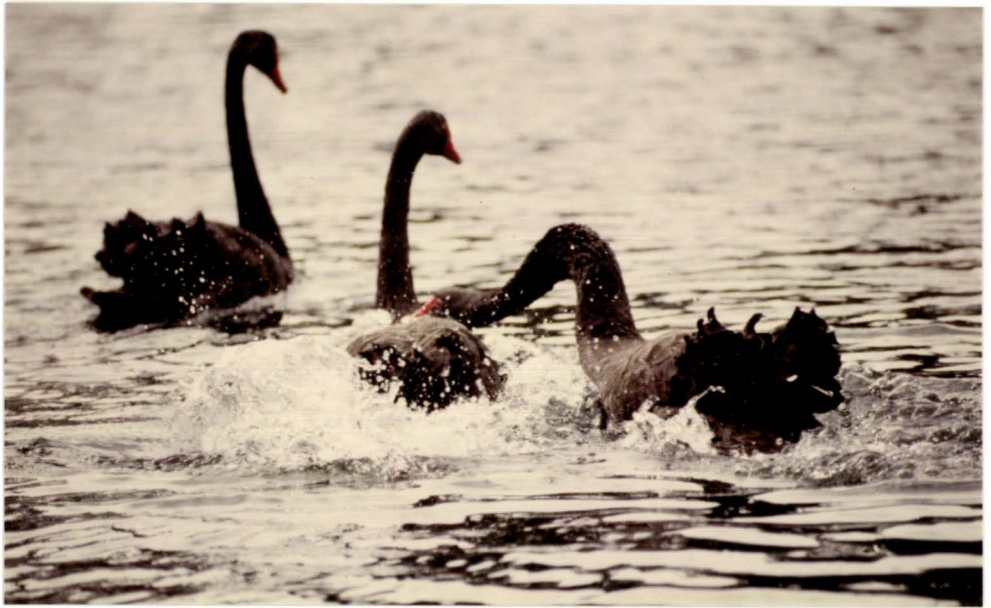


FIGURE 3.3: Threat and attack
(a) Fight, with beating wings
(b) Slow-Wing-Flap

PLATE 3.1: Parade display (PAR) by two
territorial males

PLATE 3.2: Pecking Lunge

PLATE 3.3: Trumpet display (TRU) by female
with brood



3.3.1f Intention-movement-to-peck (IMP): seen occasionally during disputes over feeding and loafing sites. The swan raises its wings slightly and draws its head back ready to strike, but then relaxes. (Fig. 3.2a)

3.3.1g Pecking Lunge (PEL): a swan pecking another raises its wings in threat, cocks its head, drawing its neck back, and then lunges forward. Its bill may be closed, to deliver a blow, or open to peck. (Plate 3.2)

3.3.1h Flapping Lunge (FL): may occur in association with THR_{me} and THR_{hi}. The wings are opened and flapped, both to increase speed and to strike the victim, and the neck is lunged forward in a peck to seize the other swan's feathers. A FL, with the swan never actually rising to fly, may extend for 50m or more. (Fig. 3.2b)

3.3.1i Fight, with beating wings (FBE): during a parade the opponents may come to blows, rearing back, beating at each other with open wings, and pecking at head and shoulders. Fights are brief and the PAR resumes immediately. (Fig. 3.3a)

3.3.1j Slow-Wing-Flap (SWF): much slower than the comfort movement of wing-flapping and involving only 1-4 beats. It is accompanied by a call (a "Ka-thunggg" note: Johnsgard 1965) and occurs frequently after a chase and after the brief preening that immediately follows much aggressive activity. Braithwaite (1981b) observed SWF occurring after the Triumph ceremony (Ch. 4); I have not seen it at all in this context, and only rarely after a Greeting ceremony. (Fig. 3.3b)

3.3.1k Trumpet (TRU): a trumpeting swan has its neck fluffed and wings raised in THR_{me}, and flings its neck forward along the water surface in the direction of the threatened bird. The accompanying call is in two parts, the louder note given as the head is flung forward and the softer second note coming as the neck returns to an

upright position. TRU is often performed by swans on or near the nest site or with cygnets. Either sex may give TRU and follow it up with further threat, although Braithwaite (1981b) views it as an "inciting" action directed to the male by the female of a pair. (Plate 3.3)

Examination of the reactors' responses to various threat displays may be used in assessing threat intensity. A total of 1716 actor-reactor diads, derived from sequences (2 or more acts by actor) and single incidents, were combined in Table 3.1. (The use of single incidents, as well as sequences, will give marginal proportions for the different threat forms differing from those in Table 3.2).

Without any statistical analysis it is apparent that certain reactor behaviours follow a given actor behaviour pattern more frequently than others. Increasing intensities of avoidance (alert) behaviour in reactors, shown by the degree of feather flattening and body streamlining shown in the group REU - ANU (description Ch. 2), are the product of increasing intensities of threat display. A FL results almost exclusively in avoidance by flapping flight (FF). In general, THR_{lo} is followed by REU, THR_{me} by ALU, and THR_{hi} by either ANU or THR_{hi} (or PAR, if along a shared boundary). Identity and status of the aggressor will have some effect on the reactor's response e.g. THR_{me} from a strongly territorial swan may elicit the high-intensity ANU in avoidance, usually produced as a reaction to THR_{hi} from other individuals. Some displays from the actor produce no overt change in the reactor's behaviour; this does not mean that they have no effect, however.

3.3.2 Sequence analysis

3.3.2a Transition matrix analysis of total aggressive sequences

The relationships between aggressive display patterns are not always obvious. Some statements made in the

literature are apparently not borne out by my own observations. To clarify the nature of pattern linkages I performed a transition analysis of 900 aggressive sequences* to seek for any dependence between pairs of acts. The results are presented in Table 3.2; Table 3.3 gives the standard behavioural abbreviations used in this and other analyses.

The cells of Table 3.2 are not independent of each other since the same marginal totals are used in the calculation of a number of expected values. In some cases these marginal totals have very high values, inflating the value of "expected" data. Only the diagonals would be fully independent. Thus, significance levels are probably not as high as they appear. A significance level of $\alpha = 0.01$ was chosen; pairs of acts occurring with $p < 0.01$ were assumed to be linked. The results are presented in Fig. 3.4 a & b, where arrows indicate the direction of transitions.

Context must be taken into account in interpreting these results. For example, PAR will follow THR_{hi} only when another territorial male is present on or near a common boundary; THR_{hi} and PAR will lead to TRI only if the bird's mate is also present.

Of particular interest are the relationships between other acts and i) TRU, ii) SWF.

i) The transitions $TRU \leftrightarrow THR_{me}$ and $TRU \rightarrow THR_{hi}$ occur significantly more often than expected on a random basis ($p < 0.001$, $p < 0.01$ respectively). Since both THR_{me} and THR_{hi} often involve movement towards the threatened individual, and TRU is performed by both σ and Q , this contradicts Braithwaite's (1981b) assertion that TRU is a Q inciting display.

ii) SWF is significantly linked with FL ($p < 0.001$), preening ($p < 0.001$), and bathing ($\#$) more often than expected, and less often with THR_{lo} and GRE ($p < 0.001$ and $p < 0.01$ respectively). There is no more than a random association with TRI, again contrary to Braithwaite's

* i.e. sequences containing some aggressive acts

findings. The linkage with aggression-related preening and bathing is expected, since SWF probably arose from the wing-flap seen as a comfort movement during "normal" preening or bathing bouts.

Figures 3.4 a & b also show that

- i) low-intensity activities (THR_{lo} , ALU) and high-intensity threats (THR_{hi} , PAR) are not directly linked.
- ii) Feeding is tied to THR_{lo} , REU, PEL but not to preening or high-intensity threats.

3.3.2b Single Link Cluster Analysis

SLCA (Morgan et al. 1976) of the transition matrix used above gives clusters of acts which are assumed to be related to a greater or lesser extent. Some of the clusters are similar to those produced in the relationships of 3.3.2a. Thus a dendrogram based on the sequential relationships of various acts (Fig. 3.5), with a cutoff at the 50% level, produces the groups

(REU DR) (SWF P B) (ALU FF)
 (IMP THR_{lo} THR_{me} THR_{hi} FL Feed GRE)
 PEL FBE TRI PAR

PAR may fit in with the major group of threats if viewed as a special case of THR_{hi} .

This breakdown again demonstrates the contiguity of the groups P, B and SWF. It also places Feeding and GRE with a group of threat displays. The positioning of Feed is due to its close relationship with THR_{lo} , usually during flock disputes over feeding areas. GRE, also with this group, is known to be linked with disturbances and/or separation of the members of a pair (Ch. 4), which would accompany any fight or chase.

Further examination of Fig. 3.5, using a higher % cutoff point, reveals the following groupings:

TABLE 3.1 REACTOR RESPONSES TO ACTOR AGGRESSION (Data from both sequences and point records)

actor behaviour	Reactor behaviour patterns							row total	
	none	REU	ALU	ANU	FF	THR _{hi}	THR me/lo		other
approach (N)	1	5	3	1	0	0	0	2	12
(%)	8.33	41.67	25.00	8.33	0	0	0	16.67	
THR _{lo}	47	123	60	20	2	0	23	17	292
	16.10	42.12	20.55	6.85	0.68	0	7.88	5.82	
THR _{me}	19	133	237	109	7	6	55	29	595
	3.19	22.35	39.83	18.32	1.18	1.01	9.24	4.87	
THR _{hi}	5	29	55	123	16	134	41	33	436
	1.15	6.65	12.61	28.21	3.67	30.73	9.40	7.57	
IMP	1	7	7	0	2	2	1	0	20
	5.00	35.00	35.00	0	10.00	10.00	5.00	0	
PEL	2	0	27	25	8	2	6	2	72
	2.78	0	37.50	34.72	11.11	2.78	8.33	2.78	
FL	1	1	10	36	184	1	0	0	233
	0.43	0.43	4.29	15.45	78.97	0.43	0	0	
FBE	0	0	0	3	1	0	2	18	24
	0	0	0	12.50	4.17	0	8.33	75.00	
TRU	1	2	5	6	1	2	3	3	23
	4.35	8.70	21.74	26.09	4.35	8.70	13.04	13.04	
SWF	1	0	3	2	1	0	0	2	9
	11.11	0	33.33	22.22	11.11	0	0	22.22	
column total	78	300	407	325	222	147	131	106	1716

FOLLOWING ACTION

	ALU	IMP	THR _{lo}	PEL	THR _{me}	THR _{hi}	FL	FBE	PAR	SWF	TRU	TRI	GRE	REU	preen	feed	drink	bathe	avoid	row total	
ALU		1 1.20 ns	50 33.99 ***	4 4.85 ns	43 40.55 ns	6 20.29 ***	12 17.05 ns	1 1.38 ns	1 8.30 **	7 10.61 ns	5 4.67 ns	0 4.48 ns	20 30.27 ns	29 12.44 ***	25 25.91 ns	34 30.49 ns	2 0.90 ns	4 3.44 ns	2 0.84 ns	246	
IMP	1 1.21 ns		2 2.63 ns	0 0.37 ns	0 3.44 ns	0 1.57 ns	0 1.32 ns	0 0.11 ns	3 0.64 ns	0 0.82 ns	0 0.36 ns	0 0.35 ns	2 2.34 ns	2 0.96 ns	2 2.00 ns	7 2.35 ns	0 0.07 ns	0 0.27 ns	0 0.06 ns	9	
THR _{lo}	63 33.94 ***	3 2.59 ns		6 10.50 ns	110 96.34 ns	16 4.387 ***	30 36.87 ns	0 2.98 ns	0 17.95 ***	11 22.95 ns	3 10.09 ns	3 9.69 ns	65 65.45 ns	46 26.90 ns	61 56.03 ns	105 65.94 ***	3 1.94 ns	4 7.44 ns	3 1.81 ns	532	
PEL	8 5.10 ns	0 0.39 ns	4 11.05 ns		14.49 ns	7 6.60 ns	2 5.54 ns	1 0.45 ns	0 2.70 ns	6 3.45 ns	0 1.52 ns	3 1.46 ns	9 9.84 ns	4 4.04 ns	10 8.43 ns	17 9.92 ns	0 0.29 ns	0 1.12 ns	0 0.27 ns	80	
THR _{me}	48 52.83 ns	2 4.02 ns	130 114.41 ns	9 16.34 ns		64 68.28 ns	103 57.38 ***	3 4.63 ns	25 27.94 ns	30 35.72 ns	36 15.71 ns	17 15.09 ns	171 101.87 ***	21 41.82 ***	75 87.20 ns	102.63 ns	3.01 ns	5 11.57 ns	8 2.81 ns	3 2.81 ns	828
THR _{hi}	16 28.77 **	0 2.19 ns	35 62.32 ***	11 8.90 ns	66 81.67 ns		74 31.26 ***	4 2.52 ns	51 15.22 ***	9 19.46 ns	9 8.56 ns	16 8.22 ns	72 55.49 ns	5 22.80 ***	36 47.50 ns	40 55.90 ns	2 1.64 ns	4 6.30 ns	1 1.53 ns	451	
FL	13 19.78 ns	0 1.51 ns	26 42.84 ***	17 6.12 ns	74 56.14 ns	66 25.56 ***		5 1.73 ns	7 10.46 ns	32 13.37 ns	1 5.88 ns	11 5.65 ns	18 38.14 ***	3 15.67 ns	20 32.65 ns	6 38.42 ns	3 1.13 ns	10 4.33 ns	1 1.05 ns	310	
FBE	2 1.91 ns	0 0.15 ns	1 4.15 ns	0 0.59 ns	4 5.43 ns	7 2.47 ns	2 2.08 ns		5 1.01 ns	0 1.29 ns	0 0.57 ns	0 0.55 ns	2 3.69 ns	0 1.52 ns	3 3.16 ns	3 3.72 ns	0 0.11 ns	1 0.42 ns	0 0.10 ns	30	
PAR	5 12.12 ns	3 0.92 ns	12 26.25 ns	6 3.75 ns	22 34.41 ns	39 15.67 ***	10 13.17 ns	8 1.06 ns		5 8.20 ns	1 3.61 ns	15 3.46 ns	35 23.38 ns	1 9.61 ns	16 20.01 ns	8 23.55 ***	0 0.69 ns	3 2.66 ns	0 0.65 ns	190	
SWF	6 10.21 ns	1 0.78 ns	27 22.11 ns	0 3.16 ns	24 28.97 ns	7 13.19 ns	8 11.09 ^{ns} ns	0 0.89 ns	3 5.40 ns		1 3.04 ns	4 2.92 ns	5 19.68 ***	10 8.09 ns	50 16.85 ***	12 19.83 ns	0 0.58 ns	2 2.24 ns	0 0.54 ns	160	
TRU	4 7.02 ns	0 0.53 ns	6 15.20 ns	1 2.17 ns	37 19.92 ***	18 9.07 ns	12 7.62 ns	1 0.62 ns	1 3.71 ns	2 4.75 ns		2 2.00 ns	17 13.53 ns	2 5.56 ns	2 11.59 ns	5 13.63 ns	0 0.40 ns	2 1.54 ns	0 0.37 ns	110	
TRI	1 3.83 ns	1 0.29 ns	3 8.29 ns	0 1.18 ns	13 10.87 ns	8 4.95 ns	2 4.16 ns	0 0.34 ns	3 2.02 ns	1 2.59 ns	1 1.14 ns		4 7.38 ns	3 3.03 ns	10 6.32 ns	8 7.44 ns	0 0.22 ns	2 0.84 ns	0 0.20 ns	60	
GRE	29 29.22 ns	1 2.23 ns	60 63.29 ns	5 9.04 ns	114 82.94 ns	39 37.77 ns	5 31.74 ns	0 2.56 ns	19 15.46 ns	9 19.76 ns	8 8.69 ns	3 8.35 ns		23 23.16 ns	41 48.24 ns	84 56.77 ns	2 1.67 ns	6 6.40 ns	3 1.56 ns	458	
REU	19 9.44 ns	5 0.72 ns	32 20.45 ns	6 2.92 ns	17 26.80 ns	6 12.20 ns	3 10.26 ns	0 0.83 ns	0 4.99 ns	6 6.38 ns	2 2.81 ns	0 2.70 ns	4 18.21 ns		23 15.59 ns	24 18.34 ns	1 0.54 ns	0 2.07 ns	0 0.50 ns	148	
preen	10 14.48 ns	0 1.10 ns	43 31.37 ns	4 4.48 ns	45 41.11 ns	17 18.72 ns	2 15.73 ns	0 1.27 ns	8 7.66 ns	30 9.79 ***	0 4.31 ns	0 4.14 ns	13 27.93 ns	19 11.48 ns		22 28.14 ns	0 0.83 ns	13 3.17 ns	0 0.77 ns	227	
feed	14 13.46 ns	3 1.03 ns	66 29.16 ***	11 [#] 4.16 ns	47 38.21 ns	13 17.40 ns	2 16.62 ns	0 1.18 ns	8 7.12 ns	6 9.10 ns	9 4.00 ns	0 0.23 ns	10 38.4 ***	19 25.96 ***	3 22.22 ***		0 0.77 ns	0 2.95 ns	0 0.72 ns	211	
drink	1 0.89 ns	0 0.07 ns	2 1.93 ns	0 0.28 ns	1 2.54 ns	0 1.15 ns	0 0.97 ns	0 0.08 ns	0 0.47 ns	0 0.60 ns	0 0.27 ns	0 0.26 ns	0 1.72 ns	5 0.71 ns	2 1.47 ns	3 1.74 ns		0 0.20 ns	0 0.05 ns	14	
bathe	3 3.13 ns	0 0.24 ns	3 6.77 ns	0 0.97 ns	6 8.87 ns	2 4.04 ns	0 3.40 ns	0 0.27 ns	0 1.65 ns	17 [#] 2.11 ns	1 0.93 ns	0 0.89 ns	3 6.03 ns	0 2.48 ns	14 5.16 ***	0 6.07 **	0 0.18 ns		0 0.17 ns	49	
avoid	5 0.77 ns	0 0.06 ns	0 1.66 ns	0 0.24 ns	2 2.17 ns	0 0.99 ns	0 0.83 ns	0 0.07 ns	1 0.40 ns	0 0.52 ns	0 0.23 ns	0 0.22 ns	3 1.48 ns	0 0.61 ns	1 1.26 ns	0 1.49 ns	0 0.04 ns	0 0.17 ns		12	
column total	248	20	502	80	634	315	268	23	135	171	77	74	453	199	394	456	15	57	14	4135	

PRECEDING ACTION

TABLE 3.3 ABBREVIATIONS USED IN SEQUENCE-,
TRANSITION MATRIX-, AND SLCA ANALYSES

Abbreviation	Expansion (Described in Ch. 3 unless stated otherwise)
REU	Relaxed-Upright
ALU	Alert-Upright
IMP	Intention-movement-to-peck
PEL	Pecking Lunge
THR _{lo}	low-, medium- and high-intensity threat displays
THR _{me}	
THR _{hi}	
FL	Flapping Lunge
FBE	Fight, beating with wings
PAR	Parade (boundary display)
SWF	Slow-Wing-Flap
TRU	Trumpet
TRI	Triumph ceremony
GRE	Greeting ceremony
P	preen
F	feed (in some cases associated with aggression)
DR	drink
B	bathe
FF	Flapping Flight (high-intensity avoidance)
AV	Avoidance

The terms preen-avoidance (inclusive) are general ones and no description is given.

FIGURE 3.4a: Behaviour-pattern transitions occurring significantly more often ($p < 0.01$) than expected in aggressive sequences (Derived from Table 3.2)

- transition occurs significantly more often than expected, in both directions
- transition occurs significantly more often than expected, in one direction only
- transition occurs significantly more often than expected in one direction, and significantly less often in the other

FIGURE 3.4b: Behaviour-pattern transitions occurring significantly less often ($p < 0.01$) than expected in aggressive sequences. (Derived from Table 3.2)

- transition occurs significantly less often than expected, in both directions
- transition occurs significantly less often than expected, in one direction only

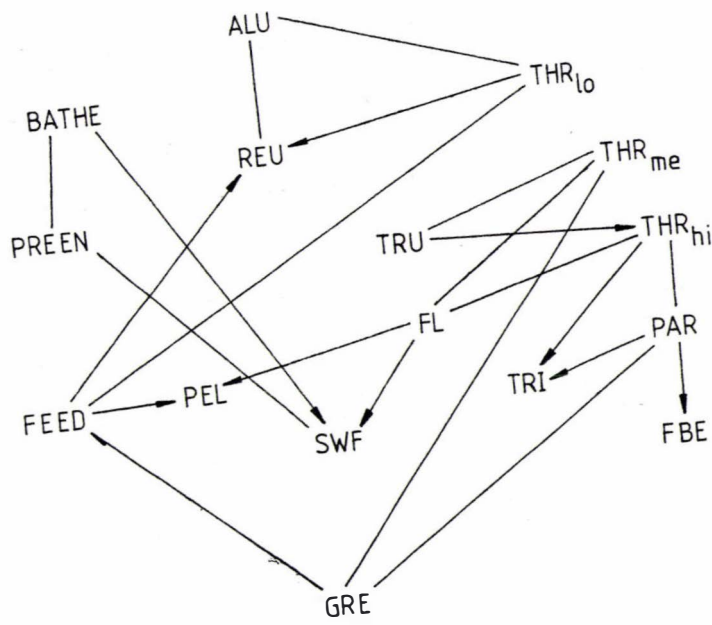


FIGURE 3.4a

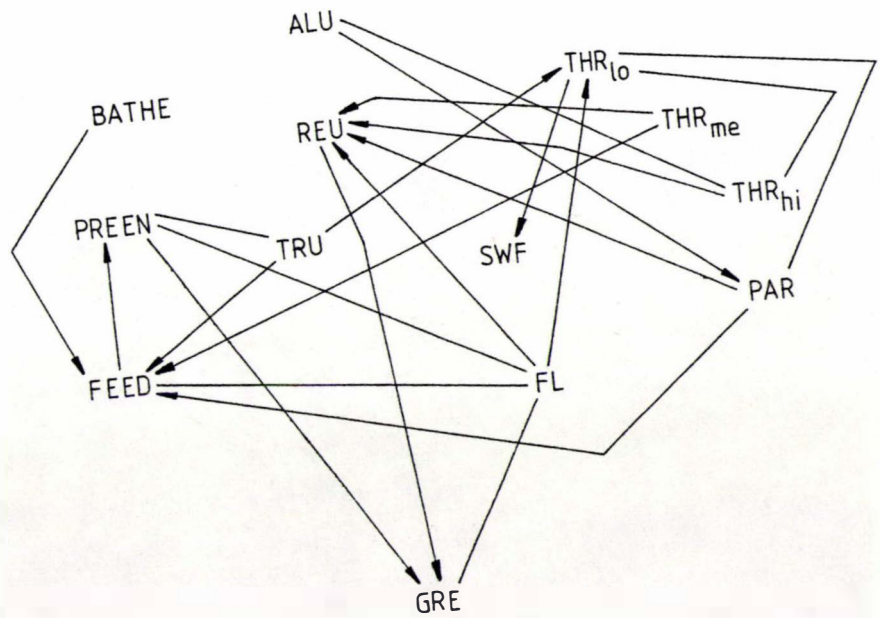
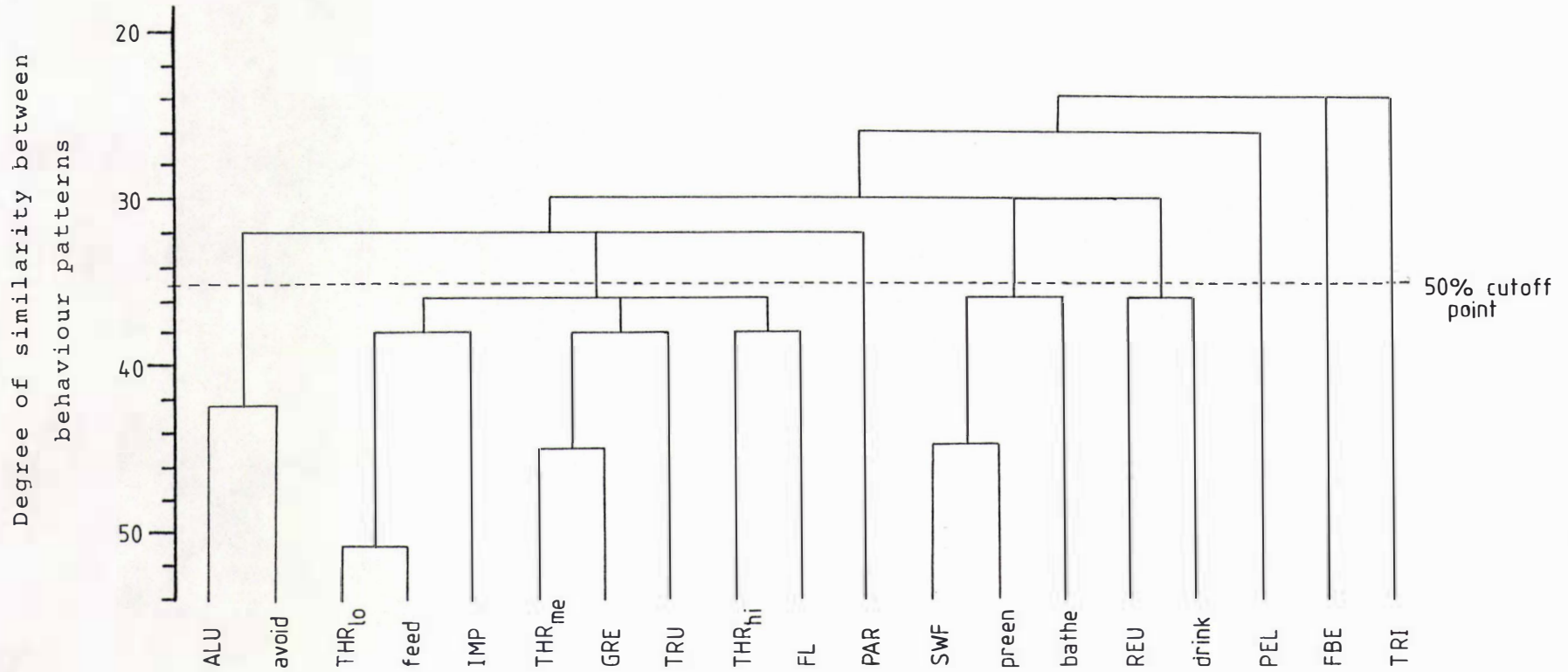


FIGURE 3.4b

FIGURE 3.5: Single-Link-Cluster Analysis dendrogram based on similarities (temporal and/or sequential contiguity) between behaviour patterns occurring in aggressive sequences (see Table 4.5 for abbreviations; Appendix III for data)



THR _{lo} - Feed	}	SWF - preen	}	PEL
IMP		bathe		FBE
THR _{me} - GRE	}	ALU - avoid	}	TRI
TRU		REU - drink		
THR _{hi} - FL	}		}	
PAR				

This groups IMP with THR_{lo} and Feed, an association not shown by transition analysis. It also shows that GRE is brought into the threat group through its link with THR_{me}. The transition from ALU to movement away (avoidance) is one I had frequently observed, but is not shown up in transition analysis, because with the exception of both members of a Parade the sequences used are those of aggressors not reactors.

3.3.3 Territorial and flock activity

Once the territorial swans can be recognised as such, it is possible to divide sequences into those by known, active territorial pairs and those by non-territorial or flock birds. The number of constituent acts, sequence composition and seasonal distribution in the two classes may then be examined.

3.3.3a Number of components

Table 3.4 presents 957 sequences separated into territorial (T) and non-territorial (NT) sequences; for April and May 1978 the NT category includes both flock birds and those whose identity was uncertain. In 1979 data for May-June and October-November were combined since the number of sequences for May and November was very small.

There is no statistical difference between the mean number of acts contained in the two sequence categories, as values for standard deviation overlap in all cases. (T sequences tend to contain a greater number of acts than NT.) There is little, if any, relationship with time of year although \bar{x} is greatest early in the 1978 incubation

period and reaches a second, lower peak as territories are re-established in February-April of the following year.

3.3.3b Monthly proportions of NT and T sequences

The proportion of T and NT sequences making up monthly totals does show some seasonal variation (Fig. 3.6), with aggressive sequences in the flock peaking over summer and T sequences comprising most of the total during the breeding season.

However, since only aggressive sequences, excluding isolated threats or notes of occurrence, are examined here, this analysis gives only an approximation of changes in the monthly proportions of T and NT behaviour. Examination of seasonal or monthly variations in sequence composition is also valuable (3.3.3c).

3.3.3c General composition of T and NT sequences

Only known T and NT sequences were used, totalling 933 (T = 552, NT = 381) sets of data.

To examine the overall frequencies of various displays, T and NT sequences were broken down into their component acts, giving the total occurrence of each display pattern or act (Table 3.5). This gives a total of 3375 components in T sequences and 1684 in NT sequences i.e. 66.7% of the total acts occur in T sequences, and 33.3% in NT. Any comparative analysis must be on the basis of total acts in each sequence type:

If H_0 : the composition of both sequence types is identical,

then the expected (e) distribution of each act, in T and NT sequences, should follow the same distribution as total acts:

$$\text{e.g. } e(T_{\text{ALU}}) = 0.667 \times \text{total}(\text{ALU})$$

$$e(NT_{\text{ALU}}) = 0.333 \times \text{total}(\text{ALU})$$

The e values presented in Table 3.5 are calculated on this basis.

To compare the occurrence of acts in T and NT total sequences a series of $2 \times 2 \chi^2$ tests was performed, testing each act (T and NT) against all others ($\nu = 1, \alpha = 0.01$) (Brown et al. 1967). The other e values were obtained by subtracting those calculated by the above method from the remaining marginal totals.

This series of tests shows that significant differences exist in the frequency with which certain acts occur in aggressive sequences attributed to territorial and flock swans:

i.e. flock (NT) sequences contain significantly more IMP, PEL, REU and Feed incidents than expected for the null hypothesis of equal display frequency ($p < 0.01$, $p < 0.001$, $p < 0.001$, $p < 0.001$ respectively), while territorial (T) sequences contain significantly more THR_{me} , FL, SWF and PAR than expected ($p < 0.01$, $p < 0.001$, $p < 0.001$, $p < 0.001$ respectively). The behaviour patterns THR_{lo} , THR_{hi} , FBE, TRU, TRI, and GRE occur as predicted by H_0 .

Thus T sequences are characterised by a higher frequency of THR_{me} , FL, PAR and SWF threat forms, while NT sequences typically contain more PEL and IMP, and more Feeding and alert (REU) behaviour.

3.3.3d Monthly breakdown of aggressive-sequence components

The monthly frequencies of individual acts comprising T and NT sequences are presented in Fig. 3.7.

It has already been shown (3.3.3c) that T and NT sequences differ significantly in their makeup with respect to at least some components. Fig. 3.7 shows that these differences are based on differing frequencies in some months, with some evidence for seasonal distribution:

- i) IMP and PEL occur at too low a level for examination of seasonal trends.
- ii) THR_{hi} (T and NT) peaks in the disturbed breeding season of 1978 (Aug.-Sept.) and in Feb.-March 1979, with the establishment of territories.

TABLE 3.4 NUMBER, MEAN LENGTH (no. of behaviour patterns), AND STANDARD DEVIATION (length) OF AGGRESSIVE SEQUENCES RECORDED EACH MONTH

Month	total sequences			T ¹ sequences			NT ² /unknown seqs.		
	N	\bar{x}	sd	N	\bar{x}	sd	N	\bar{x}	sd
Apr. '78	24	6.38	3.39				24	6.38	3.39
May	11	7.00	2.32	4	6.00	1.83	7	7.57	2.51
June	39	8.72	5.12	23	10.30	5.97	16	7.06	3.04
July	37	8.23	6.39	18	10.44	8.30	19	6.10	2.60
Aug.	12	8.58	4.46	4	8.75	2.99	8	8.50	5.24
Sept.	14	7.64	3.71	4	9.75	4.50	10	6.80	3.22
Oct.	48	5.62	2.68	37	6.00	2.79	11	4.36	1.86
Nov.	81	5.94	3.11	68	6.46	3.12	13	3.23	0.83
Dec.	65	5.72	3.46	51	6.25	3.68	14	3.79	1.25
Jan. '79	139	4.38	1.96	71	4.86	2.07	68	4.28	3.91
Feb.	98	4.93	2.49	37	6.05	3.06	61	4.43	2.07
Mar.	34	4.91	2.23	6	7.83	2.48	28	4.29	1.63
Apr.	68	5.32	2.70	37	6.03	3.12	31	4.34	1.93
(May) June	40	4.78	1.87	23	4.91	1.93	17	4.59	1.84
July	97	4.71	2.13	59	5.42	2.34	38	3.67	1.06
Aug.	67	4.99	2.56	39	5.51	2.78	28	4.25	2.05
Sept.	33	4.77	1.79	32	4.72	1.82	1	-	-
(Oct) Nov.	50	5.00	2.20	39	5.31	2.14	11	3.91	2.17
totals	957			552	$\Sigma(\bar{x}) = 6.11$		405	$\Sigma(\bar{x}) = 4.42$	

1: T = territorial sequences

2: NT = non-territorial (flock) sequences

TABLE 3.5 OBSERVED (o) AND EXPECTED (e) VALUES FOR THE OCCURRENCE OF AGGRESSIVE DISPLAY SEQUENCE COMPONENTS

oN_T : observed number of times component occurred in territorial sequences

oN_{NT} : observed number of times component occurred in non-territorial sequences

behaviour pattern	oN_T	eN_T	oN_{NT}	eN_{NT}	total displays
ALU	199	205.44	109	102.56	308
IMP	* 7	12.67	**12	6.33	19
THR _{lo}	415	412.87	204	206.13	619
PEL	**37	53.36	**43	53.75	80
THR _{me}	*631	591.63	*256	295.37	887
THR _{hi}	309	297.48	137	148.52	446
FL	**246	204.77	**61	102.23	307
FBE	14	19.34	15	9.66	29
PAR	**171	128.73	**22	64.27	193
SWF	**144	122.73	**40	61.27	184
TRU	73	75.37	40	37.63	113
TRI	61	50.69	15	19.74	76
GRE	317	332.17	181	165.83	498
REU	**135	163.42	**110	81.59	245
preen	284	284.14	142	141.86	426
feed	**274	364.18	**272	181.82	546
other	58	55.36	25	27.64	83
totals	3375		1684		5059
% of total displays	66.71		33.29		

*: displays occur at a significantly greater or lesser frequency than expected

* $p < 0.01$ ** $p < 0.001$ $2 \times 2 \chi^2$ test $df = 1$ $\alpha = 0.01$

Displays performed by T swans comprise 66.71% of total acts recorded in aggressive sequences; NT acts comprise 33.29% of the total. Calculation of T/NT display composition (e values) must take this into account (see section 3.3.3c).

FIGURE 3.6: Territorial and non-territorial aggressive sequences as a proportion of monthly totals

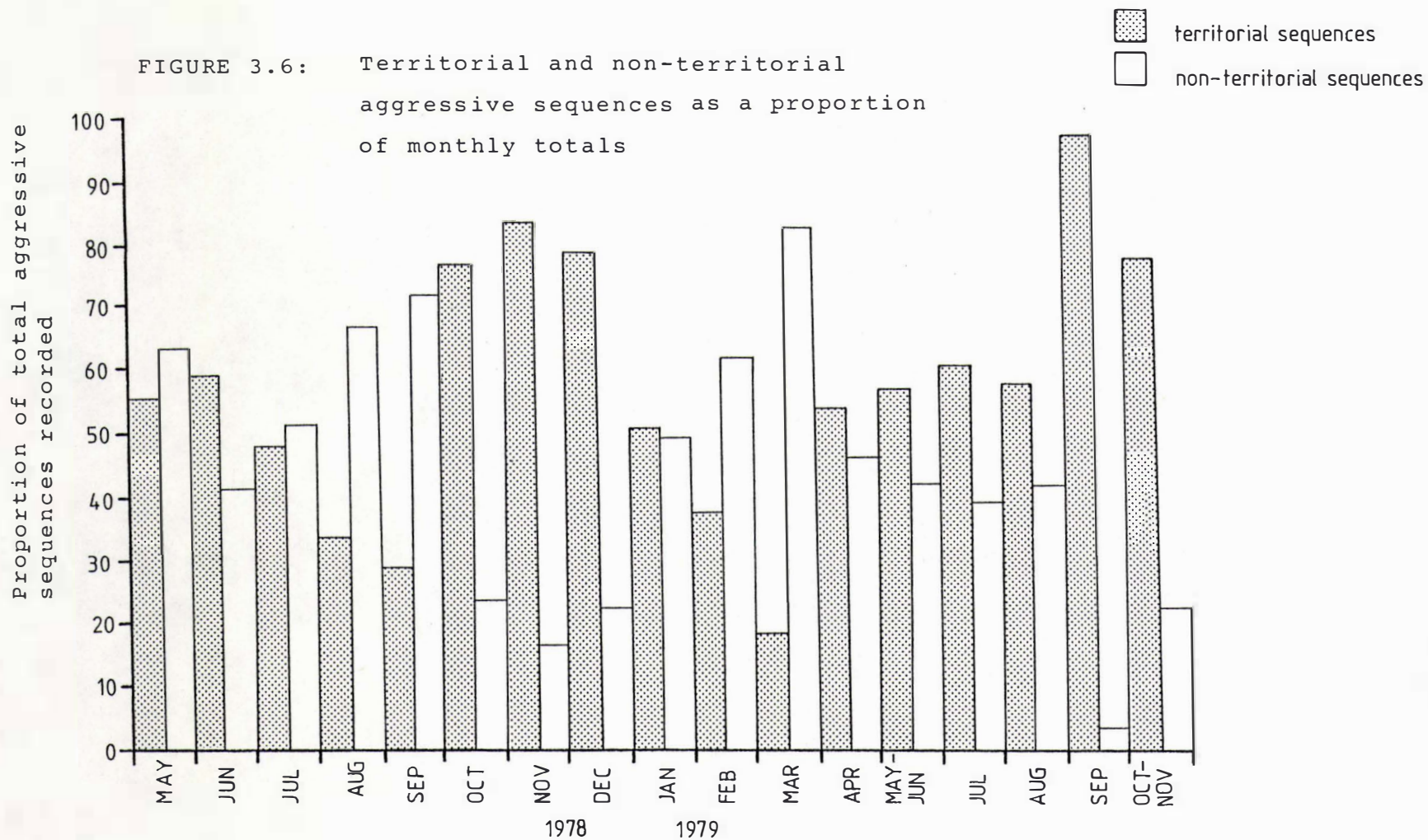
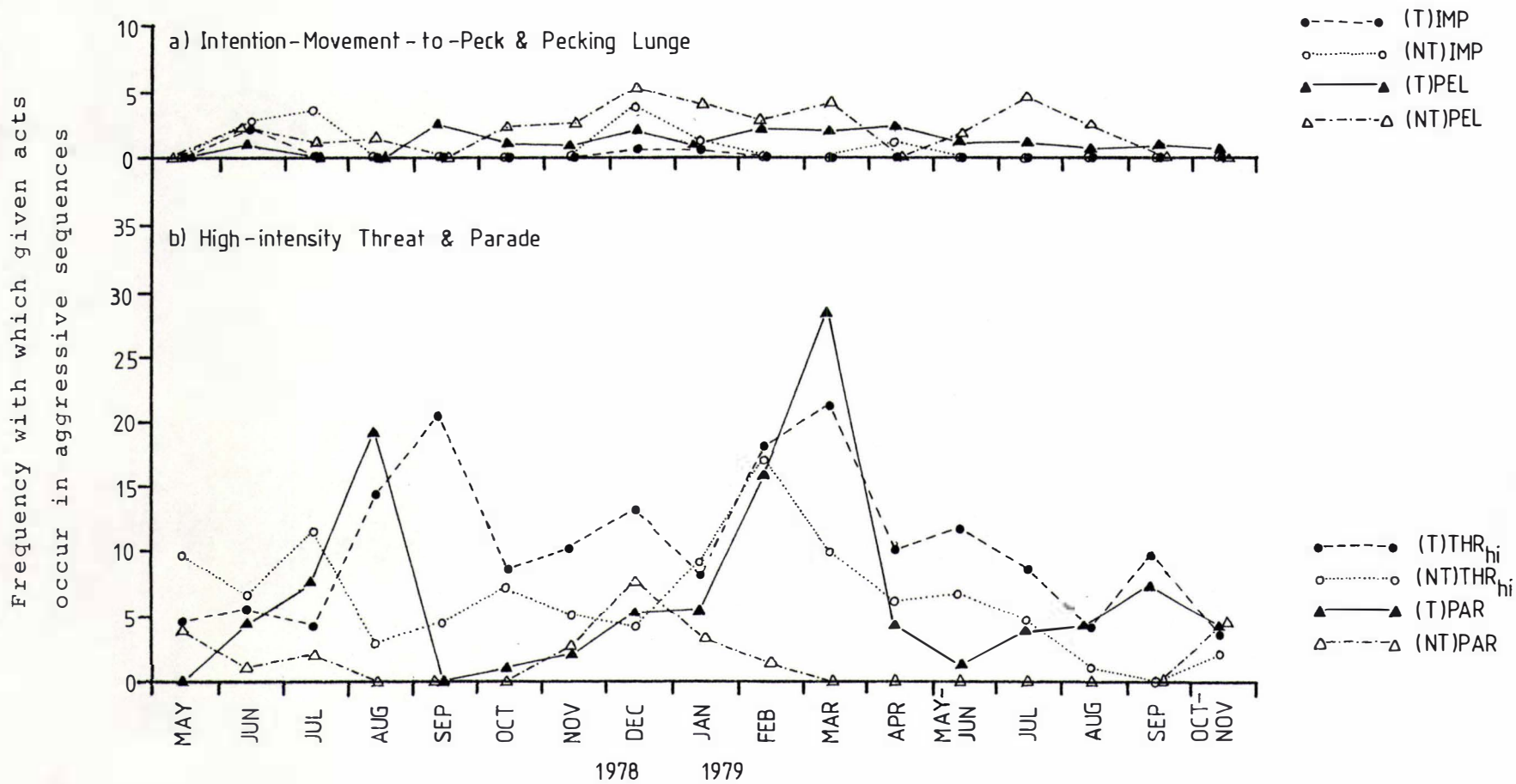
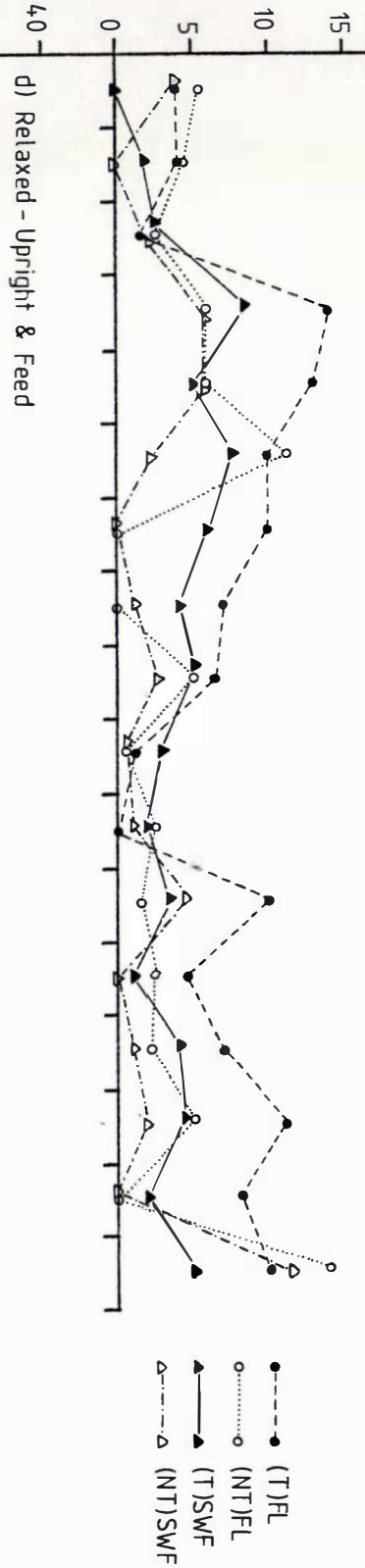


FIGURE 3.7: The monthly frequencies with which given acts occur in territorial (T) and non-territorial (NT) sequences of aggression

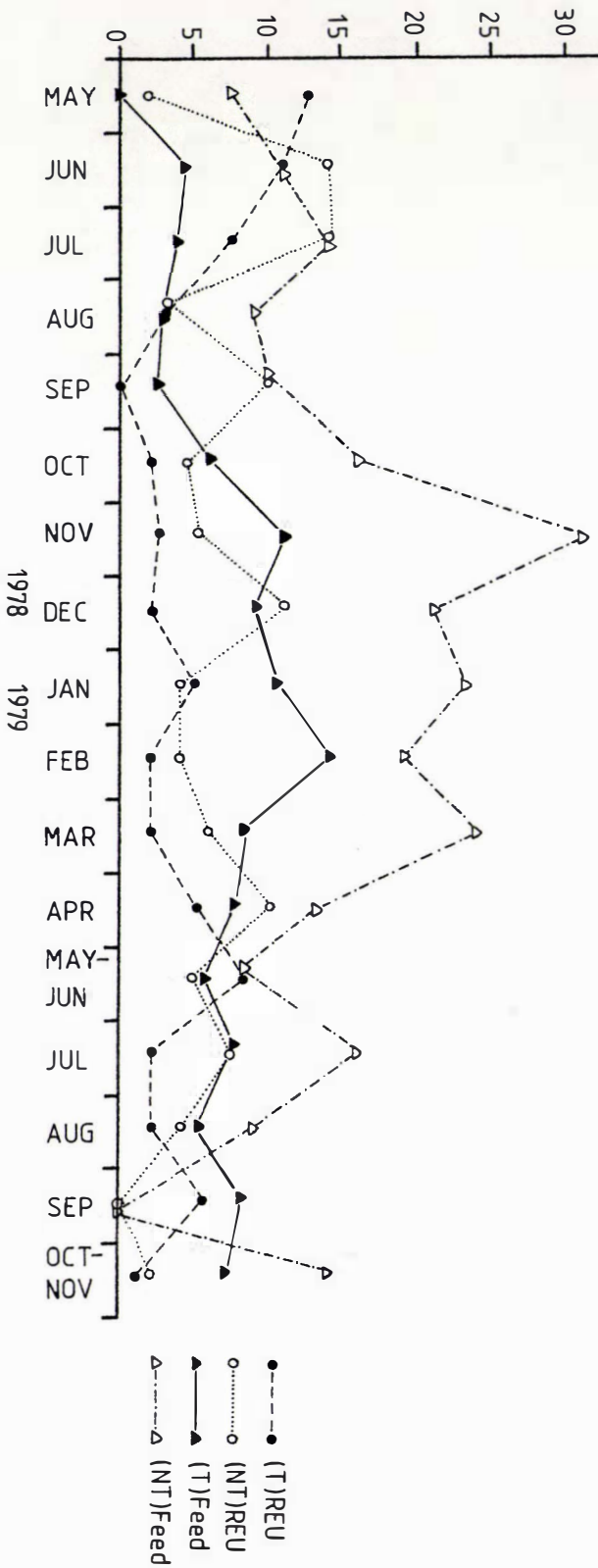


Frequency with which given acts occur
in aggressive sequences

FIGURE 3.7 cont'd.
c) Flapping Lunge & Slow-Wing-Flap



d) Relaxed - Upright & Feed



iii) PAR follows a similar pattern to THR_{hi} , with the late 1978 peak reflecting a disturbed period following several clutch removals. The 1979 peak represents an increase in activity with the establishment and marking of territories: once neighbours recognise each other's boundaries, the need for PAR is reduced. Parades in NT sequences could represent a) unrecognised territorial swans; b) mutual THR_{hi} by two birds, rather than a boundary display. This is a likely explanation for brief incidents involving little movement; c) defence of feeding, as distinct from breeding, territories.

iv) FL occurs at high levels from August into summer. It is a frequent finale of THR chases by territorial birds (3.3.2 a&b) and probably represents expulsion of intruding flock birds during the presence of broods.

v) SWF is fairly constant over the study period. Its predominant use by territorial swans may relate to longer, more intense aggressive activity and concomitant feather wetting, which provides a stimulus for some preening-derived display.

vi) REU by non-territorial swans is generally higher than in T sequences but shows no seasonal trends.

vii) Feed as a component of aggressive sequences is consistently more frequent among non-territorial swans, and peaks in the period Nov.-March. Territorial Feed shows a similar, lower peak. This is not the period when general feeding occupies the greatest proportion of a swan's time (Ch. 2), and I would in fact expect feeding as a component of aggressive sequences to peak when feeding activity is also at its highest. The effects of crowding (reduction of individual distance) due to greater swan numbers over summer may be important here.

3.3.4 Establishment, extent, and persistence of territories

3.3.4a Territorial establishment and maintenance

Using the definition of a territory as "any defended area", territory establishment is recognised when an

individual begins to exclude others from a given area, using behaviour which may or may not be peculiar to territorial defence. A Black Swan (♂ or ♀) beginning to defend an area will use a number of behaviour patterns, some of which are exclusive to territorial individuals and some which are used by the whole population but which occur at a higher frequency in territorial swans' displays.

Neighbours with contiguous boundaries mark their borders by the use of mutual PAR, possibly involving FBE/FL, and some (apparently) displacement feeding. To encroaching flock birds, the boundary is that series of points beyond which the owner will not continue a chase, and within which threat and attack are probable. THR_{me}, FL (a physical attack) and SWF (a long-distance vocal and visual display) are used here.

Using these displays as indicators, selection and establishment of territories begins in February. By this time families have broken up and some swans have completed their moult. Not all pairs begin defence at the same time. Defence continues until broods are fledged, and there is then a lull in the activity of known resident pairs. However, prospecting pairs may try out areas; also, since territorial ownership appears to be a prerequisite for mate selection (Ch. 4), young single males may attempt to take up a territory of their own. Size of the chosen territory may depend upon

- i) the resources it has to offer (b below);
- ii) the economic viability of its defence (b below);
- iii) the individual "personalities" of its holders (c below).

3.3.4b Characteristics of a breeding territory

Black Swan territories on Pukepuke Lagoon have the following characteristics:

- i) Shelter: provided by tall stands of raupo and flax and, in one case, a large stand of willow. The

dense vegetation offers shelter from the weather and from detection by predators. Access is provided by narrow waterways between flax and raupo clumps: the shoreline vegetation is not an unbroken mass.

ii) Nest sites: since ♀ choice of nest sites prospected by the ♂ seems likely (c.f. *C. olor*: MacSwiney 1966), at least one and probably several potential nest sites will be available.

iii) Food: is available for adults and cygnets. Both age classes are vegetarian; however, very young (< 14d.) cygnets are incapable of feeding below water for extended periods of time (Ch. 5), and ample shallow-water feeding areas may be a prime factor in territory choice.

iv) Field of view: territories are placed so that the owners may observe the distant approach of other swans from on, or just within, the shoreline.

v) Defendability: territories must be of such a size that, during incubation and early brood care, one member of a pair can successfully defend it without excess effort. A pair may spend up to 20% of the day in defence (Appendix I), or as little as 5%.

3.3.4c Size of breeding territories

This can be determined only approximately, since boundaries could only be mapped on the open water of the lagoon. Few fights or noisy threats were heard from within the raupo: the dense growth means that intruders run little risk of detection unless owners actively patrol the internal waterways.

However, the known territorial areas can be shown to vary with time, with the identity of owners, and depending on whether or not defence of moving broods is regarded as "territorial defence".

Table 3.6 presents the approximate size, in hectares, of territories defended on Pukepuke Lagoon in the 1978 and

1979 breeding seasons. Defence of an area about a brood is included in territorial defence (3.4.4). For some pairs both ♂ and ♀ were active in defence. In 1978 the maximum size of a breeding ♀'s territory ranged from 10.41ha to 0.55ha (10.41ha-0.03ha if all territories are considered), and in 1979 from 4.79ha to 0.03ha (4.79-0.03ha). In both years the largest territory, occupied by ♀1, was larger by a factor of 10^2 than the smallest. Generally, territories reached their greatest extent some time after their initial establishment.

Only pairs 1 and 6 could be recognised confidently in both seasons. Of the others, ♀GC in 1978 were both banded and collared (although the collar of the ♀ was not unique); the ♂ did not appear in 1979 although the ♀ may have done so.

Variation in territory size may be related to the "personality" of the occupiers. Pair 1 were extremely aggressive and, when their territory was at its largest, tolerated no intrusions. In 1979 ♀GC2 showed similar behaviour once their brood hatched; their presence restricted the size of ♀1's area. Pair GC2 were unusual in that they appeared to occupy two areas, one before and one after hatching. Most other pairs, although performing some boundary-marking (PAR) displays, did not exclude flock birds from their small territories. However, they usually acted against any approaches to the cygnets. One pair (♀Ra) did not defend an area at all, and ♀A showed only limited aggression. Both flock and territorial swans approached both broods closely and harassed them on occasion: both broods died.

Differences in the treatment of flock birds by territorial swans become apparent when flock use of the lagoon is related to the positions and maximum extent of territories (Fig. 3.8; Ch. 2). Flock birds were excluded by ♀1 (1978 and 1979) and ♀GC2 (1979). Once breeding and defence ended, flock birds spread onto almost all the available water area.

TABLE 3.6 AREA (ha) OF KNOWN TERRITORIES, 1978 AND
1979 BREEDING SEASONS

a) 1978 season

identity	Months								
	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.
♂1	2.41	4.05	4.11	5.88	9.01	8.06	10.41	4.46	-
♀1	-	0.71	-	-	1.54	7.25	8.91	4.96	-
♂6	0.08	0.26	0.35	1.75	4.20	1.69	1.60	0.88	-
♀6	-	0.07	-	-	0.79	0.69	0.99	0.53	-
♀MM1-2	0.26	0.20	-	0.10	-				
♀SE?	0.33	0.41	0.50	-					
♂GC			0.64	0.46	0.08	-			
♀GC			-	0.07	-	-			
♂Dh					-	0.99	-		
♀Dh					-	0.76	-		
♀U					-	0.55	-		
♀Y						-	0.03	0.16	-
♀Lge						-	0.08	0.36	-
♀?A						-	0.05	0.10	-
♀?B						-	0.12	-	
raupo ♂							-	0.05	-
♀ at hide raupo							-	0.20	-

average size of all ♂ territories

$$\bar{x} = 1.43 \text{ ha, sd} = 2.91$$

average size of breeding ♂s' territories

$$\bar{x} = 3.36 \text{ ha, sd} = 4.22$$

TABLE 3.6 cont'd.

b) 1979 season

identity	Months						
	Mar.	Apr.	May/June	July	Aug.	Sept.	Oct./Nov.
♂1	-	-	0.89	2.48	2.89	3.98	4.79
♀1	-	-	0.63	1.75	-	2.33	4.73
♂6			-	0.20	0.30	0.75	1.00
♀6			-	-	-	0.10	-
♂GC2		-	0.46	0.21	0.13	0.97	3.50
♀GC2		-	-	0.20	-	0.07	2.79
♀T		-	0.03	0.07	0.03	0.08	-
♀A			-	0.05	0.03	-	
♀7				-	0.05	0.07	0.08
♀Ph		-	0.05	0.04	0.12	0.25	0.05
♀R7		-	0.05	0.04	0.07	0.08	-
♂ R of Willows		-	0.05	-			
♀8					-	0.13	-
♀Uk						-	0.03
♀Ra							no obvious territory defended

average size of all ♂ territories

$$\bar{x} = 0.86 \text{ ha, sd} = 1.65$$

average size of breeding ♂s' territories

$$\bar{x} = 0.94 \text{ ha, sd} = 1.72$$

FIGURE 3.8a:

Maximum extent of breeding territories held in 1978, with cores of major territories and areas suitable for young (< 14d.) cygnets to feed (Territories not at maximum size concurrently)

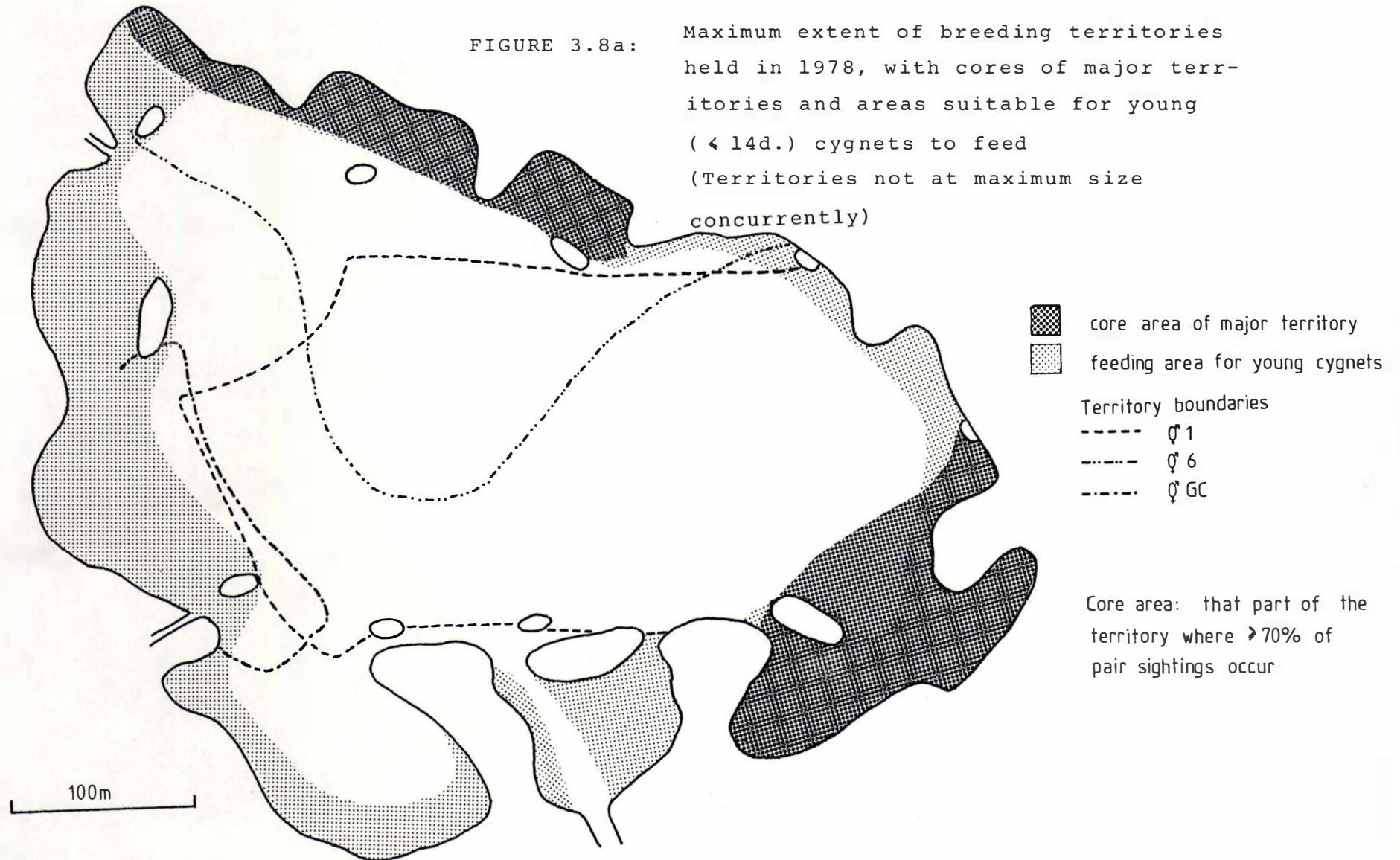
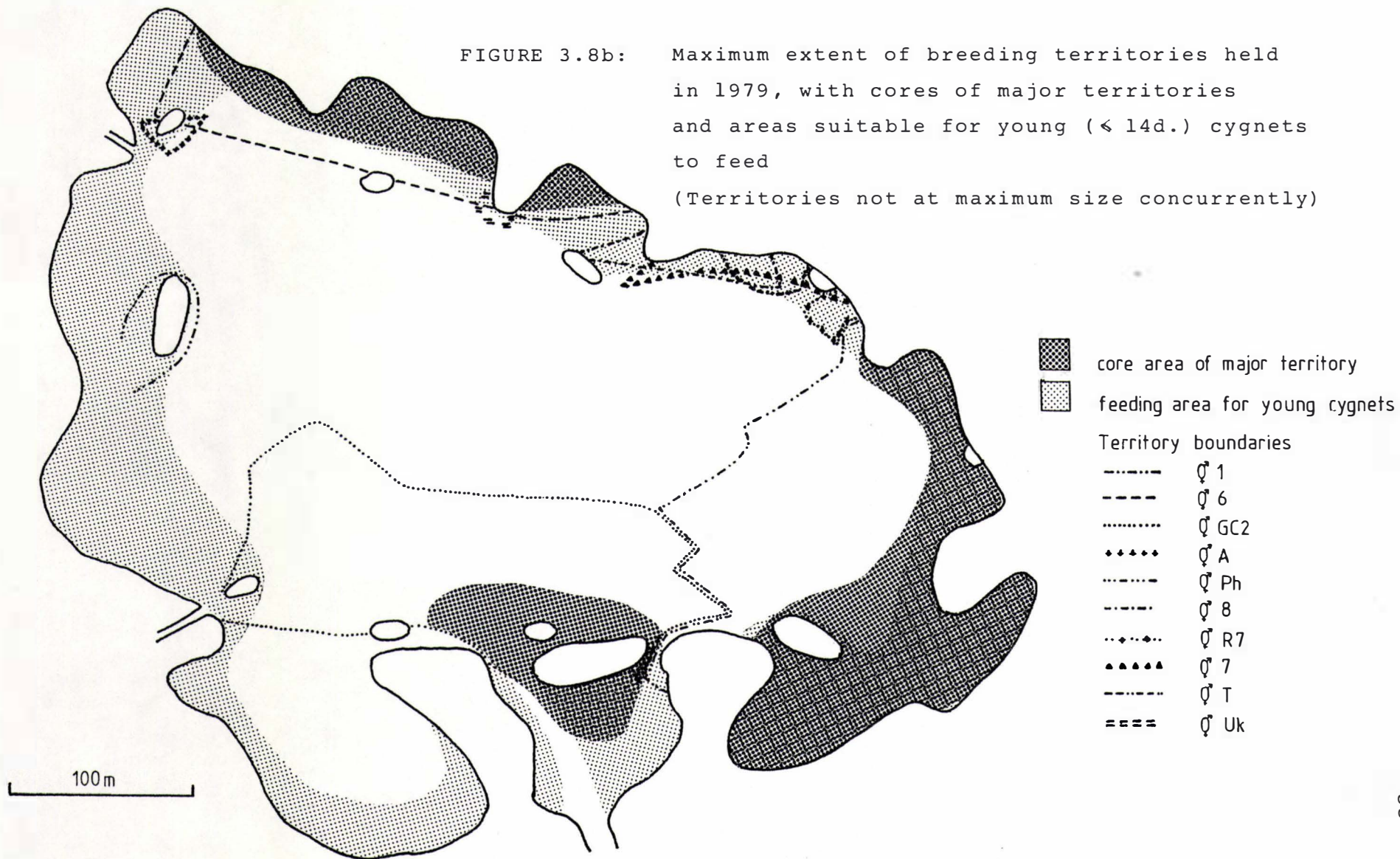


FIGURE 3.8b: Maximum extent of breeding territories held in 1979, with cores of major territories and areas suitable for young (< 14d.) cygnets to feed
 (Territories not at maximum size concurrently)



3.4 DISCUSSION

3.4.1 Differences in the behaviour of flock and territorial swans

Aggression may be defined as "behaviour directed towards [and elicited by] another individual which could lead to physical injury to the latter and often results in settling status, precedence, or access to some object or space between the two" (Hinde 1970: 335; see also Rosenzweig 1977). "Aggressiveness" can be described as a tendency to attack (Wilson 1975). Both territorial and flock birds exhibit aggressive behaviour, which may vary in form, frequency and objective between the two groups.

It is apparent that territorial and flock (non-territorial) Black Swans on Pukepuke Lagoon vary considerably in the nature and frequency of some behaviour patterns used in aggressive interactions, while other acts show no such differences.

Some of the acts involved indicate the presence of a pair bond (Greeting and Triumph ceremonies: Ch. 4). Since pairs are present in the flock as well as on territories, both in and out of the breeding season, they would be expected to perform these displays as often as the breeding birds. In fact, since flock disturbances, for whatever reason, are common, GRE by pairs may be even more frequent than is indicated by the data.

Physical fighting is rare in both groups, as would be expected for potentially damaging acts. The link between Parade and fighting (FBE) (Table 3.2, Fig. 3.5) makes it likely that any FBE seen in "non-territorial" sequences occurred during PARs which could not be attributed to known territorial swans.

Non-territorial sequences tend to involve close-range threats. They contain significantly more IMP

and PEL ($p < 0.01$ and $p < 0.001$ respectively) which, with their slight postural changes and/or soft vocalisations, are probably effective over only short distances. Together with THR_{10} they often occur in brief, localised disputes over feeding sites (Single-Link-Cluster-Analysis shows a close linkage between Feed and THR_{10} : Fig. 3.5). The Feed acts seen in territorial sequences may sometimes be due to feeding disputes (especially the slight summer peak: Fig. 3.8), or may occur during brief breaks in aggressive activity. In some cases, especially during PAR displays, they may well represent displacement activity. Non-territorial Feed also shows a summer peak. Again, this most probably represents feeding disputes, although since the swans spend less time feeding over the summer (Ch. 2), the reason for an increase in food-related threats is unclear. A possible explanation is that, with the greatly increased swan population present over the summer months, encroachment of individual distance while feeding, and associated threatening behaviour, become more common.

Where PEL occurs in territorial data, its linkage with Flapping Lunge (Table 3.2, Fig. 3.4) places it at the end of a long-range chase and attack. Slow-Wing-Flap, with its associated bugling call, is common in territorial sequences and is also likely to be effective over long distances. The same is true of Trumpet, a prelude to other threats, but this display is not limited to territorial swans. TRU is usually performed by one member of a known or apparent pair, and may, like GRE and TRI, be largely confined to the repertoire of paired or family birds.

I had expected that the high-intensity THR_{hi} display would be a discriminant for territorial activity, anticipating that such activity would be more likely than flock disputes to escalate to high-intensity displays, and was surprised to find this true only for the special

case of PAR. The equivalence of THR_{hi} in the two display groups is then difficult to explain: it may again represent the activity of pairs, both on territories and in the flock. The threat form THR_{me} is instead a major characteristic of territorial interactions ($p < 0.01$), linked significantly with the long-distance threat of TRU and the attack of FL ($p < 0.001$ for both).

The overall frequency of territorial and non-territorial sequences changes with time (Fig. 3.6). This may indicate either a) a preoccupation on my part with the "more interesting" activity of pairs, or b) an actual difference in the frequency of events. Since I attempted to remove observer bias in data collection (Ch. 1), b) is more likely. Although sequence counts are not a completely accurate measure of aggressive activity (section 3.2), this result implies that aggression by flock birds is more frequent over the summer, and that at other times prolonged aggression is more likely to involve territory holders. The territorial low is probably the result of decreased activity during the pairs' moult period.

3.4.2 Territory establishment

The display patterns THR_{hi} , PAR, and FL (Table 3.3) are markedly seasonal in occurrence. The latter two are characteristic of territorial behaviour. Their seasonality may be related to the selection, establishment and defence of breeding territories.

THR_{hi} peaked in the disturbed breeding season of 1978 (Aug.-Sept.) and again in Feb.-March of 1979. PAR showed a similar pattern. In both cases, for territorial swans (the major actors at this time: Fig. 3.6), this activity will represent (re)establishment and delineation of territories, marking them off from neighbouring pairs. The later 1978 peak is due to renewed activity by pairs whose clutches were removed, prior to resettlement or renesting attempts. Once territories

are recognised by neighbours the need for boundary displays will fall off, although other intruders must still be driven away. In February 1979 pairs (Q) 1 and 6 were in their moult but five new territories were in settlement, with considerable PAR activity. In March and April no distinct territories could be delineated although there was again much aggressive behaviour. Seven (potential) breeding territories were occupied and defended in May-June, after which high-intensity threats and boundary-marking decreased, although lower-intensity threats remained at a relatively high level.

Another display, FL, decreased only slowly over the 1978 season (Aug.-Jan.), and increased again in 1979 as boundary displays decreased. This activity, a "long-distance" display, is an attack effective in driving off non-territorial intruders and, in addition to other less mobile threats, is important in territory defence over the time of incubation and brood care.

The late-summer - early-autumn establishment of territories is probably important in pair-bond formation and the maintenance of these bonds (Ch. 4). The highly visible and audible behaviour involved is an advertisement for the presence of a potentially compatible mate, capable of at least the defence of some sort of territory. (Simple "ownership" of an area may not be of paramount importance: the quality of the area will influence the Q's choice, as well as her assessment of the O himself. Nest sites, shelter, and perhaps food supply will be evaluated.) If the area is exclusive with respect to rival breeders, once a pair has formed it will be reasonably-well isolated from interference by others. Ownership will reduce the likelihood of cuckoldry (pre-nesting) and of later forced-copulation and parasitism attempts (Mineau & Cooke 1979).

Nesting and laying do not usually follow immediately upon territory establishment. Pairs 1 and 6 established

their 1978 territories at least two months before laying and incubation began. This interval was the same in 1979 for ♂1 and ♂GC2, and possibly for ♂s T, Ph and R7. For other pairs the interval was approximately four weeks. This is calculated by working back from the date and age at which cygnets first appeared, assuming an incubation period of 36 days; for pairs where the ♀ was active in defence, the period where her activity ceased abruptly for at least a month is also a cue.

3.4.3 Colony or territory

There is no clear separation of colonial and territorial activity in the literature. Even in closely-packed breeders, an exclusive area of some sort is always defended, albeit only the nest cup (Buckley & Buckley 1977: Royal Terns *Thalasseus maxima*). In the Anseriformes, those geese which are frequently described as colonial nesters (Inglis 1976; Mineau & Cooke 1979; Ryder 1975) are often shown to defend quite extensive areas about the nest. The Black Swan itself shows a continuum of defended areas, from the several hectares seen in some Pukepuke territories, to the pecking-distance radius observed between some nests on the main Lake Ellesmere breeding grounds (Miers & Williams 1969). Similarly the usually colonial Herring Gull *Larus argentatus* is solitary and territorial where food is short, as is the Jaeger *Stercorarius* sp. if food resources are defensible (Lack 1968). Thus "territorial" and "colonial" lifestyles are separated by some ill-defined cutoff point. Pink-footed Goose territories studied by Inglis (1976) ranged in size from 2,000 to over 16,000 square feet (269-2109m²) within a large breeding colony i.e. neighbours over 30m apart are still regarded as colonial. Mineau & Cooke (1979) described as "colonial" Lesser Snow Geese nesting at a density of 22 nests/ha; the average potential territory size would then be 454m². "Overall" home ranges observed in their study ranged from 279m² to 3182m², although there was considerable overlap late in incubation. (Nest spacing is largely dependent

upon suitable sites being free of snow when the geese arrive.) Brown & Orians (1970) regard colonial and territorial social forms as extremes of a continuum, with colonial animals having a "more clumped" dispersion pattern than the distribution of resources would predict. This implies that those individuals nesting in close proximity to others may have some inherent tendency to do so i.e. their selection of an area "... is positively influenced by the prior presence of other individuals" (Brown & Orians 1970:243). The possibility that the presence of two breeding forms in Black Swans is under genetic control is discussed in Chapter 7.

3.4.4 Definition of territory

The definition of a territory, as "any defended area", is similarly open-ended. Brown & Orians (1970) regard it as having the following characteristics: a set area, which may vary slightly with time; behaviour by the owner which leads to escape or avoidance by others; exclusive possession by an individual or family. Thus rivals for ownership are excluded; what is not apparent is why the area is chosen and what is defended. Reasons for choice and defence will vary with the species. It is also uncertain whether or not the defence of a moving object should be regarded as territorial activity (Brown 1975; Hinde 1956). I have included brood defence in territorial behaviour because a) the same behaviour patterns are used in defence of a fixed area and of a moving brood, by Black Swan parents; and b) in general, exclusion of others is complete from an area (of varying size) about the brood i.e. following Hinde (1956), territorial boundaries are defined with respect to both environmental landmarks and characteristics, and the behaviour patterns used in their defence. For most pairs observed on Pukepuke Lagoon, brood movements occurred within existing boundaries, but for ♀s 1 and GC2, movement and defence of broods considerably extended territory perimeters.

There is some support for the inclusion of a mobile object in territorial defence. Cooper (1978) found in his Canada Geese that the defended area moved with the ♀; the nest site was undefended if she was absent. Defence protected the ♀ from harassment, reducing the likelihood of forced copulations and/or parasitism attempts. Owen & Wells (1979) found that ♂ Barnacle Geese *Branta leucopsis* defended both ♀ and nest site, so that defence again involved a moving body. Again, this would reduce harassment and ensure parenthood.

In addition, a territory may show variation in the degree to which parts of it are used. On Pukepuke Lagoon, the extent of defence by pairs with large territories also marked the outermost bounds of their movements. The core of each territory i.e. that area used most often and where aggressive activity centred, was much smaller. Vines (1979) demonstrated the presence of a strongly-defended core area in Oystercatchers *Haematopus ostralegus* (see also Melemis & Falls 1982). Thus the whole of a territory may not be defended to the same extent or with the same intensity.

3.4.5 Size and function of the defended area

As stated in 3.4.4, the size of territories may vary considerably within a species, and within and between habitats, with the owners able to assess habitat quality in some way. Vines (1979) suggests three reasons for differences in territory size, based on her study of breeding Oystercatchers in two localities:

- 1) there are genetic differences between the two populations (this possibility is being considered for territorial and colonial Black Swans: Ch. 7; M. Williams pers. comm.);

- 2) variations in some environmental parameter such as visibility (cover), or food distribution;

- 3) "conspecific pressure" affecting the maximum area: other birds settling at territorial margins would

compress territories and cause higher levels of aggression at the margins of now smaller territories. Vines considers 2) and 3) to be the proximate determinants of territory size in *H. ostralegus*.

She also notes that settlement in the densely nested area tended to be more synchronous. Davies (1978) also suggests that asynchronous establishment of territories may result in variable spacing, with early arrivals claiming large areas and leaving only small spaces for later breeders to occupy. This could well be the case on Pukepuke Lagoon, where ♂1 and ♂6 were considerably earlier in defining their territories*, and had earlier hatching dates, than other pairs. These later pairs, with small, closer-packed territories, had fairly synchronous brood production. This difference in timing could explain some of the observed variability in territory size; the reasons for different breeding dates must also be examined (Ch. 7).

The major environmental factors affecting breeding area on Pukepuke Lagoon are likely to be visibility, nest cover, and food resources. Owen & Wells (1979) noted that topography influenced site size in Barnacle Geese, with larger areas being claimed in open spaces giving clear and extended views of approaching intruders. Similarly Ewaschuk & Boag (1972) found that Canada Geese defended smaller areas, and nested closer together, where their view was broken by vegetation. On Pukepuke Lagoon all territory owners, if present at the raupo edge, had clear visibility; as stated earlier, I have no evidence that territories were defended very far back into the vegetation. Withdrawn in the raupo, all nests were out of view of all others. Nest cover, in the form of raupo and flax stands, was very dense in all regions except the eastern (pumphouse) shore. This lack of cover, on what was a very exposed shoreline when strong northwest winds blew, possibly influenced the choice of prospective breeders. (So may the presence of

* particularly in 1979

flock birds: this area was a major loafing ground.)

Resources available to the ♀ and/or brood may be important. Williams (1980) suggests that food supply may be a strong determinant of whether Black Swans breed colonially or defend large territories. On Pukepuke Lagoon, pairs 1, 6 and GC2 fed within their boundaries for the duration of the breeding season, mainly using a fairly central core area. This is evidence for the presence of an adequate food supply, in these territories at least, and one which did not comprise the whole of the defended area i.e. these pairs appeared to defend far more area than was needed for feeding by adults. This is also true for areas where young (< 14d.) cygnets may feed i.e. that area where the cygnets can feed at the surface, with no need for diving or prolonged head and neck submersion. It was determined by observing where cygnets could feed and where adults fed in obviously shallow water, and may be an underestimate due to the adults' habit of pulling up submergent vegetation and leaving it at the surface, an act which they perform more frequently when cygnets are present (Kear 1972). The "cygnet-feeding-area" defended varies greatly between territories (Fig. 3.8 a & b). At present, the question of whether food supply is a major determinant of territory size on Pukepuke Lagoon cannot be completely settled.

In terms of ultimate breeding success, females and young may also be regarded as resources, to be defended or not by the ♂ and/or pair. Under this viewpoint (3.4.4) mate and offspring become the focus of territorial activity. Constant attendance on, and defence of, the ♀ has already been demonstrated for many Arctic-breeding geese. In these birds defence of a food reserve is of minimal importance since the geese arrive at their snow-covered breeding grounds in a state of hypertrophy (e.g. Raveling 1979), and once young appear there is usually a superabundance of food. Strong defence of the

Q reduces the probability of cuckoldry, forced copulations and parasitism. It is notable that defence weakens once the optimum time for these acts is past (Eisenhauer & Kirkpatrick 1979; Mineau & Cooke 1979).

Reduction of harassment by, and the harassment of, others may also be important. On both Pukepuke Lagoon and Western Springs (Auckland), flock and other territorial birds often attack and may drown undefended cygnets, or else harass them so much that they cannot feed adequately. Poor parental defence may result in lost parental investment. This does not appear to be important in most geese, where broods may pass close by each other, or intermingle, without harm. Harassment of other breeders, or competition with them (Verner 1977), is less likely, since although it would be of direct benefit at the time this characteristic is a "spiteful" one and would be disadvantageous if widespread. In any case, Verner's hypothesis is not borne out by my results, as it predicts that territories should be established at their maximum size, while on Pukepuke Lagoon they tend to get larger later in the season.

Both proximate and ultimate determinants of territory size must be mediated by behaviour. This too is variable and may itself affect the area defended (Mineau & Cooke 1979). Thus O1 and Q1 were a highly aggressive pair, vigorously defending a very large area. Other pairs appeared considerably less aggressive, held smaller territories and did not exclude all comers from them. Flock birds usually had free access to the cluster of territories on the southern shore, although breeding neighbours were often threatened.

In addition, where territories were relatively large, both O and Q were active in their defence (Qs 1, 6, GC, GC2, Dh). Active interest by both sexes may be essential if a large area is to be maintained. It would be interesting to examine the roles of O and Q in territory defence in Black Swan colonies.

The reasons for territorial breeding by part of New Zealand's Black Swan population, and the factors on which these individuals base their selection and defence of an area, are thus not clearly defined. Williams (1980) offers a list characterising the habitats of the two breeding types: territories are established on small water bodies (5 - 20ha); on larger areas where food plants are limited; on larger areas where a flock is not present in the breeding season; and on areas where water levels are constant in the breeding season. Colonial swans, however, are found on large water areas with a large non-breeding flock present throughout the year; where water levels fluctuate during breeding and drop markedly over summer; where food is extremely plentiful; and on estuaries. This does not account for additional differences which must exist in the birds' social behaviour, nor is the reason for entering one breeding mode or the other immediately apparent. The answer may be found in genetic differences, or early learning, or a combination of the two (Ch. 7).

On Pukepuke Lagoon itself, the only way of determining whether large territories are inferior to others with respect to some resource, or just held by more aggressive individuals, would be to combine a lake-wide vegetation survey with removal experiments: if, for example, $\phi 1$ was replaced by several new pairs on the same initial area, it would suggest that the size of large territories is in part dependent on the aggressiveness of the defending individuals. The origins of the replacements should be closely monitored.

Chapter 4

MATE SELECTION, PAIR-BONDING, AND BREEDING ACTIVITY

4.1 INTRODUCTION

Successful reproduction is the ultimate aim of all organisms and their life-styles, directly or indirectly, are influenced by and organised towards this end. Selection of a suitable mate, formation and maintenance of the necessary bond, and integration of breeding activity are of vital importance, and may occupy a considerable portion of an animal's time.

It is important to make the best possible choice of available mates, in order to minimise loss of genetic and personal investment through breeding failure. Such failure could be due to behavioural incompatibility, lack of physical condition or experience, or to infidelity. A courtship period of variable length, prior to breeding, will serve to lessen the chances of failure, as courting individuals have the opportunity to assess potential mates and reject those found to be unsuitable. They should not, however, be infinitely selective. Burley (1981), studying criteria for mate choice in pigeons, concludes that "it is probably advantageous for birds to accept as mates any individuals of the quality they, on average, can expect to attract".

Discussing mate choice in Anatidae, McKinney (1975) lists five criteria likely to be used by females in selecting suitable mates:

- "1. vigour, skill and persistence in courtship;
- "2. healthy physical condition ...;
- "3. attentiveness, compatibility and constancy in reaffirmation of the bond;
- "4. success in competition with other males;
- "5. efficiency in copulation."

Males would use similar criteria in their selection of females.

For species with parental care, Burley (1981) adds "the quality and quantity of care an individual is likely to provide". Choice in this matter may be based on the length of time an individual invests in courtship, for a lengthy pre-copulatory investment is likely to be followed by prolonged post-copulatory attentiveness (Trivers 1972). This will be an important mate-choice criterion in those species where both male and female must contribute to clutch and brood care if the young are to survive. Burley (1981) also found that the dominance status of the potential mate could be used as a basis for selection, particularly by females, which observed male agonistic interactions before making their choice.

Courtship and pre-copulatory displays may serve a number of functions other than simple attraction and excitation of a mate. Beer (1975) proposed five functions for male courtship displays: deterrence of rival males and spacing out of the breeding population; attraction of, and bonding with, an unmated female; stimulation of the female's gonads, and synchronisation and integration of the pairs' breeding activities; stimulation of other conspecifics, which affects timing of breeding in the population as a whole; prevention of interspecific hybridisation.

In the Anserinae preliminary courtship and pair-formation frequently take place in wintering flocks (Minton 1968), where birds of each sex have a large number of potential mates to choose from. Mate selection may also occur when the young birds arrive on the breeding grounds (Braithwaite 1981b; Braithwaite & Frith 1969b; c.f. Nelson 1966: Gannets). Courtship is a lengthy process in anserines, as a poor choice may prevent breeding or reduce its success for at least that year. The male must often play

a large part in rearing the brood (Kear 1972), which may take up to 6 months (in the Black Swan), and which calls for strong and enduring bonding within the pair.

Initial pair-bond formation includes some elements of aggression, as male and female tend at first to be hostile to each other. The development of mutual greeting and triumph ceremonies, the latter having some aggressive motivation (Fischer 1965; Radesäter 1975 a & b), is seen in swans and geese as bond formation progresses. Other behaviour patterns seen at this time include elements of precopulatory display, and copulations also occur as members of the pair test each other's physical competency. These displays continue for the duration of the pair bond, which in anserines is often for several years (Minton 1968; Reynolds 1972), or even a lifetime (M.Evans 1975). Copulatory activity can be expected to peak in frequency when it becomes functional in fertilisation as well as in testing and maintaining the pair bond.

In this chapter I list and describe the behaviour patterns of courtship and breeding in the Black Swan population of Pukepuke Lagoon; analyse their occurrence and frequency; and discuss the biological functions of the pair bond in relation to the territorial lifestyle of the breeding pairs.

4.2 METHODS

Data on behaviour patterns seen in courtship, pair-bond maintenance and copulation were collected over the course of the study on a focal-individual basis (Ch.1; Altmann 1974). Thus the lagoon was scanned constantly between half-hourly counts until an individual was seen in one of the chosen categories of behaviour, which was then followed through to completion. Casual notes on the occurrence of acts heard (greeting, post-copulatory call) or glimpsed during focal-individual sampling were also collected. Combining these data then permits an examination of the frequency of behaviour patterns, description

of the acts involved, and analysis of sequences.

Pair-bond maintenance may have been under-represented with this method as the relevant displays are low-key, often fairly brief, and inconspicuous, and thus easily missed. Copulations are longer, visually and aurally conspicuous, and occur on open water. The total count of completely and briefly observed copulations is likely to be an accurate measure of total sexual activity. Greeting and Triumph ceremonies are also highly audible. However, more than one family or pair may greet at a time and such counts will be inaccurate unless visually confirmed.

4.3 RESULTS

4.3.1 Courtship

4.3.1a Behaviour patterns of courtship

I observed courtship only once. Most pairs taking up breeding territories on Pukepuke Lagoon are already of an age to be established breeders, as shown by their size and plumage characteristics (Braithwaite 1981a) and are likely to be mated for at least several seasons. All adults breeding in 1978 and 1979 were pair-bonded when they first became active territorially.

The pair observed courting were both young birds, with all flight feathers black-tipped, and the male began to defend a territory a week before courtship activities were observed. Their courtship contained the same elements of precopulatory display as pair-bond maintenance, plus aggression towards each other and other individuals and also the development of shared Greeting and Triumph ceremonies. One copulation was seen, towards the end of the liaison.

4.3.1ai Precopulatory elements

A full description of precopulatory behaviour is given

in 4.3.3: Copulation. Those elements of precopulatory display regularly observed in both courtship and pair-bond maintenance are Facing-Together (FT), Cheek-Rub-Lateral-Preen (CRLP), Head-Dip (HD), and Head-Shake (HS). Neck-Dip (ND) occurs in some sequences.

4.3.1aii Aggressive displays

These are described fully in Ch. 3. The displays used in courtship, directed towards either the prospective mate or other individuals, are the low-, medium-, and high-intensity (THR_{lo} , THR_{me} , THR_{hi}) threat displays.

4.3.1aiii Greeting ceremony

The Greeting ceremony (GRE) is performed by paired or courting birds, within family groups and, after generalised flock disturbances, by apparently unrelated swans (perhaps trying to regain contact with mates or siblings). The birds involved have usually been separated for some period of time, or else alerted by some disturbance.

Birds performing a GRE approach each other closely, necks erect and fluffed and bent just below the head so that this is in a "pendant" position (Boase 1959). Their wings may be slightly raised. From the pendant position each bird jerks its head repeatedly upwards, giving a bugling call with each jerk (Fig. 4.1).

There appear to be two greeting calls, although further analysis is needed to resolve this point:

The first is used by paired or family birds. It is quite melodious and ends on a falling note. Neck and head are not fully vertical as the call is given.

The second call is given in alarming, and possibly in hostile, situations, or when a swan is alone, and is harsher and louder than the first, ending on a rising note. The neck is vertical or pulled slightly back (c.f. threat posture), so that the head is pointed straight up after each call. I have heard it after Trumpet and Slow-Wing-Flap threat displays by other, distant, swans, and it is

also given by lone birds as they approach a group.

Swans performing a GRE ceremony usually call alternately. In most cases they call while facing each other, but occasionally they swim round in a circle. At the end of the display the birds relax and commence preening or feeding.

4.3.1aiv Triumph ceremony

After aggressive incidents a GRE may develop into a Triumph (TRI). I have seen this display given only by paired birds which are defending territories. If present, cygnets may join in with greeting calls.

One partner, usually the male, returns to the other after an aggressive incident still in a threat posture (TRI occurs significantly more often than chance after high intensity threats - $p < 0.01$ - and boundary Parades - $p < 0.001$; see Ch. 3). The other partner may also be giving a threat display. They begin with GRE calls, but do not relax their plumage and end the series of calls by curving their necks well over so that their heads point at the water, with wings still raised in threat (Necks-Curved-Over: NCO). A similar posture is sometimes seen after copulation, but this lacks the raised-wing component. During TRI the male and female are oriented so that they threaten past, not directly at, each other (Fig. 4.2). Finally the birds relax slowly and begin preening or feeding, although further threats may also ensue. I have not observed Slow-Wing-Flaps immediately following the TRI (c.f. Braithwaite 1981b) although they may occur during subsequent preening.

4.3.1b Sequence of events during courtship

The male of the courting pair observed on Pukepuke Lagoon began to defend a territory on or around 24 - 25/1/79, while still alone. A pair of adults was already resident in the area, and may have gone on to breed there. The young male's (OY) defence activities involved a series of

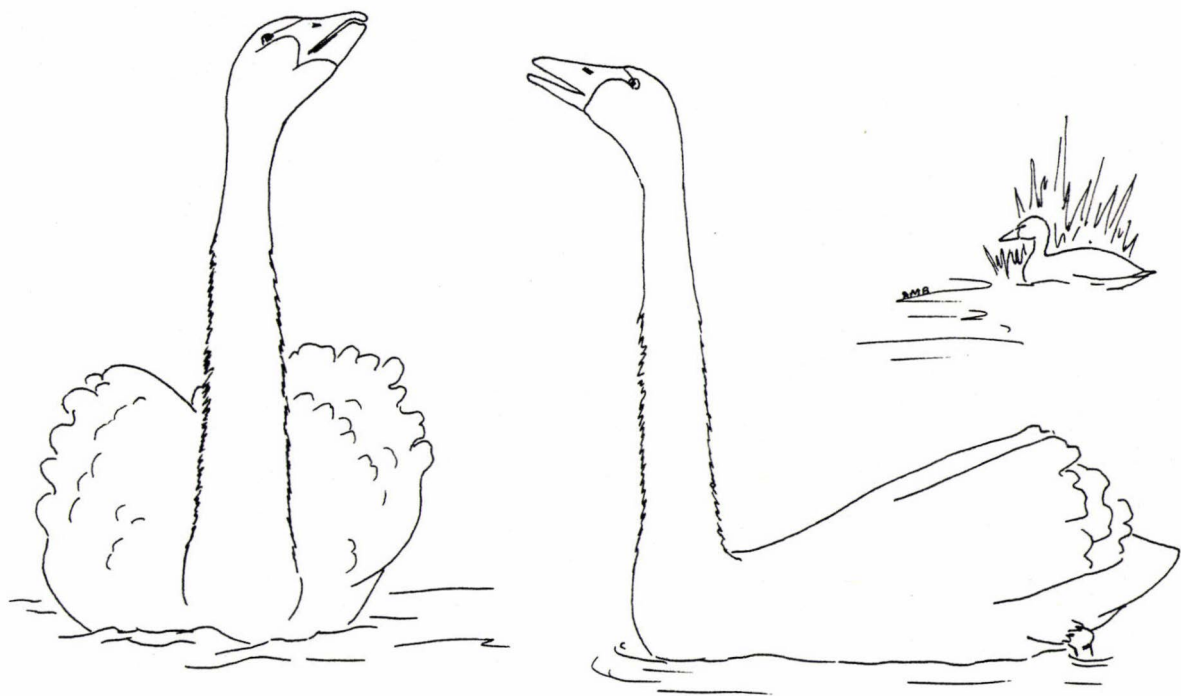


FIGURE 4.1: Greeting ceremony

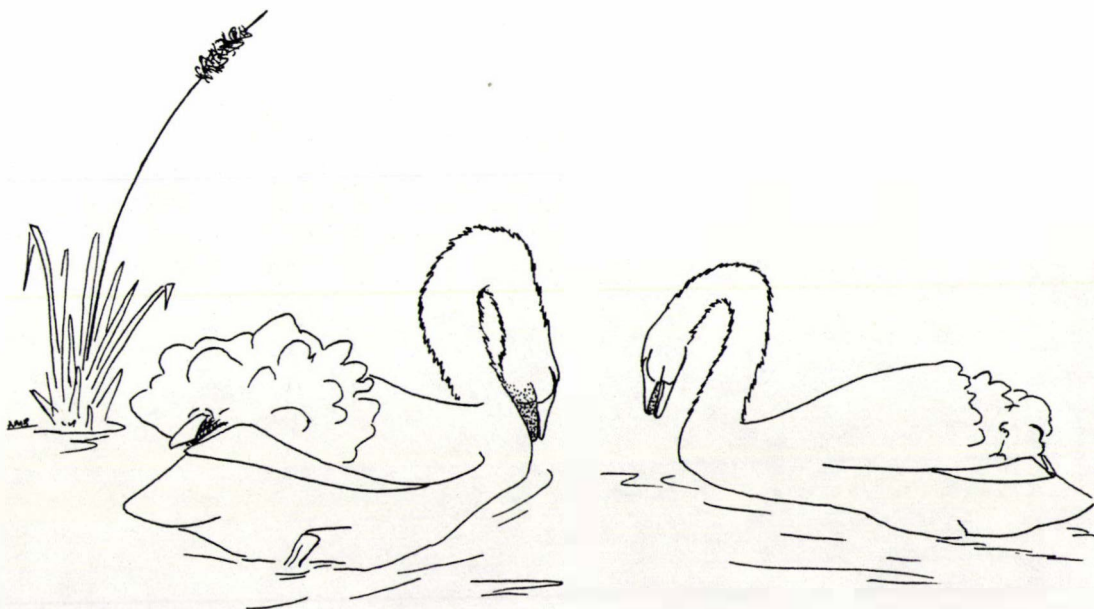


FIGURE 4.2: Triumph ceremony: Necks-Curved-Over
end-posture

Parades (PAR) with the ♂ of this pair. A week later (31/1 - 1/2/79) a young female (♀Y) was seen in the area, frequently approaching ♂Y in either an Alert-Upright (ALU) or low-intensity threat (THR₁₀) posture. Male Y responded by chasing her, using medium- or high-intensity threat; she avoided him in ALU or THR₁₀ but did not go far and quickly returned. Between these incidents, both performed brief pair-bond maintenance display sequences (4.3.2). The ♂ also threatened other birds who entered his territory. Female Y did not "incite" these actions although she twice chased intruders herself. Following such incidents the aggressor approached its partner giving greeting calls and a mutual GRE ceremony developed. Pair (♀) Y also greeted after threatening each other.

Pair Y remained together on the territory, actively defending it, for at least two weeks after ♂Y's arrival. They were also seen copulating once, on the territory, on 14/2/79. On 28/2/79 ♀Y was not present on the territory. Male Y was still active in defending it, using PARs and frequent threats at other swans in the vicinity, but after 1/3/79 he too was gone. His defended area was incorporated into the territory of an adult, breeding, pair.

4.3.2 Pair-bond maintenance

The behaviour sequences considered in this section, although consisting largely of displays seen early in pre-copulatory sequences, showed no sign of advancing to copulation. They were brief, with little repetition of displays. Usually one partner performed at a higher intensity than the other, who might not join in at all. It is possible that these sequences may represent unsuccessful attempts by one member of the pair to solicit copulations.

Pair-bond maintenance behaviour, as defined here, was observed relatively infrequently (N = 54 c.f. 127 copulations), perhaps because the behaviour patterns involved are inconspicuous. It is quite possible that some went completely unnoticed or were erroneously classified as preening or

comfort movements.

4.3.2a Behaviour patterns of pair-bond maintenance

A full description is given in 4.3.3 (Copulation). Like courtship, pair-bond maintenance involves Head-Dip, Head-Shake, Facing-Together, Cheek-Rub-Lateral-Preen and Relaxed-Upright (REU). Neck-Dips occur in some sequences, and Slow-Wing-Flap, Greeting or Triumph, and crossing of the ♂'s neck over the female's (♂/♀) are infrequent additions.

4.3.2b Sequence of events during pair-bond-maintenance display

Pair-bond maintenance displays are often brief (a few seconds) and not obvious. One swan faces its partner in REU or Facing-Together, and then gives a brief series (1 - 4 repetitions) of Head-Dip - Head-Shake and Cheek-Rub-Lateral-Preen. The preening component may continue for some time, and may be followed by another HD-HS series. Although these acts are similar to normal comfort movements used in preening and bathing (McKinney 1965), they differ in that they are performed more slowly and are exaggerated in form. The birds may then begin preening in earnest, or return to feeding or some other activity.

4.3.2c Involvement of ♂ and ♀ in pair-bond maintenance

Performance of these sequences was often one-sided. Of 54 sequences 37 (68.52%) involved ♂ and ♀, but 17 (31.48%) were given by the ♂ only.

Table 4.1 compares the composition of sequences performed by the ♂ and by the pair. There is no significant difference ($\alpha = 0.01$, $\chi^2 = 4.9106$, $df = 6$; NS) between the two.

4.3.2d Context of pair-bond maintenance display

Pair-bond maintenance display appeared to be closely related to feeding and preening. Table 4.2 suggests that

the activity preceding a sequence is often returned to once that sequence is ended. The exception is aggression, after which pair-bond maintenance turns to preening. Table 4.2 examines the relationship between activities preceding and following pair-bond maintenance sequences. It shows that pair-bond sequences are most likely to occur within bouts of feeding and preening (Fischer exact probability test, $p = 0.00039$). Then it is likely that the "Not recorded" (NR) row, for preceding acts, comprised mainly feeding and preening. Aggression is not likely to be a component of NR as most threat sequences observed ($N > 900$: Ch. 3) were followed through and subsequent actions noted. Only 9 were observed to precede "pair-bond maintenance" sequences, although many more led into Greeting ceremonies.

4.3.2e Composition of pair-bond sequences

Displays were generally of low intensity, and some acts seen in most copulatory sequences were rare or absent (Table 4.3 a&b). The most common (in 50%+ of sequences) patterns were predominantly those derived from washing and preening: HD, HS and CRLP.

This result may be compared with the same behaviour patterns from 82 copulations for which lengthy sequence data are available (Table 4.3b: data from Section 4.3.3). It is apparent that some behaviour patterns occur in copulatory sequences with greater or lesser frequency than they do in pair-bond maintenance sequences. Table 4.4 demonstrates that the frequency composition of the two sequence types is different in some respects. Examination of $\frac{\text{observed}}{\text{expected}}$ scores for each cell suggests that the difference lies mainly with the frequencies of CRLP, σ/Q , ND and ND_{hi} (see Table 4.5 for abbreviations).

A series of 2x2 contingency tables, comparing the number of sequences containing a given display pattern, produces the following results: REU, FT, σ/Q , ND and ND_{hi} occur at a significantly higher frequency than in pair-

TABLE 4.1 FREQUENCY OF PAIR-BOND MAINTENANCE DISPLAY PATTERNS IN SEQUENCES PERFORMED BY THE PAIR AND BY THE MALE ONLY

	display patterns ^a							
	REU	FT	HD	HS	CRLP	ND	OTHER	total
♂ only (N)	8	7	14	15	15	4	4	67
(f)	11.94	10.45	20.90	22.39	22.39	5.97	5.97	
♂ and ♀	24	22	27	36	35	27	15	186
	12.90	11.83	14.52	19.35	18.82	14.52	8.06	
total	32	29	41	51	50	31	19	253

H_0 : no difference exists between ♂ and ♂-only sequences in the frequency of display patterns

$\alpha = 0.01$ $df = 6$ $\chi^2 = 4.9106$

Accept H_0

a: see Table 4.5 for standard behavioural abbreviations

TABLE 4.2 AN EXAMINATION OF THE LINKS BETWEEN
PAIR-BOND MAINTENANCE DISPLAY SEQUENCES
AND OTHER ACTIVITIES

initial data

		act following display sequence					
		REU (R)	aggn ¹ (A)	feed (F)	preen (P)	other (O)	Σ_r
preceding act	REU	1	0	2	1	1	5
	aggn	1	0	2	6	0	9
	feed	0	0	5	0	1	6
	preen	1	0	0	3	0	4
	other	1	0	0	3	1	5
	Σ_c	4	0	9	13	3	29

1: aggression

These data must be manipulated before statistical analysis can be performed, as the observed numbers in many cells are low. D. Drummond (pers. comm.) suggested combining some data on the basis of their $\frac{\text{observed}}{\text{expected}}$ ratios. The data so combined are (REU-aggn-other) and (feed-preen).

A Fisher exact probability test was performed on the resulting table:

	REU-aggn-other	feed/preen	Σ_r
self	2	8	10
other	17	2	19
Σ_c	19	10	29

$$p = 0.00039$$

i.e. there is an extremely low probability that the observed relationship between pair-bond maintenance display and those activities frequently preceding and following the display is a random one; pair-bond maintenance display is frequently preceded and followed by preening and feeding.

TABLE 4.3a FREQUENCY OF OCCURRENCE OF THE BEHAVIOUR PATTERNS SEEN
IN PAIR-BOND MAINTENANCE DISPLAY SEQUENCES (N = 54)

	display patterns ^a											total acts
	REU	FT	HD	HS	CRLP	♂/♀	wing- flap	ND	ND _{hi}	GRE/ TRI	DR	
no. sequences where display seen	32	29	41	51	50	2	8	23	8	7	2	253
frequency (n/54) of display	59.26	53.70	75.93	94.44	92.59	3.70	14.81	42.59	14.81	12.96	3.70	

TABLE 4.3b FREQUENCY OF THOSE BEHAVIOUR PATTERNS SEEN IN COPULATORY SEQUENCES
(N = 82) WHICH ALSO OCCUR IN PAIR-BOND MAINTENANCE SEQUENCES

	display patterns ^a											total acts
	REU	FT	HD	HS	CRLP	♂/♀	wing- flap	ND	ND _{hi}	GRE/ TRI	DR	
no. sequences where display seen	68	79	69	82	41	77	0	81	61	0	0	558
frequency (n/82) of display	82.93	96.34	84.41	100.0	50.00	93.90	0.00	98.78	74.39	0.00	0.00	

a: see Table 4.5 for expansion of abbreviations

TABLE 4.4 COMPARISON OF BEHAVIOUR PATTERNS COMMON TO PAIR-BOND MAINTENANCE AND COPULATORY DISPLAY SEQUENCES

	pair-bond		copulation		total
	observed	expected	observed	expected	
REU	32	29.72	68	70.28	100
FT	29	32.10	79	75.90	108
HD	41	32.69	69	77.30	110
HS	51	39.53	82	93.47	133
CRLP	50	27.05	41	63.95	91
♂/♀	2	23.48	77	55.52	79
ND	23	30.91	81	73.09	104
ND _{hi}	8	20.51	61	48.49	69
total	236		558		794

H_0 : there is no difference in the frequency of behaviour patterns occurring in pair-bond-maintenance and copulation sequences.

$$\alpha = 0.01 \quad df = 7 \quad \chi^2 = 77.8250 \quad \text{reject } H_0$$

At least some cells vary from the values expected under H_0 . From examination of $\frac{\text{observed}}{\text{expected}}$ values these appear to be CRLP, ♂/♀, ND, and ND_{hi}. A series of 2x2 χ^2 tables, comparing the number of sequences having a given display pattern, produces the following results ($\alpha = 0.01$, $df = 1$): REU, FT, ♂/♀, ND, ND_{hi} occur significantly more often than expected ($p < 0.01$ for REU, $p < 0.001$ for all others) in copulatory sequences, while CRLP occurs significantly more often ($p < 0.001$) in pair-bond maintenance sequences. (See Table 4.5 for expansion of abbreviations.)

NOTE: pair-bond maintenance displays are brief, intimate sequences performed by already-bonded birds. They comprise acts seen early in pre-copulatory sequences but do not proceed further.

TABLE 4.5 EXPANSIONS OF ABBREVIATIONS USED IN
CHAPTER 4 (Descriptions given in Ch.4,
unless stated otherwise)

Abbreviation	Expansion
ALU	Alert-Upright: vigilant posture (Ch. 2)
CALL	Post-copulatory call
CRLP	Cheek-Rub-Lateral-Preen: precopulatory act
DR	Drink (general term; no description)
FT	Facing-Together: precopulatory
GRE	Greeting ceremony
HD	Head-Dip: precopulatory
HS	Head-Shake: precopulatory
MO	Mounting: copulation
NCO	Necks-Curved-Over: occurs in both TRI and copulatory display; post-copulatory
ND	Neck-Dip: has low (ND) and high (ND _{hi}) intensities; precopulatory
NOS	Necks-Outstretched: post-copulatory
NPP	Nibble-Preen-Partner: precopulatory
PAR	Parade: high-intensity threat used in boundary disputes (Ch. 3)
PP	Post-copulatory preening
REU	Relaxed-Upright: vigilant posture (Ch. 2)
THR _{lo, me, hi}	Low-, medium-, and high-intensity threat displays (Ch. 3)
TRE	Treading: copulation
TRI	Triumph ceremony
TRU	Trumpet: threat display (Ch. 3)
♂/♀, ♀/♂	♂ neck crosses base of ♀'s, or vice versa, during HD or ND
♀PRO	♀ in prone position, for mounting

bond maintenance sequences, while the reverse is true for CRLP (Table 4.4).

4.3.3 Copulation

A large number of displays, and temporally-related non-display behaviour patterns, are involved in copulation.

4.3.3a Behaviour patterns of copulation

A. Precopulatory display

- (a) Neck feathers are fluffed, giving the neck a bloated appearance, up to and including the post-copulatory call.
- (b) Head-Dip (HD): the head is lowered and dipped briefly into the water (Fig. 4.3a).
- (c) Neck-Dip (ND): occurs at two intensities. In the lower of these (ND) only the neck is immersed, dipping near-horizontally under water. At higher levels of excitement (ND_{hi}), both neck and shoulders are plunged forward under water. The movements are similar to the plunging seen when swans are bathing (Fig. 4.3b).
- (d) Head-Shake (HS): occurs after HD and ND. Seen as the head is raised from the water, it is slower than head-shakes seen in normal (preening) situations (Fig. 4.3c).
- (e) Male-neck-over-female (σ/Q): at times the σ may perform HD or, more usually, ND, with his neck over the base of the Q 's. In NDs the Q is often pushed down into the water. This situation is reversed in some copulations, with the Q 's neck crossing the σ 's, but the more usual σ/Q is given before mounting occurs. σ/Q may stimulate the Q to enter the prone position, prior to mounting (Fig. 4.3d).
- (f) Facing-Together (FT): occurs between HD, ND and/or ritualised preening. The partners face each other with a slow deliberate movement, necks and heads in the Alert-Upright (ALU) posture but with necks fluffed

and heads slightly below horizontal (Fig. 4.4a).

- (g) Cheek-Rub-Lateral-Preen (CRLP): this is a slow preening movement, rolling the head as well as moving head and neck backwards and forwards along one side - not necessarily the side closest to the mate (Fig. 4.4b).
- (h) Nibble-Preen-Partner (NPP): occasionally the ♂ nibbles at the base of the ♀'s neck, often while she performs ND. This is similar to the action of grasping the ♀'s neck prior to treading, except that the base, rather than the middle of the neck, is held (Fig. 4.4c).
- (i) Female Prone (♀PRO): instead of rising up from a ND the female remains prone on the water, with neck outstretched. She may actively manoeuvre herself under the ♂. Mounting does not always follow immediately after ♀PRO (Fig. 4.4d).

B. Copulation

- (j) Mounting (MO): usually occurs after the ♀ has entered the ♀PRO position, although a ♂ may attempt to MO before his mate is ready. The ♂ pushes himself onto her back, seizes her neck (usually in the middle: 73/76 treadings) with his bill, and tail-wags (TW) to evert his penis. The ♀'s tail is lifted, facilitating cloacal contact; her body and neck are submerged (Plate 4.1).
- (k) Treading (TRE): intromission is signalled by several downward-&-forward thrusts of the ♂'s tail. At the same time the ♀ begins to raise head and neck out of the water (Fig. 4.5a).

C. Postcopulatory display

- (l) Postcopulatory call (CALL); this and one or both of the two following displays occur if TRE is successfully completed. Either sex may call first, or else the ♂ and ♀ begin calling together. The number of calls varies from 2 to 12 (Fig. 4.6a; Plate 4.2).

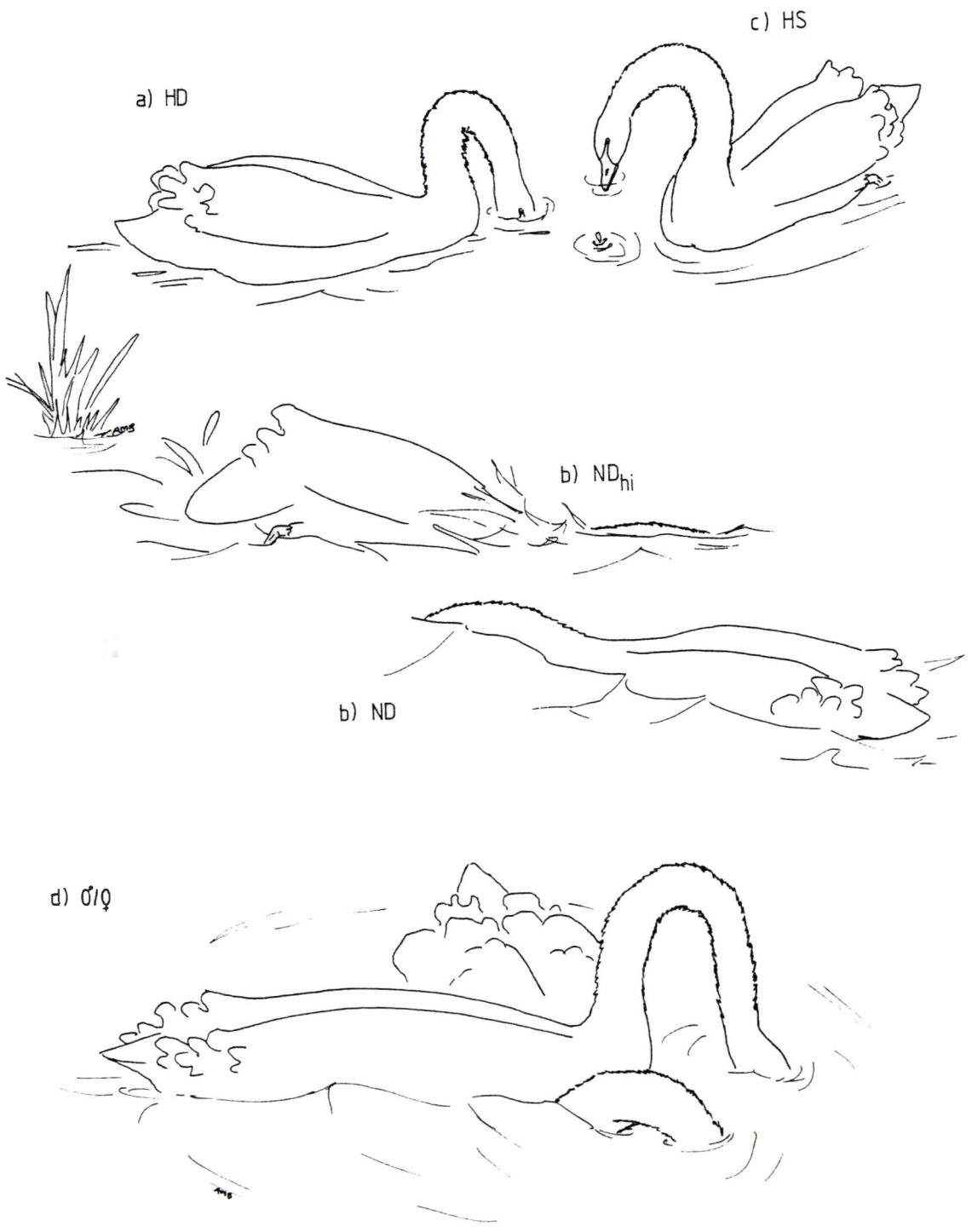
FIGURE 4.3: Precopulatory display

(a) Head-Dip

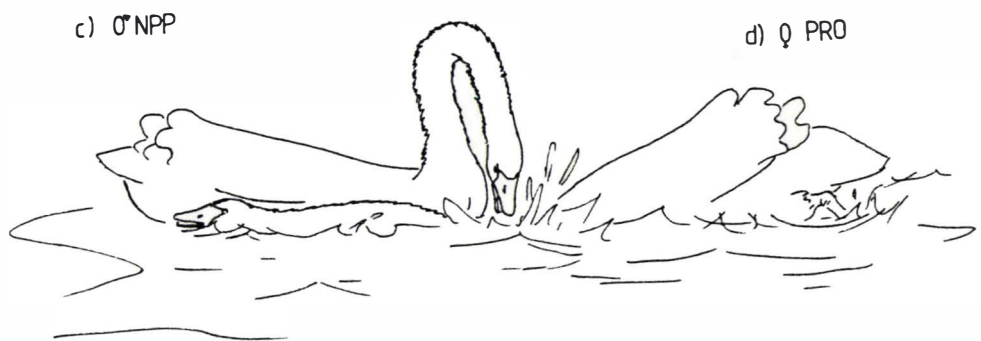
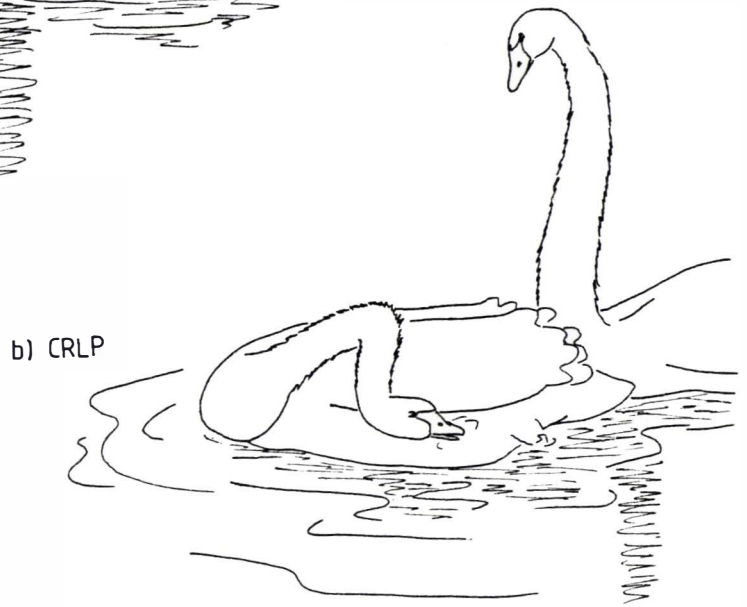
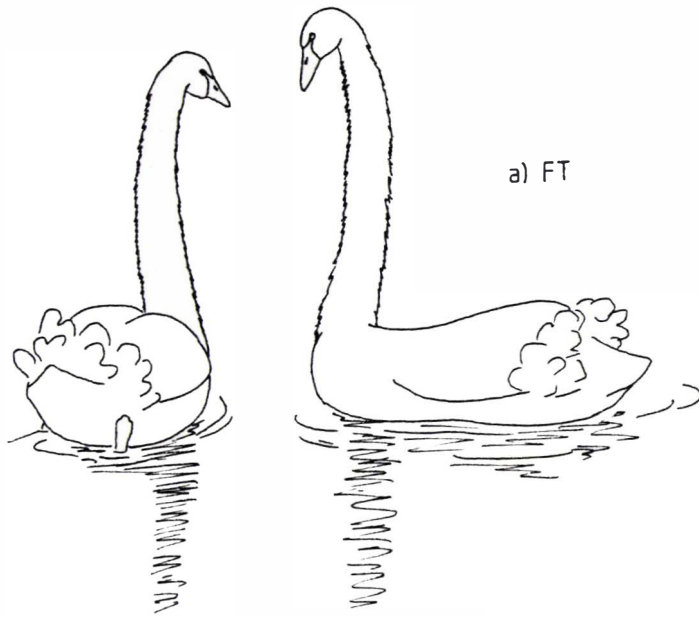
(b) Neck-Dips, low and high intensity

(c) Head-Shake

(d) ♂ neck over female's



- FIGURE 4.4: Precopulatory display
- (a) ♂ and ♀ Facing-Together
 - (b) Cheek-Rub-Lateral-Preen
 - (c) ♂ reaching to Nibble-Preen-Partner
on neck
 - (d) ♀ entering Prone position



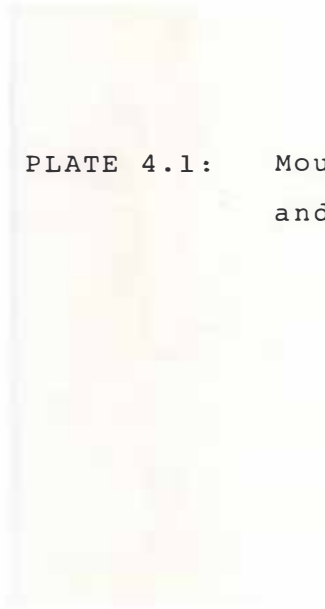


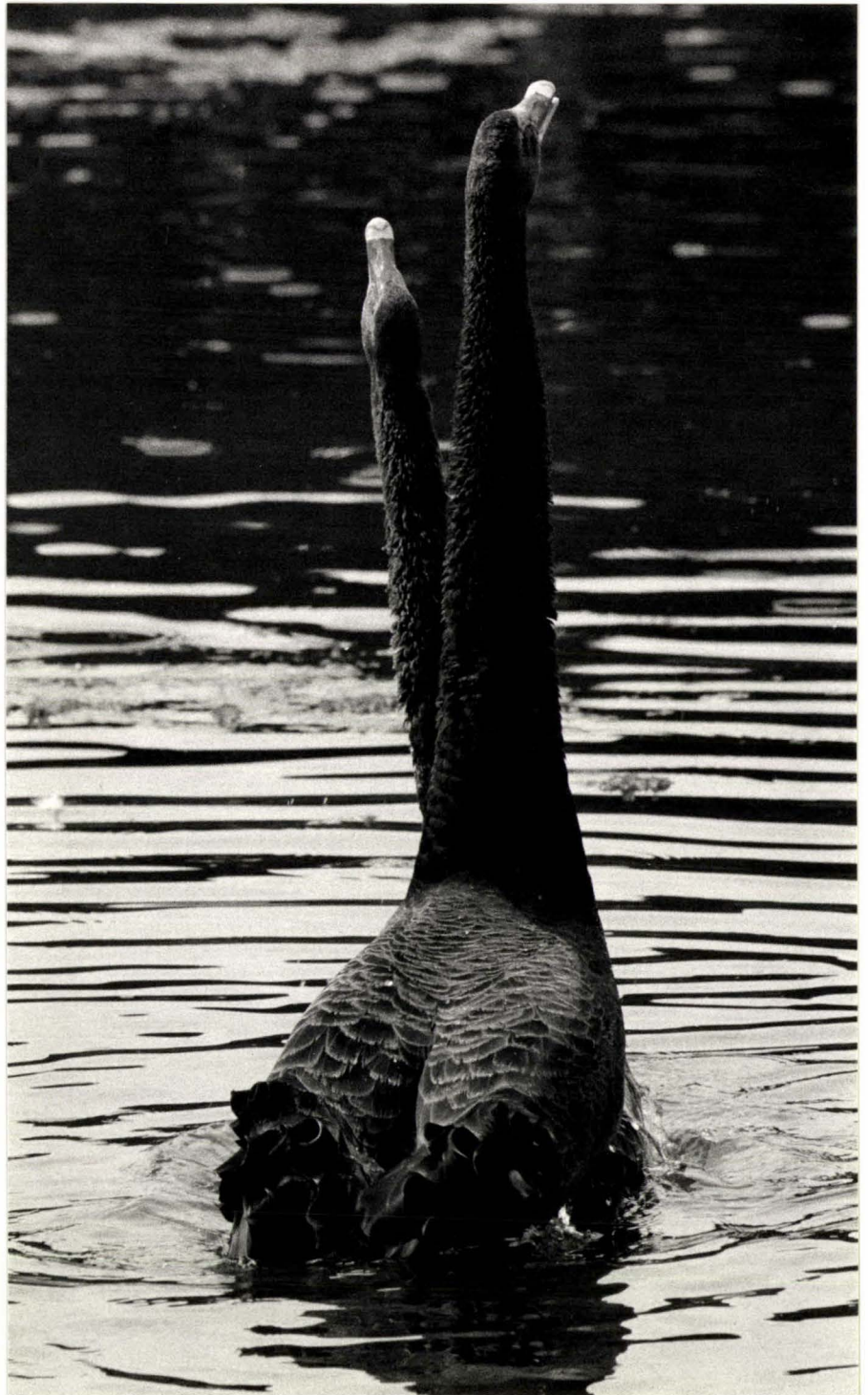
PLATE 4.1: Mounting (MO), with the male on the female's back
and tail-wagging to evert his penis



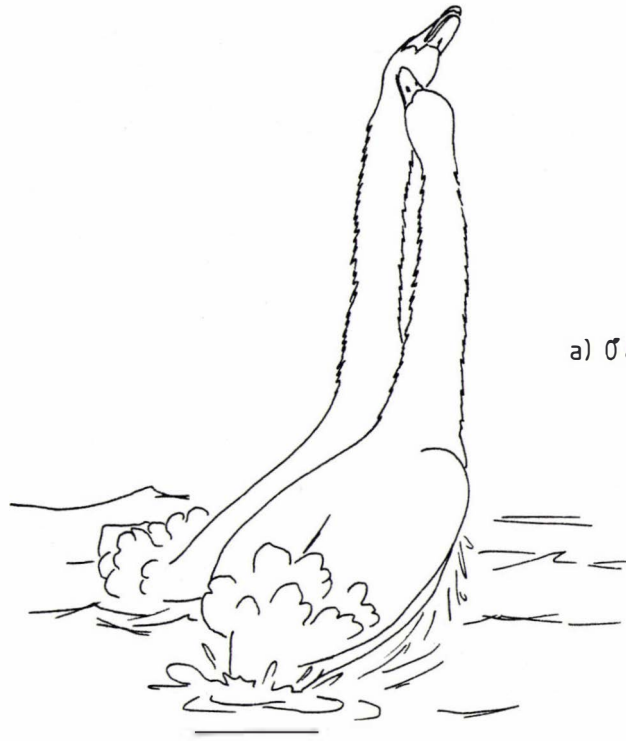


FIGURE 4.5: Treading

PLATE 4.2: Post-copulatory Call (CALL), with
the male closer to the camera



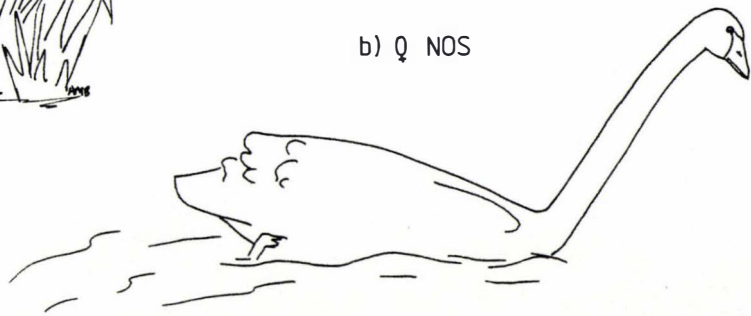
- FIGURE 4.6: Post-copulatory display
- (a) Post-copulatory Call by ♂ and ♀
 - (b) Neck-Outstretched (♀)
 - (c) Neck-Curved-Over (♂)



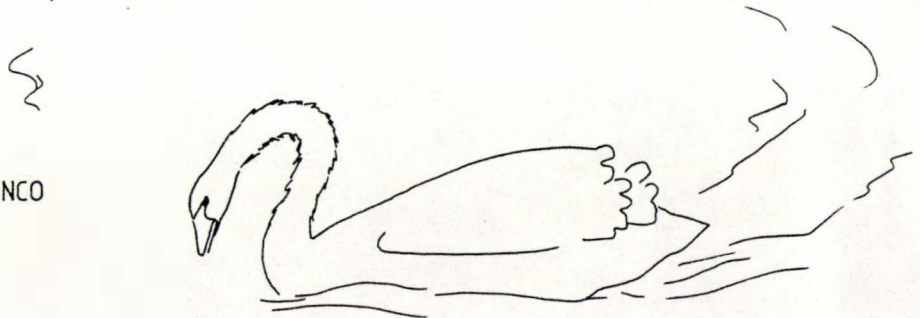
a) ♂ & ♀ CALL



b) ♀ NOS



c) ♂ NCO



- (m) Necks-Outstretched (NOS): after CALL the partners swim in a circle about each other, necks outstretched at about 45° below vertical and heads horizontal or pointing downwards (Fig. 4.6b).
- (n) Necks-Curved-Over (NCO): replaces or precedes NOS in a small proportion of matings (26.50%: 30/117 sequences with sufficient data for analysis), usually when other swans are close by. Male and female sit facing each other, or swim in a circle, with necks curved well over and bills pointing to the water. This display may be performed by the σ° only, while the ϕ gives NOS (Fig. 4.6c).

Subsequently the pair becomes more relaxed, usually passing through the ALU posture, and then commences preening and bathing. Preening starts at the cloacal region and then becomes more generalised. There is some uncertainty as to whether postcopulatory bathing is "a normal, functional response or ... an irrelevant activity" (McKinney 1965).

4.3.3b Sequence of events during copulation

A Black Swan pair intending to copulate swims apart from other birds, in a particularly erect posture and with their neck feathers starting to fluff. Other swans rarely approach with the apparent intent of disrupting the copulation, but may feed or watch nearby. The sequence of events in a copulation is shown diagrammatically in Fig. 4.7. Once a copulation reaches the stage of $ND\sigma^{\circ}/\phi$, it is usually completed. (See Table 4.5 for abbreviations.)

4.3.3c Duration of sequences

Data on duration are available for only 18 pair-bond maintenance sequences (\bar{x} = 125.56 seconds, range 30-240 secs., standard deviation 67.49 secs.). When compared with 18 randomly-selected copulations (\bar{x} = 322.00 secs., range 90-585 secs., s.d. = 114.99 secs.), it is apparent that copulations are considerably longer than the pair-bond

sequences, since there is no overlap of standard deviations.

4.3.3d σ and Q involvement

Both σ and Q displayed in all those copulatory sequences where at least a part of the pre-mounting sequence was observed (N = 98 of 127).

4.3.3e Context

Four copulatory sequences immediately followed aggression involving the mating pair. Preening and/or feeding preceded all others where the preceding activity was known. Four, different, matings were followed by aggression towards or by the pair, while preening bouts of variable length followed all others.

4.3.3f Composition of copulation sequences

The total number of behaviour patterns is greater than that seen in pair-bond maintenance. For some acts variations in form are apparent, which may in some cases depend on the presence or actions of other swans.

Table 4.6 shows that some behaviour patterns, or variations of them, occur in less than 50% of copulations. These are σ/Q (N = 27, 32.93%), NPP (N = 21, 25.61%), TRE with wings drooped about the Q (10, 12.19%), and σ holds base of Q neck during TRE (3, 3.66%). There is also some variation in the sex of the first to give CALL and the first to preen after TRE.

Table 4.7 investigates an apparent relationship between the presence or absence of other swans and the pair's performance of NOS or NCO as a postcopulatory display. The analysis shows a significant relationship ($p < 0.001$) between the presence of other swans and the performance of NCO, or NCO and NOS, by one or both members of the pair, while NOS alone occurs more often in the absence of other birds. The activities of the onlookers may also be important:

feeding or threatening was associated with NCO by the pair, while NOS was given if the others were drinking or preening.

4.3.3g Transition analysis of copulation sequences

The overall sequence of events in a copulation is shown diagrammatically in Fig. 4.7. There is a change as the sequence proceeds from the relatively low-intensity displays of HD, FT and CRLP to the higher-intensity ND, ND_{hi} and σ/Q prior to TRE. FT regularly occurs between the other acts (Fig. 4.7; Appendix IV).

Eighty-two of the total matings recorded contained sufficient data to permit a transition analysis of the effects of σ actions on Q behaviour, and *vice versa*. The method used is described by Radesäter (1975a). It is of particular interest in determining the possible function and derivation of such behaviour patterns as NPP and σ/Q . For example, a positive significant link between σ/Q and $QPRO$ would suggest that the σ display does stimulate the Q to become prone.

The results of this analysis are given in Appendix IV. Note that the cells are not independent of each other, since the same marginal totals (which in some cases are very high and inflate expecteds accordingly) are used in the calculation of a number of expected values. This decreases the power of the test. Only the left-right and right-left diagonals in each table are fully independent.

The data are more easily interpreted in the form of Table 4.8, a&b, which indicates that the Q tends to duplicate σ actions during the sequence, while σ actions following a given Q behaviour pattern are much more variable. Thus, up to the point where the Q is ready to enter $QPRO$, the patterning of a precopulatory sequence is initiated by the σ and confirmed by the Q . If the Q responds suitably to a display (i.e. with a similar display) the σ goes on with the sequence. The forms of the post-TRE displays are

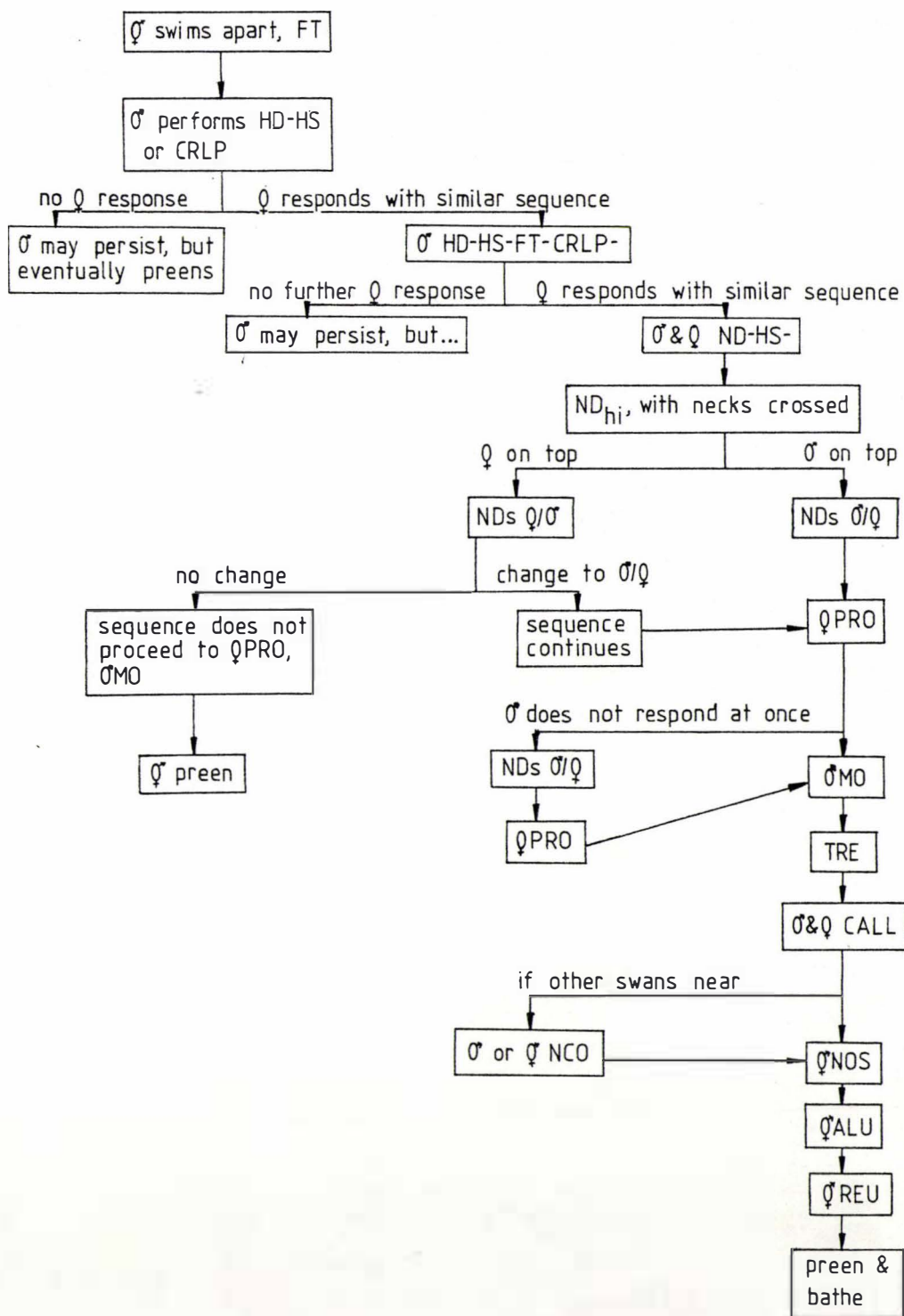


FIGURE 4.7: Diagrammatic representation of events in a copulatory sequence (see Table 4.5 for abbreviations)

TABLE 4.6 DISPLAYS OCCURRING IN 82 COPULATORY SEQUENCES
(Data also used in transition analysis)

behaviour pattern	number of sequences where behaviour seen	proportion of sequences including behaviour
other swans	{ not recorded 8	9.75
	{ present 27	32.93
	{ absent 47	57.32
HD	69	84.41
HS	82	100.00
ND	81	98.78
ND _{hi}	61	74.39
♂/♀	77 ¹	93.90
♀/♂	27	32.93
CRLP	41	50.00
NPP	21	25.61
FT	79	96.34
♀PRO	79 ²	96.34
MO	78 ²	95.12
TRE	66 } 76 ³	80.49
TRE, wings drooped	10 }	12.19
holds base ♀ neck	3	3.66
holds mid-♀ neck	73	89.02
♀CALL	54	68.85
♂CALL	53	64.63
♀CALL	23	28.09
NCO ♂ only	11 } 24*	13.41
NCO ♀	13 }	15.85
NOS ♂ only	1 } 73*	1.22
NOS ♀ only	2 }	2.44
NOS ♀	70 }	85.36
NCO & NOS	21*	25.61
tail-wag	76	92.68
REU	68	82.93
ALU	64	78.05
PP ♂ first	27 } 79 ⁴	32.93
PP ♀ first	27 }	32.93
PP ♀	25 }	30.49

TABLE 4.6 cont'd.

Notes:

Expansions of all abbreviations are given in Table 4.5

- * : 76 sequences have either NCO or NOS or both, as an end-posture.
- 1 : In two of five sequences where σ/Q was absent there was no TRE, although mounting did occur in one; Q/σ occurred in the other. In all other sequences where Q/σ was seen, there was a change to σ/Q before mounting.
- 2 : Multiple MO attempts occurred in seven sequences, multiple $QPRO$ in 17, and multiple NPP in nine sequences. Multiple MO and $QPRO$ occurred together in four sequences, NPP and $QPRO$ in two, and MO NPP and $QPRO$ in one.
- 3 : For those six sequences where no NCO or NOS was recorded,
 - in one there was no TRE because of interruption by other swans;
 - in one there was no TRE but the σ preened (NPP) the Q 's cloaca and $QCALL$ followed;
 - in two the precopulatory sequence was prolonged, with much preening, but no TRE occurred;
 - in two MO and the following behaviour patterns were not seen, although CALL was heard and the pair was seen preening.
- 4 : The total number of post-copulatory preenings was 79, plus three completed copulations where no PP occurred, while the total number of TREs was 76. The discrepancy may be explained by
 - one case where there was no TRE, but $QCALL$ followed σNPP (see 1 above);
 - two instances where the actual TRE was unseen but CALL and PP were seen and heard.

TABLE 4.7 AN EXAMINATION OF THE RELATIONSHIP BETWEEN THE PRESENCE OF OTHER SWANS AND THE PERFORMANCE OF NCO AS A POST-COPULATORY DISPLAY

initial data

	others present	others absent	total
NCO only	8	0	8
NCO & NOS	17	6	23
NOS only	15	51	66
total	40	57	97

This may be reduced to a 2x2 table for χ^2 analysis, as follows:

	others present	others absent	total
NCO seen in sequence	o^1 25 e^2 12.78	6 18.22	31
no NCO; NOS only	15 27.22	51 38.78	66
total	40	57	97

1 : observed value

2 : expected value; calculated from marginal totals

H_0 : the performance of NCO is not dependent on the presence of other swans near the copulating pair.

$$\alpha = 0.01 \quad df = 1 \quad \chi^2 = 29.22 \quad p < 0.001$$

Reject H_0 .

TABLE 4.8a TRANSITION ANALYSIS OF σ - σ INTERACTIONS
DURING COPULATION

σ act	subsequent σ act																
	HD	HD/ σ	ND	ND/ σ	ND _{hi}	ND _{hi} / σ	REU	ALU	FT	CRLP	PP	QPRO	QCALL	QCALL _{act}	NCO	NOS	other
HD	+						+			+							
HD/ σ	+		+														
ND	+		+	+						+							
ND/ σ			+	-	-							+					
ND _{hi}					+												
ND _{hi} / σ																	
REU			+				+				+						
ALU								-		+							
FT	-	-						-	+								
CRLP							+			+							
PP											+						
NPP			+														
MO												+					
TRE												+	+				
QCALL													+				
QCALL _{act}														+			
NCO	-														+		
NOS																+	
other																	+

+ : diad occurs significantly more often than expected

$\alpha = 0.01$ $df = 1$

- : diad occurs significantly less often than expected

TABLE 4.8b TRANSITION ANALYSIS OF Q-Q' INTERACTIONS
DURING COPULATION

Q act	subsequent Q' act																			
	HD	HD/Q	ND	ND/Q	ND _{hi}	ND _{hi} /Q	REU	ALU	FT	CRLP	PP	NPP	MO	TRE	QCALL	Q'CALL	NCO	NOS	other	
HD	+																			
HD/Q																				
ND		+		+	-			-	+	-			-	-	-	-			-	
ND/Q																				
ND _{hi}			-	-	+				+	-	-		-	-						
ND _{hi} /Q																				
REU							+				+	+								
ALU			-	-			+	+	-		+	+								
FT		+	+	+	+	+	-	-	-		-	-		-	-	-	-	-	-	-
CRLP	+	-		-			+			+										
PP											+									
QPRO	-		-	-	-		-	-	-	-	-		+	+		+				
QCALL	-		-	-											+		+	+	+	
Q'CALL																				+
NCO																				+
NOS			-	-			+	+	-											
other																				-

+ : diad occurs significantly more often than expected

$\alpha = 0.01$ $df = 1$

- : diad occurs significantly less often than expected

also set by the σ , at least with respect to the alternatives NCO and NOS. After relaxing through ALU and/or REU, either sex may initiate preening and bathing. The φ would be expected to do so more often, as she has experienced a greater degree of stimulation through feather-wetting and disarray, but this is not the case: Table 4.6. This is reflected in the positive association between REU, ALU and postcopulatory preening (PP) for both sexes.

The consequences of NPP, σ/φ and φ/σ are of interest. The first display is followed by φ PRO no more frequently than would be expected on a random basis but does lead to φ ND ($p < 0.001$). σ/φ may be followed significantly often by φ HD, ND or ND_{hi}, or by φ PRO ($p < 0.01$, $p < 0.001$, $p < 0.001$ respectively), and may signify σ readiness to mount. Similarly, φ PRO, performed far more often (notes to Table 4.6) than either MO attempts or TRE, probably indicates φ readiness for copulation. φ/σ has significant positive links only with σ FT ($p < 0.001$).

A large number of diads occur significantly less often than expected. The reason for many such is clear: post-TRE patterns would hardly be linked with precopulatory displays. The nature of those negatively-dependent diads remaining bears out the earlier finding that it is the σ who initiates sequences and the φ who, if willing, follows his patterning.

4.3.4 Daily and seasonal frequency of breeding activity

4.3.4a Daily

Data from each display type for the complete study period were combined in this analysis.

The raw data show a peak in numbers between 1200 - 1400h. for the pair-bond maintenance display and between 1100 - 1300h. for copulatory activity. This pattern of activity is still seen when the data are adjusted to compensate for the differing number of hours in each observation period (Fig. 4.8).

Lumping data in this manner may hide any seasonal patterning they possess. However, when data for copulations are broken down into seasonal groupings (Fig. 4.9), those in Spring and Summer are too few ($N = 15$ and 10 respectively) for analysis of whole-day patterns. (Observed pair-bond maintenance patterns are too few for this analysis.) This numerical restriction still holds when the hourly data in each season are combined into thirds-of-days: morning, middle-day, and evening (see Ch. 2). When Spring and Summer ("non-breeding") and Autumn and Winter ("breeding") are combined it becomes possible to compare parts of the day and examine them for differences in the distribution of copulatory activity, which might possibly be related to quality and/or quantity of food supplies and hence to time spent feeding and in other activities. However, no differences are apparent (Table 4.9: $\alpha = 0.01$, $df = 2$, $\chi^2 = 2.4147$; NS).

The patterning of pair-bond and copulatory display is possibly related to other activities in the time-budgets of the birds involved. No adequate time-activity budget data are available for breeding pairs. Data for flock birds' time-activity budgets are available (Ch. 2) and may be used as an overall estimate of the population's activities, as a relatively large number of flock birds is present and visible throughout the year. However, there is no apparent seasonal patterning of daily activity, in the six activity classes considered (alert, feed, preen, doze, aggression, other), which may be related to the distribution of mating behaviour. Some exogenous factor, such as light intensity (lux) may have had some effect.

4.3.4b Seasonal distribution

Figure 4.10 presents pair-bond maintenance and copulation counts, as total counts per month and corrected for the number of hours' observation in each month. A seasonal distribution of behaviour is apparent for both, with major peaks in August 1978 and July 1979 for pair-bond maintenance displays and July of both years for copulations.

FIGURE 4.8a: Occurrence of pair-bond maintenance displays over a day (total data)
 (i) displays per hour as % of total displays
 (ii) displays per hour of observation

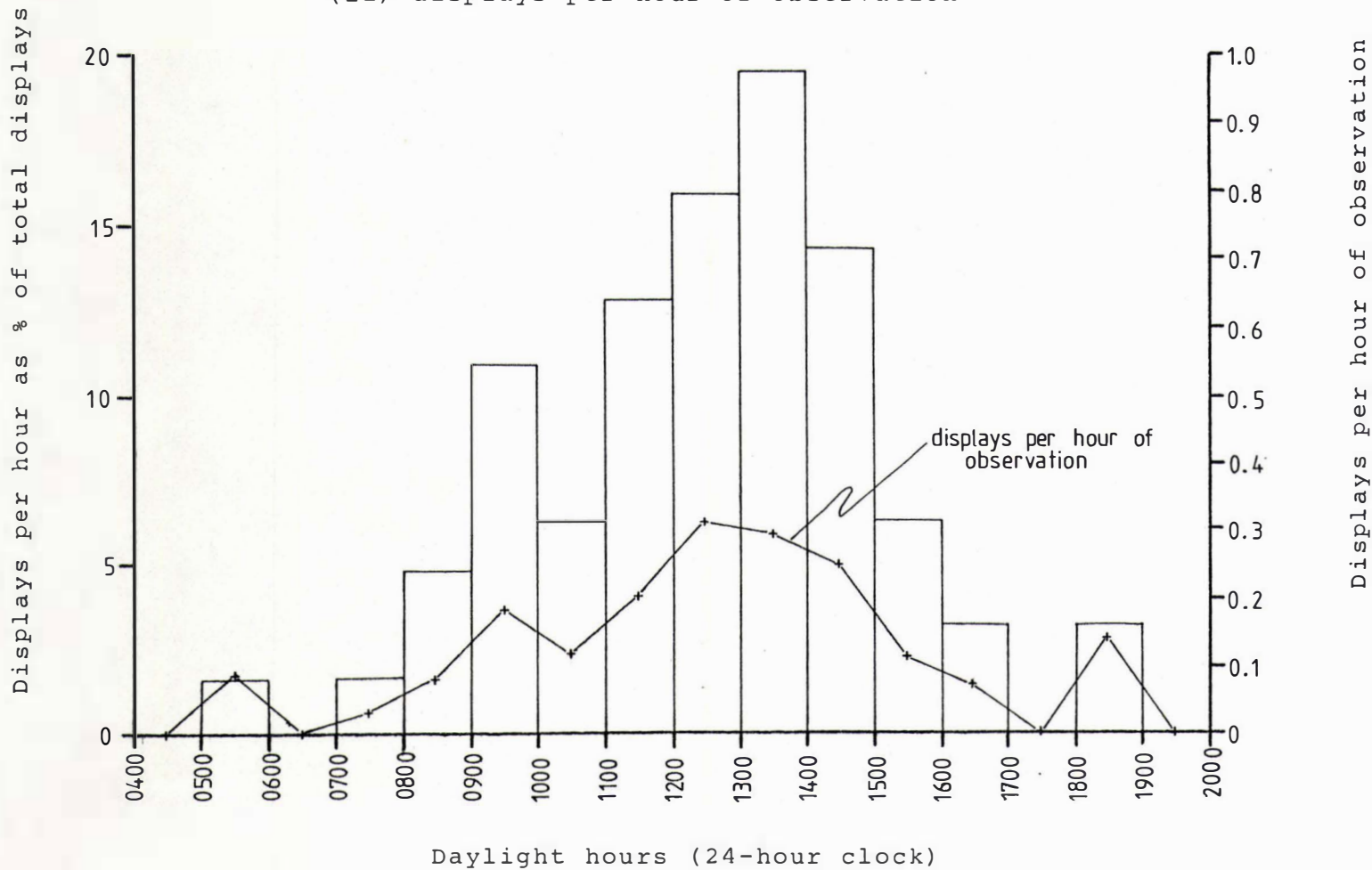


FIGURE 4.8b: Occurrence of copulations over a day (total data)
 (i) displays per hour as % of total displays
 (ii) displays per hour of observation

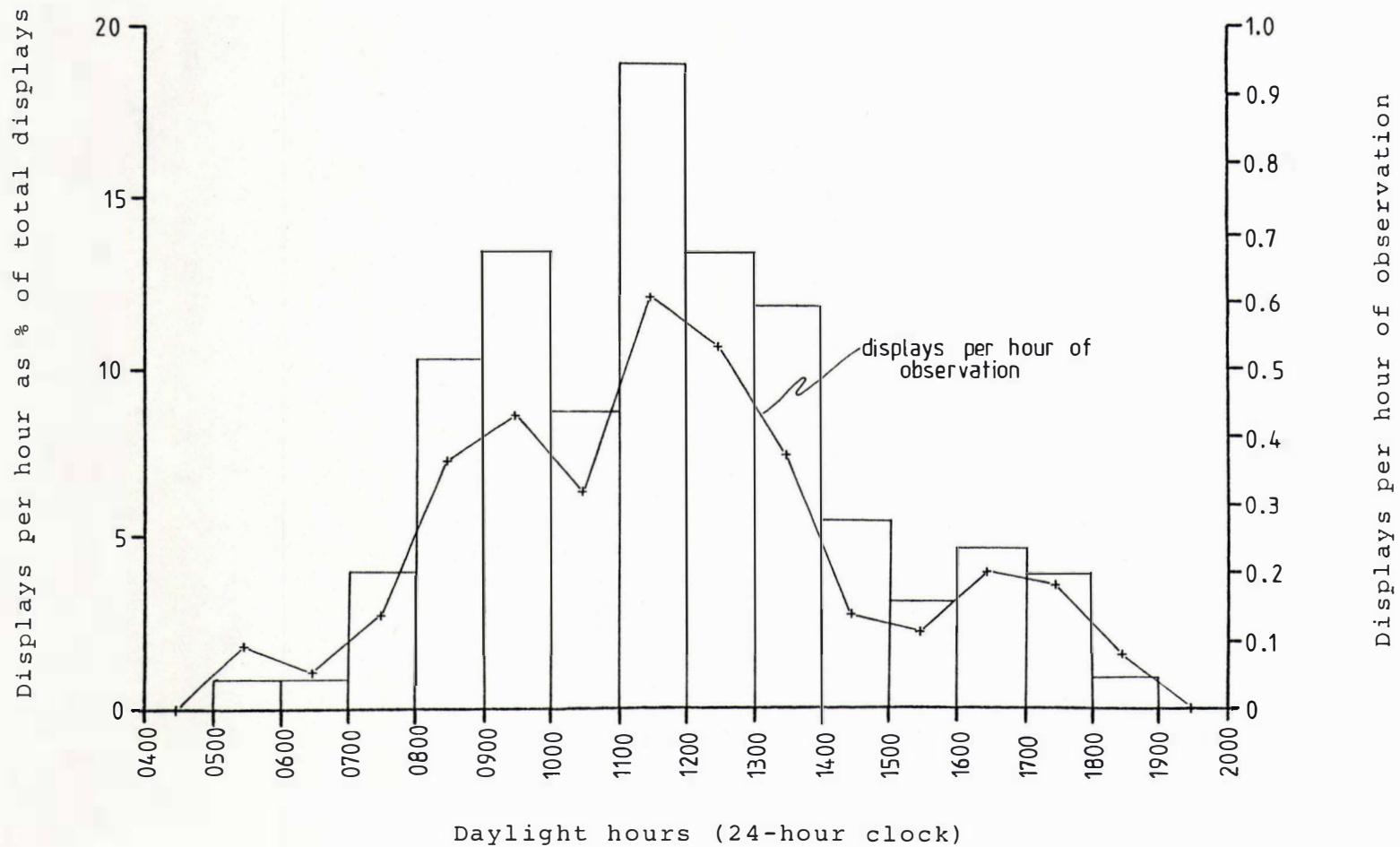


FIGURE 4.9: Spread of copulations over the hours of daylight, in each season

- a) Summer (N. copulations = 10)
- b) Autumn (N. = 34) c) Winter (N. = 68)
- d) Spring (N. = 15)

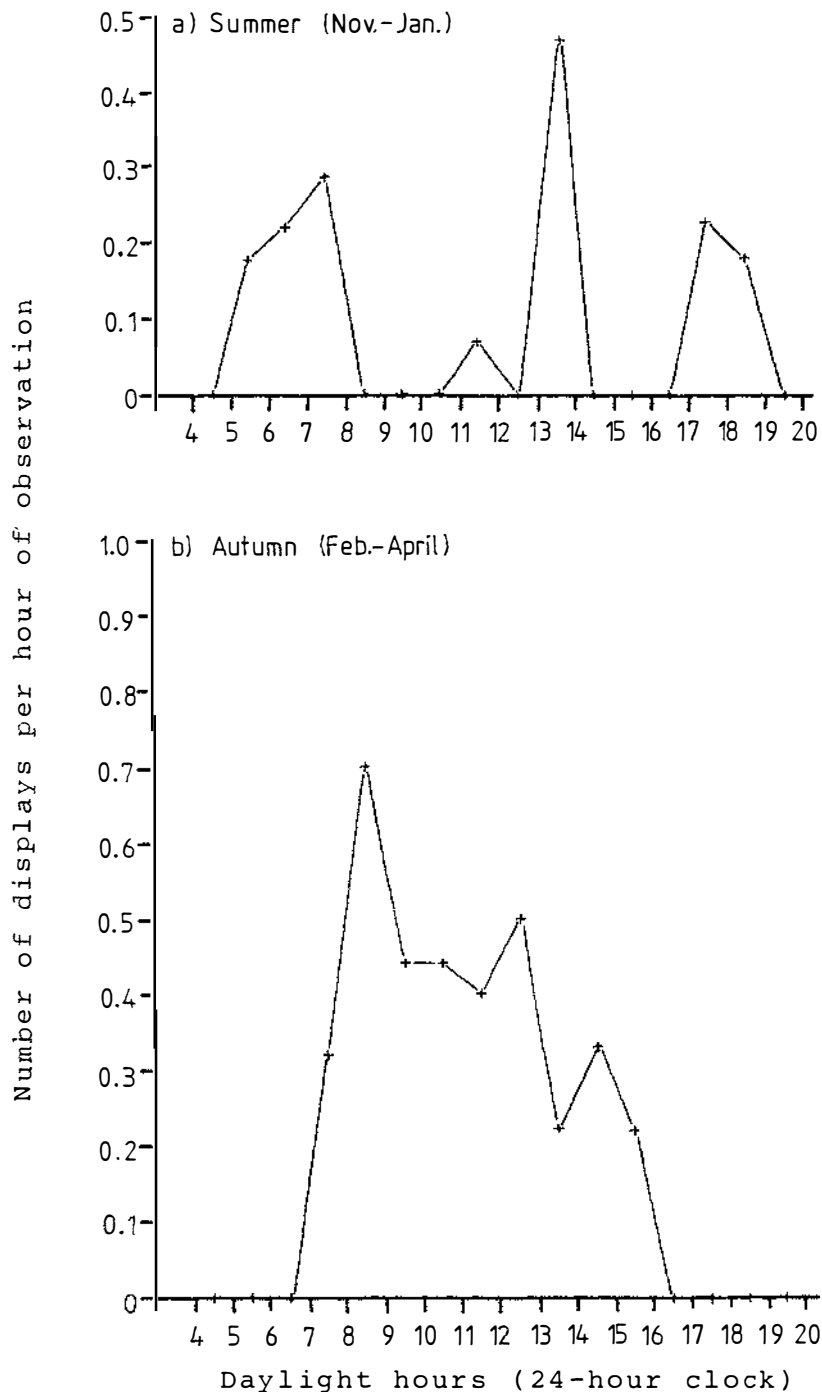


FIGURE 4.9 cont'd.

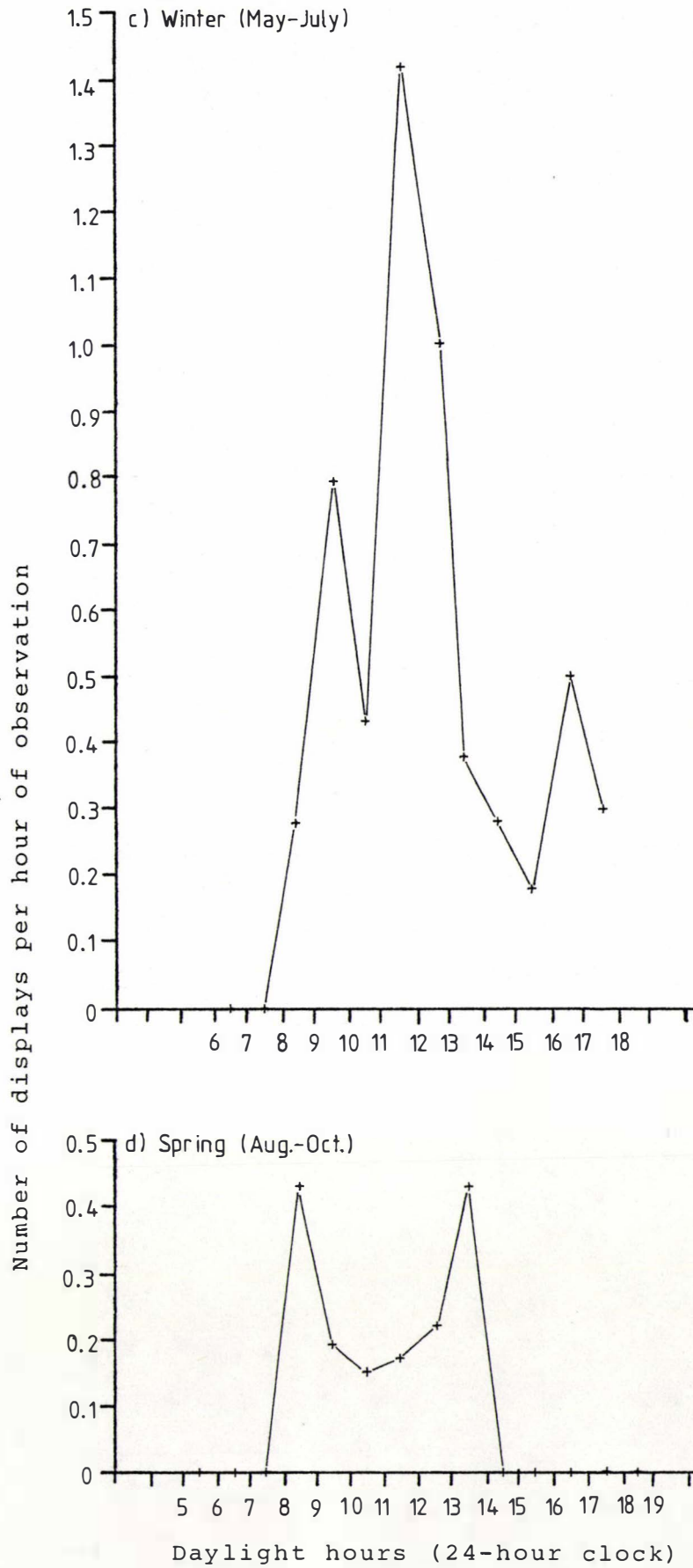


TABLE 4.9 DISTRIBUTION OF COPULATIONS OVER A DAY:
BREEDING AND NON-BREEDING SEASONS

	Non-breeding (summer & spring)		Breeding (autumn & winter)	Total
morning	o^1	9	24	33
	e^2	6.50	26.50	
mid-day		14	60	74
		14.57	59.43	
evening		2	18	20
		3.94	16.06	
Total		25	102	127

H_0 : no difference exists between non-breeding and breeding seasons in the distribution of copulations over a day.

$$\alpha = 0.01 \quad df = 2 \quad \chi^2 = 2.4147$$

Accept H_0

1: observed value 2: expected value

FIGURE 4.10a: Occurrence of pair-bond maintenance displays over the study period
 (i) displays each month as % of total displays
 (ii) displays per hour of observation

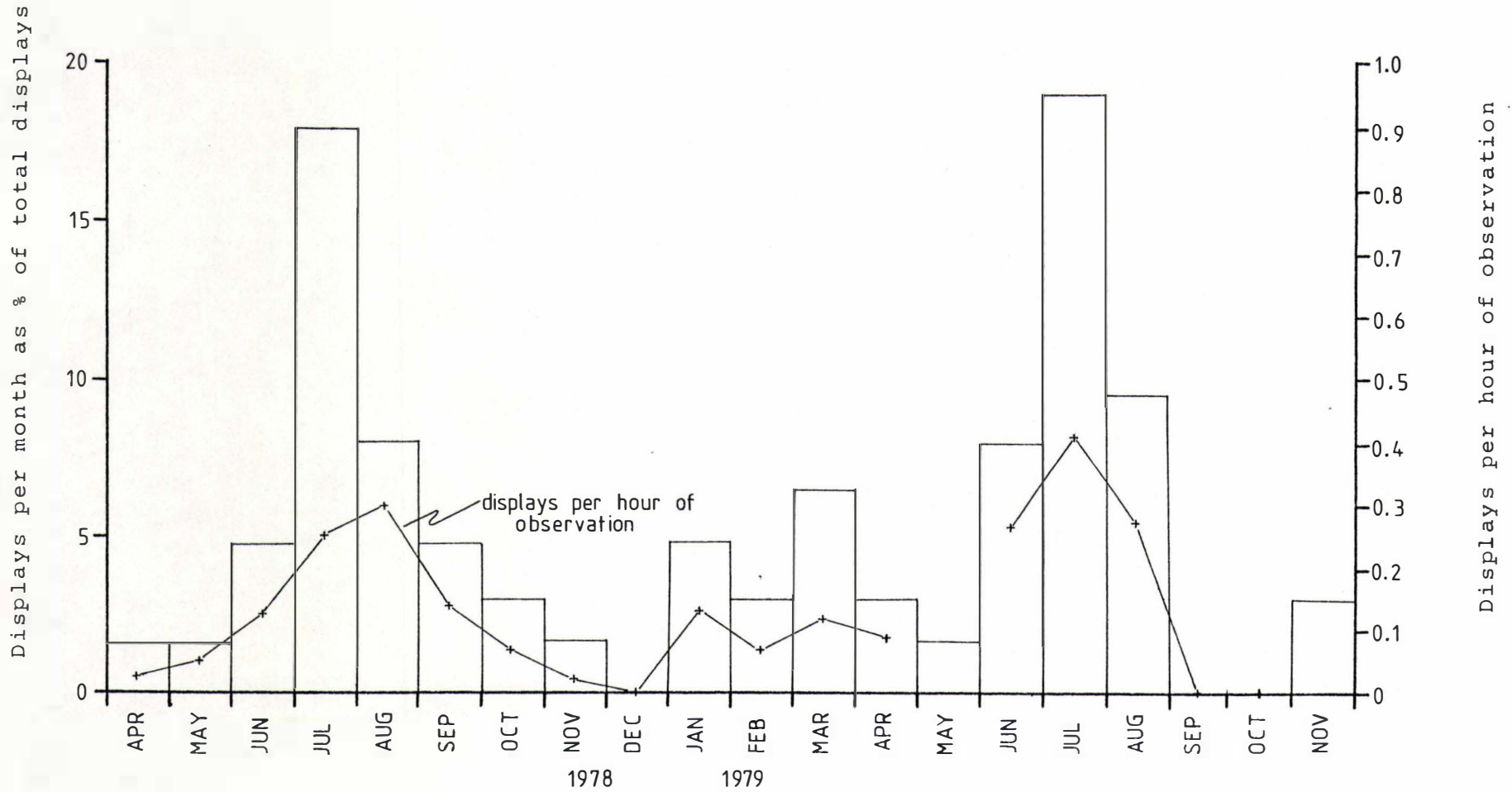
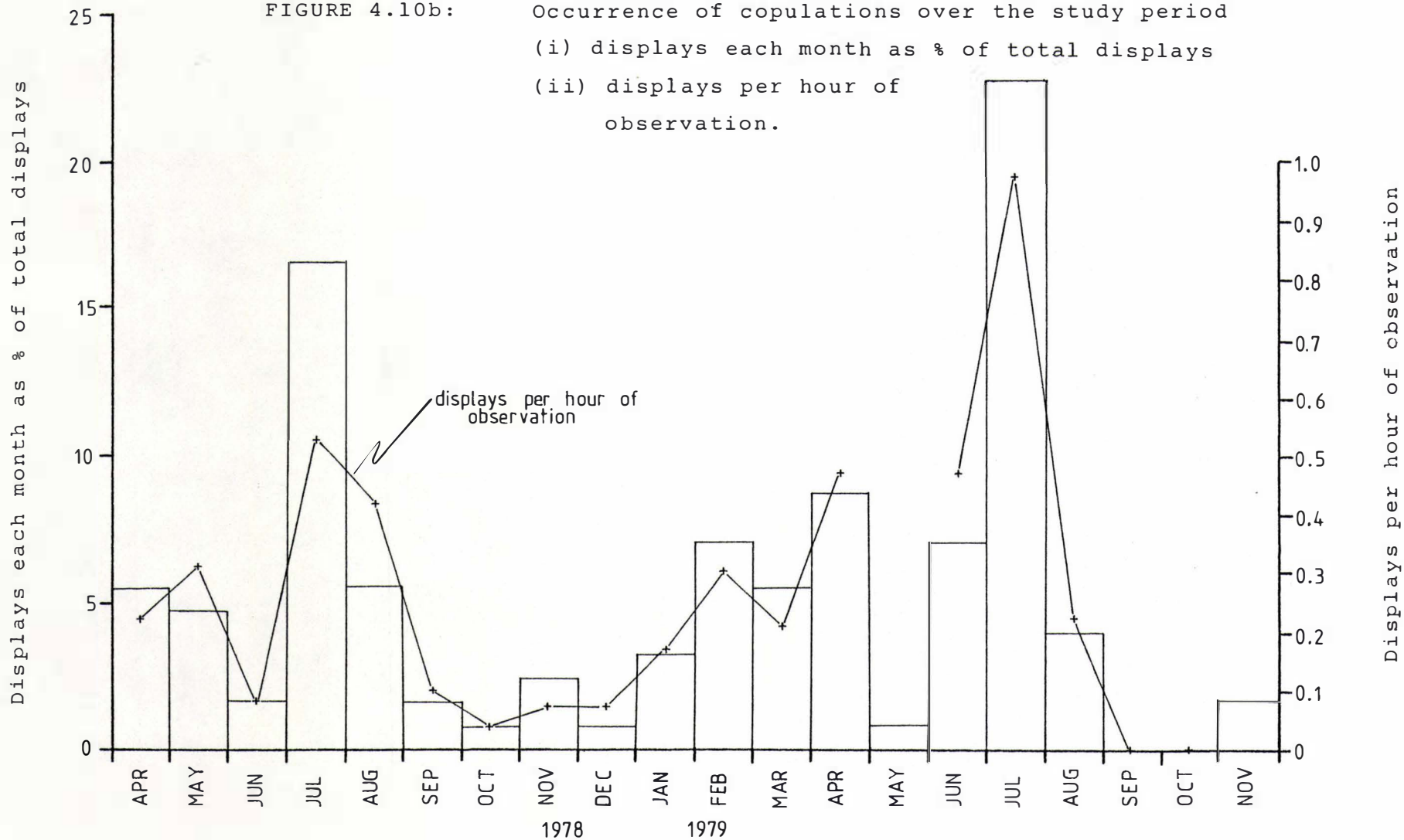


FIGURE 4.10b: Occurrence of copulations over the study period
 (i) displays each month as % of total displays
 (ii) displays per hour of observation.



4.4 DISCUSSION

4.4.1 Pair formation

Where Black Swans breed on discrete territories, as on Pukepuke Lagoon, a strong monogamous pair bond, with shared responsibilities for territorial defence and clutch and brood care, is necessary for successful breeding. In contrast, in colonial-nesting swans pair bonds may be weak and breeding associations other than the monogamous pair may prevail (Braithwaite 1970, 1981b).

In most anserines pairing occurs in large overwintering flocks, so that birds are ready to commence breeding on arrival at the nesting area. This is important in those species which nest in arctic or sub-arctic regions, where the breeding season is short. Even in the Mute Swan, which nests in temperate zones, the chances of finding a mate are enhanced if single birds enter the winter flocks (Minton 1968). However, in the Black Swan mate selection may also occur after the young birds arrive on the breeding grounds (Braithwaite & Frith 1969b). This was the case in the one incident of courtship I observed on Pukepuke Lagoon, in the early autumn of 1979.

A number of criteria are involved in mate selection (McKinney 1975). Skill and persistence in courtship, physical condition, attentiveness and compatibility, and copulatory efficiency can all be measured by prospective mates in both flock and territorial situations. Data on age and physical condition are derived from feather colour and condition and from the colour of soft parts, particularly the iris of the eye (Braithwaite 1981a). The other criteria can be tested through mutual display and sexual activity. Success in competition with others of the same sex may be measured by the frequency and results of threat and attack towards real or imaginary opponents. A female may induce a male's performance either by threatening others herself or by the use of specific "inciting" displays (e.g. Lorenz 1966: inciting by ♀ Common Shelducks *Tadorna*

tadorna and Mallards *Anas platyrhynchos*). Braithwaite's (1981b) suggestion that the Trumpet (TRU) display may be used by ♀ Black Swans to incite ♂ attack is not supported by my observations. Instead TRU, by either sex, is followed by high intensities of threat and approach (THR_{me} : $p < 0.01$; THR_{hi} : $p < 0.001$), and sometimes by physical attack, by the trumpeting swan (Ch. 3).

Possession of a suitable breeding territory, containing nest sites, shelter, and adequate shallow areas for young cygnets to feed (Section 3.4), may also be used by ♀s in mate choice. Successful defence represents ability to compete with other males, ability to provide for a family, and perhaps dominance status (Burley 1981); Collias & Jahn (1959) found that only dominant Canada Goose pairs bred successfully, perhaps because their status freed them from harassment. The young ♂ I observed courting defended an area which was later used for breeding by an adult pair, and was not joined by a ♀ until he had occupied it for some days. The presence of threats between ♂ and ♀, not observed in other, resident, adult breeding pairs, confirms that this pair bond was in the initial stages of formation.

Although aggression within the pair had lessened and a Greeting ceremony was developing, the young ♀ eventually left. Reasons for the bond's failure are unknown, but may be related to behavioural incompatibility, poor physical condition (although this was not apparent), or lack of experience. Both ♂ and ♀ were only 1 - 2 years old, an early age to start breeding (Braithwaite & Frith 1969b; Minton 1968). The ♀ Black Swan should have the final choice in mate selection: she makes the major gametic investment in breeding, spends more time in attendance on clutch and brood, and should maximise her investment by choosing the best possible mate.

The young pair's courtship lasted at least two weeks. A long courtship is expected in those species where both sexes must contribute to clutch and brood care. Trivers (1972) points out that a lengthy precopulatory period, with

considerable time invested by both sexes, is likely to be followed by lengthy post-fertilisation attentiveness. If prospective partners are compatible the courtship stage allows for cementing the pair bond and integration of physiological and behavioural states (Beer 1975).

Initial pair-bond formation includes some elements of aggression: D. Scott (1977) found Whistling Swan courtship to involve pecks and low-intensity threat. As bond formation progresses mutual Greeting and Triumph ceremonies develop, both of which reaffirm the mates' identities (Bateson *et al.* 1980: auditory cues are basic to individual recognition). Aggression is still present, in the Triumph ceremony, but threats are generally directed at real or imaginary opponents beyond the mate (Fischer 1965; Lorenz 1965; Radesäter 1975b). Male-female aggression may still occur if the ♀ does not use a suitably submissive posture (Radesäter 1975b). Aggressive elements are apparent in the Black Swan's Triumph (TRI) display, in the form of the raised-wing component and also in the significantly high frequency with which TRI follows high-intensity threats, boundary disputes, and attacks (Ch. 3). In the closely related Mute Swan the ♂ "busking" posture, a high-intensity threat very similar in form to the Black Swan's THR_{hi}, is used as a greeting or triumph display after successful defence, and also in the presence of an intruder which cannot be driven away (Huxley 1947). The use of TRI after aggression may emphasise the male's successful defeat of rivals and his continued suitability as a mate. Johnsgard (1965) notes that the triumph ceremony of *C. olor* is performed only by strongly mated birds.

4.4.2 Strength and duration of the pair bond

In most anserines the pair bond, once formed, is stable for at least the current breeding season and may persist, especially in successful breeders, for a number of years. The frequently-heard statement that swans (and geese) mate for life (e.g. Lickers 1977) is unlikely to be true, for several reasons.

Data are available which show that the Bewick's Swan

does apparently mate for life. M. Evans (1975) found that true divorce is unknown in the population wintering at Slimbridge, England. A bird may return with a new mate but the first is not seen again, although it may have wintered at the same site for many seasons. The implication here is that remating occurs after the death of a mate, but not while the original partner is alive.

Conversely Minton (1968) found that about 15% of Mute Swan pairs that bred together in one year were divorced before the next season. Individuals that were paired for several years were likely to have several mates within their lifetime, although there might be a gap of some years between the divorce or death of a mate and re-pairing. Divorces occurred between and within breeding seasons and, although more common in non-breeding pairs, sometimes happened when one mate in a successful pair was markedly younger than the other. Minton found no difference in bond strength between successful and non-successful breeders.

Inglis (1977) observed no divorces in Pink-footed Geese within a breeding season, probably because the season is too short for any advantage to accrue from remating. He concluded that, within a season, desertion is not a good alternative to fidelity. Pairs copulate before arrival at the nesting grounds and so a deserting bird (♂) could not mate again. Also the ♀ is probably too exhausted after incubation to protect the brood if alone. Overall, "staying with the same mate is ... likely to lead to a long-term increase in breeding efficiency". However, he added that divorce would be advantageous, for one or both partners depending on the reasons for failure, if breeding was unsuccessful.

Ollason & Dunnét (1978) found a significant correlation between breeding success and duration of the pair bond in Fulmars (*Fulmaris glacialis*). Ninety percent of birds breeding in one season had the same mate and nest site as in the previous year, and change of mate or site led to

decreased success. Similarly Kittiwakes (*Rissa tridactyla*: Coulson 1966) tended to retain the mate of the previous season, a tendency more pronounced in older birds. Only 33% of mate changes were due to a partner's death. Divorce was most likely if the pair had failed to hatch its eggs in a given season. However, a ♀ retaining her mate from the previous season bred earlier, laid more eggs, had a greater breeding success and showed more consistency in time of laying than a divorced or first-mated ♀. The depressive effect of a mate change lasted for at least two years. Coulson (1966) concluded that "there is a marked selective value in retaining the same mate from one breeding season to the next, but that in incompatible pairs ... there is more advantage in changing mates if by doing they are more likely to breed successfully". (See also Mills 1973: Red-billed Gull *Larus novae-hollandiae scopulinus*.)

Strength and duration of the pair bond seems to vary widely in the Black Swan. Frith (1967) and Lickers (1977) state that they may mate for life, although neither gives any supporting evidence. Braithwaite (1970) suggested that the monogamous pair bond may persist for several seasons, where breeding is territorial, but found several breeding associations in a small (N = 25) captive group (Braithwaite 1981b). The five main forms were (1) a single ♂ incubating alone, the ♀ deserting after laying; (2) a single ♀, with the ♂ deserting after mating; (3) a heterosexual pair, with fixed clutch- and brood-care roles; (4) a homosexual ♂ pair, obtaining a clutch either by mating a ♀ and forcing her desertion after laying (which cannot be classed as a true homosexual mating) or by theft; (5) a trio of 2♂ and 1♀. In this last association Braithwaite reported that, fairly soon after hatching, the brood would be left in the care of the males while the ♀ renested and incubated a further clutch. This may be an effect of captivity as records of second clutches after a successful first brood are rare in wild birds. The trio is comparable to the "ménage à trois" of Dewar (1936) and Ellis (1936) in Mute Swans. Here, however, the sex ratio was 2♀:1♂. The male mated with both females but defended one, both, or neither. In Braithwaite's

(1981b) study, the 1♂:1♀ association was the most common (37/58, over several years) at the time of egg-laying. The alternative associations were seen mainly during initial breeding attempts; they were also recorded in nests from the periphery of wild colonies, where young and inexperienced birds might be expected to nest (Nelson 1966: Gannets *Sula bassana*).

On Pukepuke Lagoon, successful breeders were paired monogamously for the duration of the breeding season. Two pairs that could be definitely recognised (♂1, ♀6) remained together for at least the 1978 and 1979 seasons, and ♂1 had apparently been together, on the same territory, for some years previously (A. Garrick pers. comm.). This pair stayed on their territory throughout the year, moulting there, although at this stage active territory defence was non-existent. The histories of other pairs could not be followed with any certainty, due to difficulties in recognition (Ch. 1). However, these pairs appeared to remain together at least until the broods hatched. In 1979 at least two broods did not survive to fledging, perhaps because poor parental defence allowed harassment by other swans (Chs. 3, 6). Whether these parents remained together after losing their cygnets is unknown. Certainly ♂GC, who lost their clutch through human interference and were prevented from re-nesting by continued harassment by ♂1, left first the main lagoon, and then a nearby small pond, together.

In such territorial situations it would be difficult for a ♂, having deserted one ♀, to carve out a new territory and remate. He could oust the first ♀ but this has obvious disadvantages in terms of his investment in the first clutch. Also, the demands of territorial defence and brood protection appear to be such that both partners must be involved in maintaining the territory and caring for eggs and brood. Thus, where features of the habitat make territoriality the favoured breeding mode, monogamy is desirable for both partners. However, given the conditions prevailing where colonial nesting is the main breeding type (e.g. Lake Ellesmere), other breeding associations may be favoured

and desertion may not be disadvantageous. Since, among other factors, food for cygnets does not appear to be a limiting resource in normal breeding years (Williams 1980) there is little need for defence of a large territory, and territory boundaries may extend only a pecking distance around the nest (Braithwaite 1970; Miers & Williams 1969). It is definitely possible for one bird to carry out incubation duties alone (Soper 1960). The advantages to a deserting partner would then have to outweigh the disadvantages (egg-loss through predation and theft or breakage, during a nest recess - mainly applicable to colonies; harassment of the brood, by other territory holders). In colonies any disadvantages would be effective during incubation, since after hatching cygnets may join a creche and the need for strong parental care is reduced. There is little evidence that ♀s lay twice in a season unless it is soon after clutch loss or removal (e.g. ♀1). The best time for colonial ♀s to desert is then straight after the clutch is completed, while the ♂ is most likely to leave once his mate is committed to incubation. Since the breeding season is relatively long both stand a good chance of being able to mate again. Strength and duration of the pair bond are thus related to the time and energy requirements of breeding. "Coy" females, with a requirement for lengthy courtship, may be expected where considerable investment by both sexes is necessary for successful breeding, while "fast" females may exist in the opposite situation.

4.4.3 Sexual activity

The seasonal distribution of sexual behaviour is related to the strictly seasonal nature of breeding on Pukepuke Lagoon, with fertilisation and laying occurring in early - mid July (shown by the behaviour of the pairs, and hatching dates), and broods appearing in August. The Spring - early Summer decrease is probably due to the pairs' preoccupation with brood-rearing and the subsequent moult, with their accompanying hormonal changes. Renewed activity through Autumn, building up to the Winter peak, may be attributed to increased activity by resident breeders and

also by transient pairs. Disturbances during the May-June shooting season produced a lull in sexual activity. Very few swans were present, in a continually alert state. In 1978 only four pairs began incubating and these were reduced to two by another researcher, while in 1979 11 pairs nested and hatched broods. This increased number of breeding pairs probably caused the rise in sexual activity in the 1979 breeding season (Fig. 4.10).

Fertilisation and laying occur in early-mid July, and broods are present for a fairly brief period, in contrast to findings for other, colonial nesting areas (Lickers 1977; Miers & Williams 1969). The timing of breeding is probably proximally related to the nature of the food supply and hence to the timing of rainfall and to water levels (Braithwaite & Frith 1969b; Miers & Williams 1969), although ultimately the influence of photoperiod must initiate gonad development. Otherwise a lag period would ensue between the appearance of an adequate food supply and full gonadal activity. Perrins (1970) found that the date of laying in some birds may be related to the date when the ♀ can find enough food to form eggs. The ♀ Black Swan lays 30% of her body weight in an average ($\bar{x} = 5.5$) clutch (data derived from appendices to P. Scott 1972). With a laying rate of two eggs in three days (Braithwaite 1977) and an incubation period of 36 days, the ♀ must have an adequate food supply at least 45 days before young are present, or else sufficient stored reserves, as is the case for arctic-nesting geese. Furthermore, laying must be timed so that young are present at a time of maximum abundance of suitable food for them (Lack 1968). Long-term defence of a territory on Pukepuke Lagoon may be important where suitable food for young cygnets is limiting (M. Williams pers. comm.; Ch. 7). Thus the July peak in copulatory activity must be functional in fertilisation, while the bulk of copulations occurring at other times will probably be "practice", affecting strength and maintenance of the pair bond by repeatedly demonstrating sexual competence (4.4.1). Those leading up to the peak will also serve to synchronise the pair's gonads as they enter reproductive

condition.

There is no easy explanation for the daily patterning of sexual activity. Possibly light intensity (lux) or temperature may be involved (B.Springett pers. comm.). There is no obvious relationship between these activities and other, major behaviour such as feeding and loafing (Ch. 2). Greeting and Triumph ceremonies occur at a low but constant level throughout the day.

Male and female spend an equal amount of time on pair-related activities (Appendix I). This investment may reflect the need, in a territorial situation, for constant and mutual testing and affirmation of the pair bond. However, although display activity is usually mutual, there may be a difference in the frequency with which one particular partner initiates, and one responds to and continues, the behaviour sequences. This is shown by an examination of pair-bond maintenance sequences, where the σ is the sole performer in 17 of 54 displays. Although there is no statistically significant difference in composition between σ -only and σ - \varnothing sequences (Table 4.1), an apparent difference for the acts Neck-Dip and ND_{hi} may be due to the fact that these are normally a mutual performance: if the \varnothing does not respond the σ will not be encouraged to continue or intensify his display. Analysis of σ - \varnothing and \varnothing - σ actions in copulatory sequences (Table 4.8 a&b) also suggests that it is the σ who initiates and the \varnothing who confirms the sequence. The chance to respond, or not, to σ behaviour will allow the \varnothing to test σ persistence; her actions will show her own interest (Halliday 1978).

An analysis of Canada Goose triumph ceremonies shows that, while the σ usually initiates the display, the \varnothing is also active and "the performance of an act by one individual initiates a behaviour pattern from the other" (Radesäter 1975b). Also, "the behaviour of the \varnothing seems to be more affected by the nature of the preceding performance by the σ than by her own behaviour, while the reverse ... is true for the σ " (*ibid.*). I did not examine the nature of σ - σ

and Q-Q chains.

Examination of Tables 4.8 a&b shows that, after a given O precopulatory display (i.e. HD, ND, ND_{hi}, FT, CRLP, NPP, O/Q), the subsequent Q precopulatory display (HD, ND, ND_{hi}, FT, CRLP, QPRO, Q/O) occurring more often than expected is the same or similar in 8 cases and different in 6. For Q-O interactions these figures are 4 and 11 respectively. This difference is not statistically significant (Binomial test, $\alpha = 0.01$, O actions $P = 0.395$, Q actions $P = 0.059$). However, there is a tendency for the O to follow any Q action with a different one, especially in the case of QFT. The Q may duplicate the O display or produce a different one, but tends to copy O actions for displays derived from bathing (variants of HD and ND: Ch. 7). In two cases where the Q response is different (ONPP - QND, OND/Q-QPRO), this response may still be specifically induced by the O action. Thus ND/Q may indicate O readiness to mount, and QPRO indicates equal readiness in the Q. It is possible that ND as a response to NPP indicates that the Q is not yet ready for treading, assuming that NPP is derived from an intention movement to mount (Ch. 7).

The presence of others may influence the final display form. Table 4.7 shows that the performance of NCO by one or both partners after copulation is linked with the close presence of watching swans. Similarities in form between this display and the NCO end-posture of Triumph ceremonies suggest some aggressive motivation, although threat displays rarely follow.

Copulatory, and possibly pair-bond maintenance, sequences may be seen as a continuing series of O actions producing, in a receptive Q, confirmatory responses, which in turn influence the nature of subsequent displays. Mutual stimulation is necessary for continuation of the sequence, but the Q should have the major role in determining whether or not it is completed (see 4.1).

4.4.4 Function of the pair bond

The successful formation and maintenance of a pair bond must ultimately affect breeding success.

A weak pair bond may prevail where Black Swans nest in colonies (Braithwaite 1970, 1981b). Here, partly because there is a good, widespread food supply for both adults and young, there is no need to hold a territory larger than that immediately around the nest (4.4.2). One bird may, if necessary, complete incubation alone and there is a reasonable chance of remating following desertion, so that pre-mating activity by the pair may be reduced in duration or intensity.

However, where birds breed in territories and share parental duties, a strong pair bond is advantageous to both sexes, and will be formed slowly over a long period to ensure correct mate choice (4.4.1). The mutual nature of all pairing and breeding displays reflects the need of both partners to make the best possible selection of mate, although it is the female who has the final decision (Butterfield 1970).

Where environmental conditions necessitate territorial breeding, a strong pair bond permits a division of labour over most breeding activities, especially territorial defence. The need for this is shown in a study of ♀1 in 1979 where, with an increased number of pairs attempting breeding, both male and female became more active in aggression, but the female's contribution over incubation increased by 200% over 1978 figures (c.f. ♂ 57%: Appendix I). The female could not have successfully defended a territory for herself and her young, and incubated the eggs, without the male's presence, and *vice versa*. D. Scott (1977) similarly concluded that "continued presence of the male appears to be necessary in anserines to ensure adequate food for the young", through territorial defence. Defence may also improve breeding success through decreasing harassment by other swans (Ch. 6); again, the actions of one parent

could be inadequate.

A strong pair bond lasting more than one season may also improve breeding success through its effects on the timing of breeding: in general experienced birds breed earlier in the season and tend to have a greater reproductive success than younger or inexperienced birds (Finney & Cooke 1978: Snow Goose *Anser caerulescens*; ; Nelson 1966: Gannets). The effect of partner-familiarity on reproductive success is well demonstrated by the results of divorce: changes of mate, in experienced breeders, lead to reduced success for at least the next one or two seasons (Coulson 1966; Ollason & Dunnet 1978).

Chapter 5

CYGNET GROWTH AND DEVELOPMENT

5.1 INTRODUCTION

Observation of the physical and behavioural development of young birds provides information on the ontogeny of various acts and the physical bases for them. Close observation of young swan broods is difficult under natural conditions, so I reared a group of young Black Swan cygnets from the hatchling stage to almost complete feather development at 60 - 70 days.

The great advantage of working with captive birds is that they can be observed at much closer quarters and for longer periods of time than birds in the wild (Johnsgard 1965). This was especially true for my study, as very young wild broods on Pukepuke Lagoon spend most of the day hidden in raupo stands around the shoreline. Using captives, data may be collected on physical parameters as well as behavioural patterns that could otherwise be missed altogether. The latter include soft vocalisations (Dilger 1962) such as hisses, "sleepy" and "contact" calls (Kear 1972), and small postural changes which cannot be detected from a distance. It is also possible to work with known individuals (it was impossible for me to mark wild birds), so that social relationships within a family group may be examined.

5.2 METHODS

I reared a single cygnet in 1979 and a group of six in 1980. The 1979 bird was obtained unintentionally and

I was unable to get others, so that her behaviour may have been affected through lack of interactions with other swans (5.4.1). This bird, named Ebony (E), spent her early life (1 - 28d.) in very unnatural conditions, particularly in that she did not have continued access to water, which was freely available to the 1980 brood. The conditions under which these birds were kept were as normal as possible (see 5.2.1).

5.2.1 Rearing

All seven cygnets were imprinted on me as their foster parent, through keeping them in physical and vocal contact with me as continuously as possible. I used vocalisations combining human speech with imitations of their own contact calls. Since the thermoregulatory ability of very young birds is poor (Ricklefs 1968) the cygnets were kept warm by my brooding them (1979) or by providing heat lamps and a warmly lined box (1980). Ebony was carried around with me a great deal, while the group was provided from the first with a large inside run. Here they had continual access to water, in the form of a pool (2m x 1.3m x 0.25m). A second, larger pool with adequate depth for diving was dug outside. Ebony was able to swim in a tank every day but not to use it continuously. This led to some plumage problems, as her down became fouled and could not be immediately cleaned, and lost some of its waterproofing.

Food was provided on an *ad lib.* basis, following the recommendations of Kear (1976) and Owen & Kear (1972). These authors state that young waterfowl require a diet containing 18-20% protein, so the cygnets were given chick-starter crumbs when small, and graduated to growers' pellets after three weeks. They preferred to have these soaked in water. Sieved egg yolk was scattered over the crumbs at first, to encourage feeding. A variety of chopped greenstuffs was provided: dandelion, lettuce, cabbage, grass. Sprouted Mung beans and grated carrots were also offered, although only one or two birds would take the carrot. Soaked whole wheat was also provided

once the oldest birds were four weeks old, and by the time the brood was six weeks old they were taking between them 1.5kg (dry weight) of wheat a day. Wheat replaced the pellets completely at this stage. In 1980 chopped greens were given on the pool, while other foods were presented in containers at some distance from the water. The run and pool were cleaned out, and food replaced, daily. Outside, all birds were free to graze over the lawn and they then added dock and puha (Appendix V) to their diet.

The cygnets were taken outside for 2 - 6 hours each day when small (0 - 3 weeks), and the period spent outside increased, with improving weather and rapid feather development, to a maximum of 13 hours a day.

5.2.2 Physical development

The cygnets were weighed at least twice weekly on a 3kg Mettler balance, until the oldest was 4 weeks old. From then till the end of the study they were weighed weekly on a 5kg spring balance. While the cygnets were small enough for the weighing to be done easily by one person they were weighed at the same time each day. Timing became more irregular when it became necessary to enlist help.

Stage of feather development and changes in bill colouration were recorded as they occurred, using colour photography for the latter. The cygnets were sexed by cloacal examination at the end of the study.

5.2.3 Behavioural development

Ebony (1979) was in some ways treated more as a pet than as a research subject. As I kept her with me for most of the day, especially when she was very young, my own activity patterns were imposed on her. In 1980 such disturbance was very limited and although I was with the birds for long periods they were left very much to their own rhythm(s) of activity. Ebony became very distressed if

left alone, but the 1980 group rapidly became accustomed to being left alone in their run for at least some part of the day.

5.2.3a Appearance and timing of behaviour patterns

In 1979 all new acts, or qualitative changes in existing acts, performed by the cygnet were noted as they occurred. However, I made no attempt to quantify such patterns as Greeting ceremonies or aggressive incidents. The former followed almost every move on my part, as well as occurring after alarms or disturbances, and as Ebony was very nervous they were probably performed at a much higher frequency than greetings by the group or by wild birds. The frequency and "direction" of aggressive acts also varied in comparison with the group, in that they were not directed at people or the household cat until much later in development.

In 1980, all new acts, or changes in earlier acts, were again noted as they occurred. However, the availability of a group meant that a number of social behaviour patterns (5.2.3b) could be examined. To distinguish individuals all six cygnets were banded, at first with make-shift bands of folded insulating tape, but later with swan bands provided by the Wildlife Service.

5.2.3b Examination of social behaviour

Although I was with the birds for varying periods (up to 14 h.) each day, data collection was generally restricted to a period of 3 - 4 h., during which all events relating to 5.2.3b, i-iv below were recorded. New or changed acts were watched for throughout the day. Aggressive acts (i & ii) were soon found to be extremely rare (N = 46 and 47 respectively, for the total 8-week study period), so that they were also noted whenever they occurred, rather than during the restricted period of more concentrated observation.

Data relevant to the cygnets' social behaviour were recorded as follows, in fortnightly blocks:

- (i) development of a peck order, if any, within the group: the identity of aggressor and victim were noted, together with the form of threat or attack, the context in which the incident occurred (e.g. feeding, moving), and the response of the victim.
- (ii) frequency of aggressive incidents directed outside the group, and the relationship, if any, between this and the peck order: the identity of the displaying bird(s), the form and object of the threat or attack, and the context of the incident were recorded.
- (iii) frequency of initiating and receiving Greeting ceremonies: Stahlberg (1974), working on Greylag Geese (*Anser anser*), suggested that there was some relationship between rank in the peck order and the number of greetings received by each bird. To examine this in Black Swan cygnets, I recorded the identities of the bird(s) initiating and responding to greetings, together with context.
- (iv) order of the birds when moving around, and any age-related changes in this order: the creche members almost always moved from place to place in single file. Their order in this file was recorded and examined for changes with age, as in the study of Mute Swan cygnets performed by de Jong & Bacon (1979). For analysis, I combined data from moves initiated by the birds and from moves begun by some action of mine.
- (v) cohesion within the group and changes, if any, in the composition of sub-groups: it appeared that some cygnets preferred to spend a large amount of time with certain of the others. To examine the truth of this, I used a method of cluster analysis described by Morgan *et al.* (1976) (see Ch. 3, 3.2.2). Every 30 minutes the position of birds were noted, relative to each other (birds alone, identities of birds in groups). Single-Link-Cluster-Analysis (SLCA) of this information was used to provide some measure of group cohesion and to determine any tendencies for individuals to associate

with certain others. The results were also examined for any changes with increasing age.

5.3 RESULTS

5.3.1 Physical development

5.3.1a Sex

The lone cygnet reared in 1979, Ebony (E), was a female. The 1980 creche consisted of 4 males, Aggro (A), Chum (C), Lazy (L), and Squeaker (S) and 2 females, Diver (D) and Placid (P). Names were given on the basis of early superficial behavioural traits.

5.3.1b Growth rates

The weights of all 7 cygnets are shown in Figs. 5.1 a&b. The 1980 cygnets were not all the same age, so data for calculation of mean weights at given ages (Fig. 5.2) were obtained by interpolation from these graphs.

These figures suggest that male cygnets were heavier than females at the same age, throughout the study period. This difference is maintained into adulthood (P. Scott 1972: 198 - Appendix I). However, a Mann-Whitney U test ($H_0: \sigma \text{ weight} = \phi \text{ weight}, \alpha = 0.01$) performed on cygnet weights at 10-day intervals showed that σ s were not significantly heavier than ϕ s, at any age.

Rates of weight increase, also calculated from mean weights at 5-day intervals, were similar for σ s and ϕ s (Table 5.1), with the only obvious difference coming in the first (11 - 15 d.) period. Growth rates, as reflected by % weight increase, slowed from more than 11% to approximately 2% per day, over the 50-day period examined. However, in terms of actual daily weight increments, there was a change from an average daily increase of about 33g (both sexes) in the 11 - 15d. period to a maximum of 127g/day for males and 74g/day for females, both in the 51 - 55d. period.

These data may be compared with figures provided by Guiler (1966) which show a range in weight increases of 3g/day to 44g/day (sexes combined) for wild cygnets in Tasmania. Unfortunately the age of Guiler's birds is unclear. However, it appears from this comparison that my captive cygnets grew at a faster rate than the Tasmanian birds. A similar slower growth rate for wild swans is seen in Lickers' (1977) work, but since he set (apparently arbitrarily) the time spent in each class at 30 days (but see Tables 5.2 and 5.3), these data cannot be reliably compared with mine.

5.3.1c Feather development

Table 5.2 gives a method of determining age classes from physical characteristics. Tables 5.3 a&b present the ages (and weights, where applicable) at which wild and captive birds entered each age class, and the time spent in each class. The captive birds developed faster than those in the wild, and clearly cygnets do not spend equal amounts of time in each age class.

5.3.1d Bill colouration

The results presented in Table 5.4 are a brief verbal summary from a series of photographs taken of the 1980 brood. They show that birds of similar ages or the same stages of feather development do not necessarily have the same bill colouration. No sex differences are apparent.

5.3.2 Behavioural development

5.3.2a Behavioural repertoire of Black Swan cygnets

Data collected from the 7 captive cygnets have been augmented where possible by information gained from wild broods. They are presented under the headings of

- (A) comfort and maintenance behaviour (including feeding);
- (B) agonistic behaviour;
- (C) behaviour influencing social relationships.

FIGURE 5.1a: Weights of 4 ♂ Black Swans, vs. age

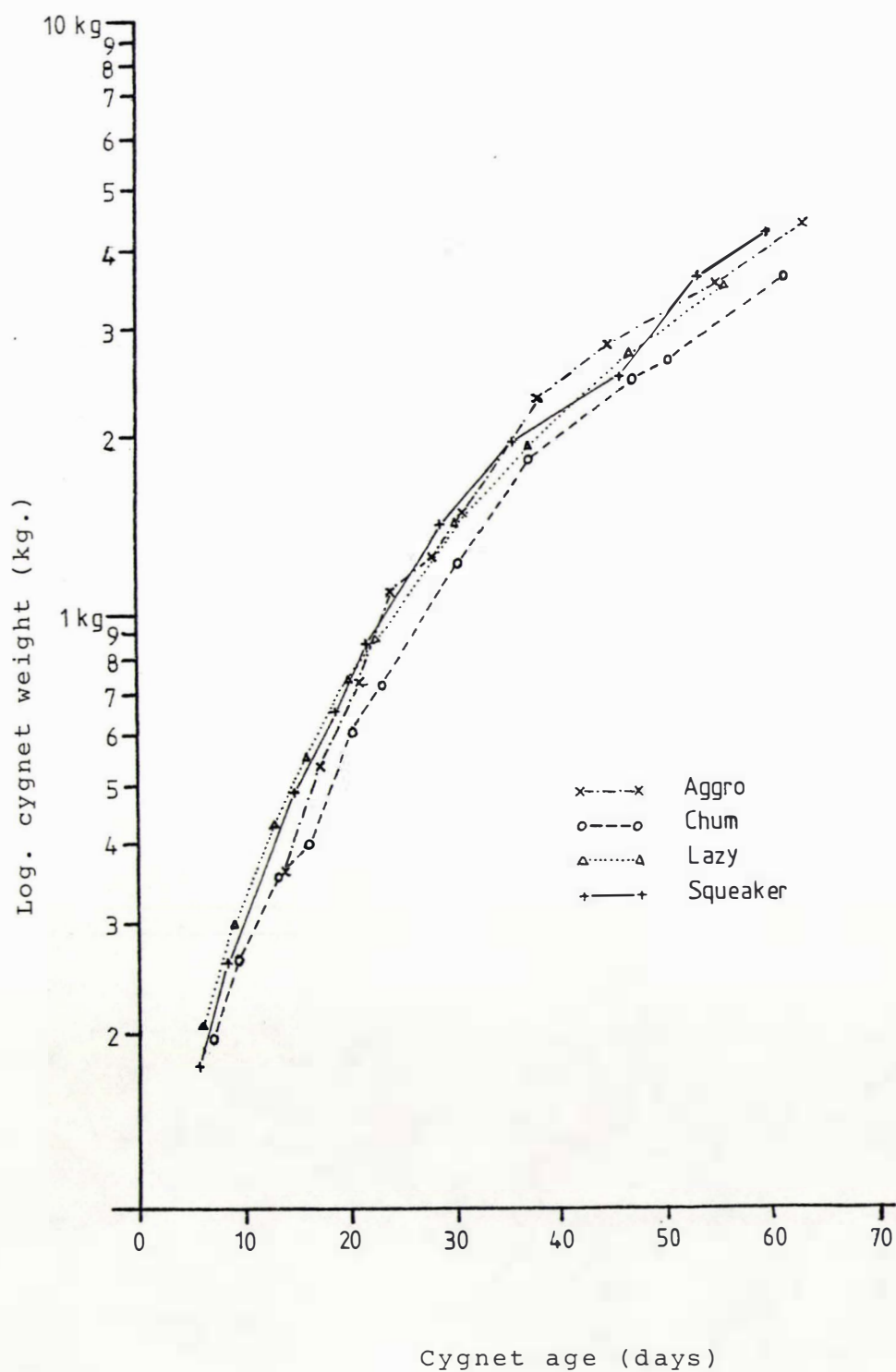


FIGURE 5.1b: Weights of 3 ♀ Black Swans, vs. age

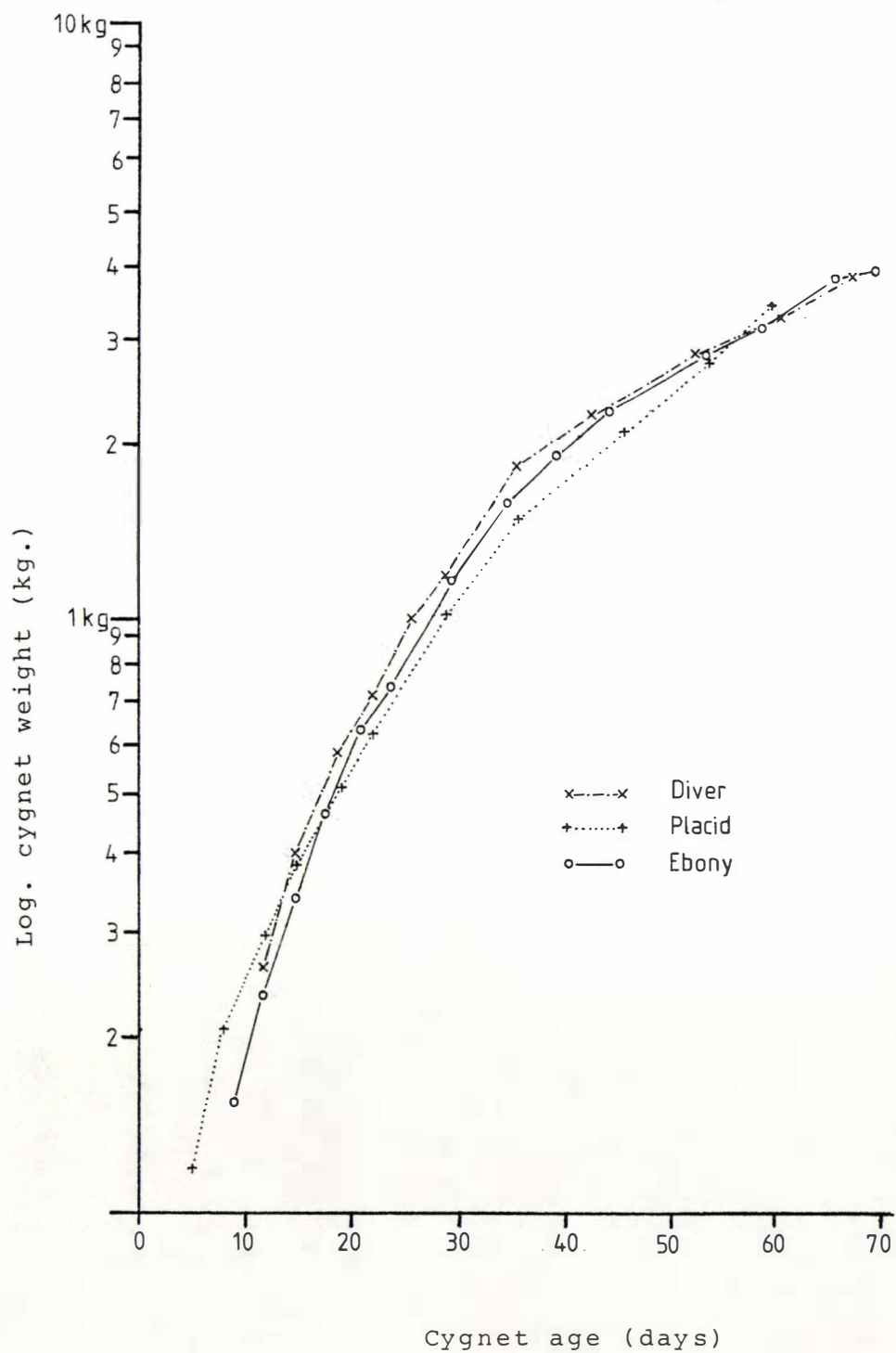


FIGURE 5.2: Mean weights (kg.) of ♂ and ♀ cygnets, vs. age

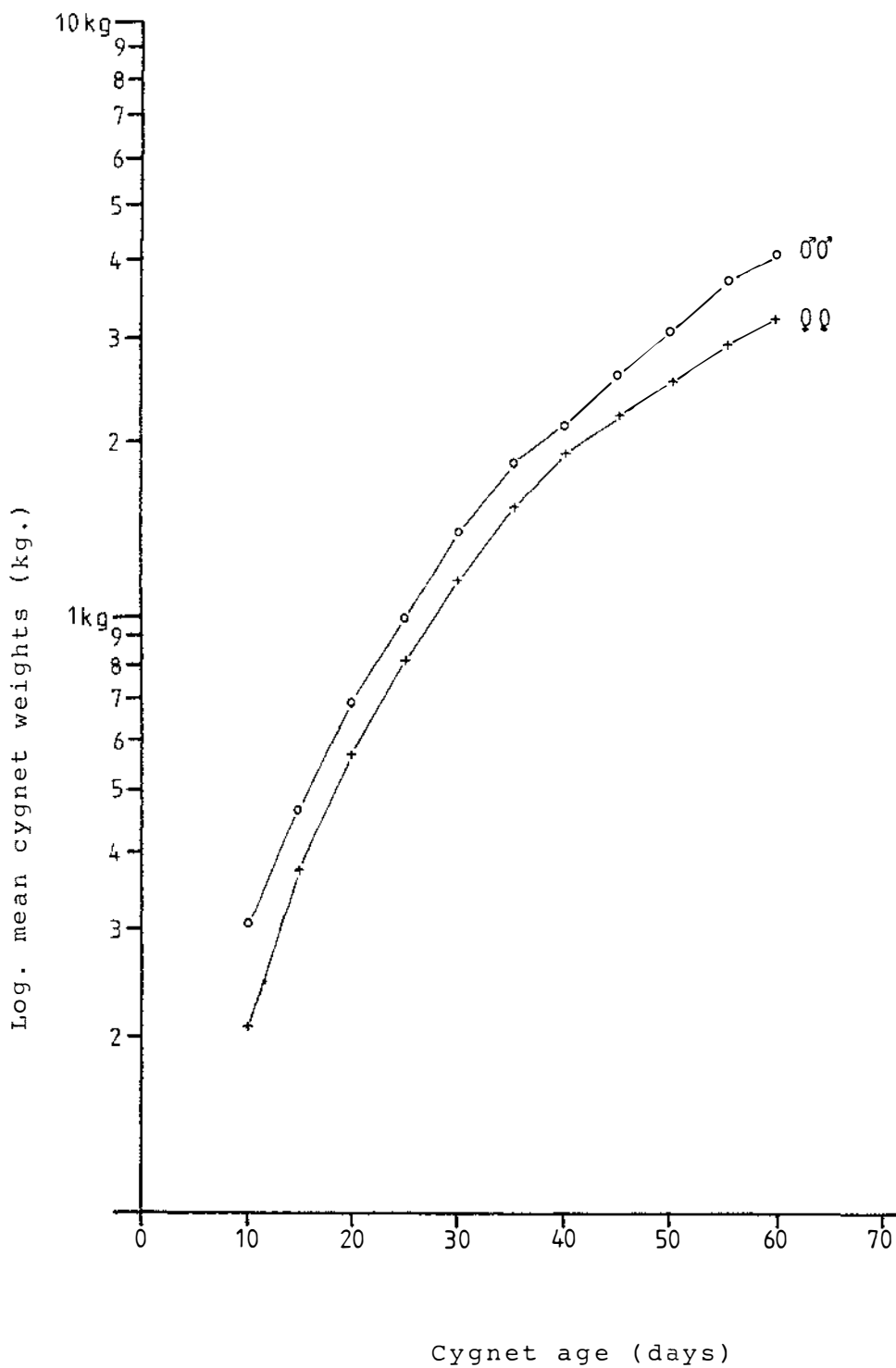


TABLE 5.1: CYGNET GROWTH RATES: AVERAGE DAILY WEIGHT INCREASE (g) & % WEIGHT INCREASE DAILY, OVER 5-DAY INTERVALS

Ages	Males		Females	
	g increase	% increase	g increase	% increase
11-15d	32.5	11	33.4	16
16-20d	50.2	11	43.6	12
21-25d	56.8	8	51.4	9
26-30d	75.2	7	60.6	7
31-35d	84.0	6	76.6	7
36-40d	73.6	4	63.4	4
41-45d	75.0	3	57.4	3

TABLE 5.2: CYGNET AGE-CLASS CLASSIFICATION
 Derived from observation of captive and
 wild birds.

Class	Physical Characteristics
I	Downy, newly hatched. Down pale grey, darker above; bill and legs dark grey/black; egg-tooth may be visible for first 3-4 days; nail of bill white.
II	No contour feathers visible. Neck and tail becoming prominent, body shape becoming oval and long. Patches of down may protrude where feathers are developing underneath.
III	Contour feathers developing on shoulders and flanks. Tail feathers quite obvious and facial feathers appearing. Still predominantly downy. Pink patches may be appearing on bill.
IV	Face and upper neck well feathered; scapular, flank and tail feathers prominent and secondaries visible; belly feathered. Down patchy but persisting from rump to nape.
V	Almost fully-feathered with primaries and secondaries well developed (a flapper). Patches of down on nape and rump. Bill pink, and white stripe may be obvious above nail.
VI	Fully feathered and just able to fly; plumage much paler than that of adults, and has a brownish tinge. All flight feathers tipped with black. Bill reddish-pink with white tip and tail. May have separated from parents.

TABLE 5.3a: AGE (d.) AND WEIGHT (g) OF CYGNETS
ENTERING EACH AGE CLASS
(as defined by plumage characteristics)

CYGNETS	Age classes (see Table 5.1)					
	I	II	III	IV	V	VI
Captive ♂♂ N=4	0d	12-15d 320- 450g	41-47d 2100- 2750g	53-58d 3550- 3850g	69d ¹ 5300g ⁴	
Captive ♀♀ N=3	0d	13-15d 300- 340g	42-48d 2100- 2200g	55-59d 2900- 3300g	66-70d 3600- 3800g ²	
Captive ♂♂ & ♀♀	0d	12-15d 300- 450g	41-48d 2100- 2750g	53-59d 2900- 3850g	66-70d 3600- 5300g ³	
Wild, 1978 N > 10	0d 125- 227g ⁵	20-24d	48-52d	70d	74-89d	100d
Wild, 1979 N > 10	0d	17-23d	49-51d	66d		100d ⁶

1: N=1. 2: N=2. 3: N=4.

4: from extrapolation from Fig. 1a; all other captive weights from interpolation of Figs. 1a & 1b.

5: data from various authors in P. Scott (1972), Append. 9.

6: see also Guiler (1966).

TABLE 5.3b: TIME SPENT IN EACH AGE CLASS

CYGNETS	Age classes				
	I	II	III	IV	V
Captive					
♂♂	11-14d	29-32d	11-12d	12d	
♀♀	12-14d	29-33d	11-13d	11d	
Wild, 1978	20-24d	28d	18-22d	19d	11-26d
Wild, 1979	17-23d	28-32d	15-17d		

TABLE 5.4: RELATIONSHIP BETWEEN BILL COLOUR AND CYGNET AGE
(From comparison of colour photographs at different dates)

<u>Cygnets</u>						
Age class and bill colour details						
date of photography	A	D	C	L	S	P
28/9/80	I;black	I;black	I;black	I;black	I;black	I;black
12/10/80	II;black	II;black	II;black	II;black	early II; black	early II; black
29/10/80	III;black at base, pink- ish-grey e elsewhere with whit- ish nail	III;black, whitish nail	II;black with faint pink areas round nares on bridge; whit- ish nail	late II; black, whitish nail	late II; black, whitish nail	II;black, whitish nail
4/11/80	late III;all over reddish- pink;white nail	late III; black, white nail	late II; as A on 29/10/80	III;black with pale areas round nares;whitish nail	III;black, whitish nail	late II;black whitish nail
20/11/80	late IV;red although paler than adult;white tip & nail	late IV;as L on 4/11/80 but with white tip as well as nail	IV;as A on 4/11/80 but base still dark grey	IV; as A on 29/10/80	IV;as L on 4/11/80 but white tip as well as nail	III;pale pink with dark base and white nail
23/11/80	V	V	IV	IV	IV	early IV

pink colouration intensified in all birds

(A) The comfort movements (preening, bathing, stretching) are the same as those recorded in adult swans (Ch. 2, 2.3.1; see also McKinney 1965). The timing of their appearance is affected by the physical development and needs of the cygnets. Two acts are of particular interest.

The first of these was frequently seen while the cygnets were still downy (Cl. I-II). When preening while sitting together or huddled together in a close group, cygnets were observed several times preening each other on breast, shoulder or flank (Plate 5.1). This often required that the cygnet performing the preen should reach across another body to the recipient. This activity might be described as allopreening with some signal function (McKinney 1965), possibly agonistic in nature (Harrison 1965), or may simply be a response to the sight of a patch of wet down on another bird. There was no evidence of presentation behaviour or mutual preening (McKinney 1965).

The second pattern is a series of acts occasionally seen during bathing, which McKinney (1965) called "dashing-&-diving". His study of anatidine comfort movements does not record this pattern in swans, although he states that it probably does occur. It consists of frequent dives interspersed among heavy flapping over the surface, together with dashing about in an Alert-Upright or Anxiety-Upright position (Ch. 2, 2.3.1), and is contagious. McKinney (1965) states that dashing-&-diving may occur at any stage of a bathing sequence. However, although the captive cygnets would bathe two or more times a day in their outside pool (the interior one was probably too shallow), dashing-&-diving was usually seen only during the first bathe of the day. One individual would begin a bout, usually by a splashy dive, and would be joined not only by others already bathing, but also by those who had not yet entered the water or had finished bathing and left the water to preen and dry themselves. Thus dashing-&-diving would appear to be a socially-facilitated act and could possibly be termed play (Ficken 1977). Interestingly, it could be

stimulated by spraying the birds with water or splashing them thoroughly. Dashing-&-diving motions also occurred in very shallow (3 - 5cm) puddles where the water depth was quite inadequate for bathing. On three occasions I observed the captive brood hurry to such puddles from preening or moving about on the lawn and begin running about in alert postures or attempting to dive. Dashing-&-diving play occurs quite often in wild cygnets but I have seen it performed only 3 times by adults, during bathing sequences.

Feeding behaviour patterns are the same as those of adults (Ch. 2, 2.3.1).

(B) Agonistic behaviour

(a) Intention-Movement-to-Peck (IMP): was the most common threat display seen in the 1980 brood; data on threats by wild cygnets were insufficient for both quantitative and qualitative comparison. In IMP the neck is drawn back slightly with head lowered a little and wings raised, but no blow follows (Fig. 5.3). In intrabrood aggression this threat is seldom accompanied by a hiss or call ($N_{\text{IMP+hiss}} = 4$ in threats at other cygnets, $N = 2$ at humans; c.f. $N = 11$ at birds or cat).

(b) Head-Jerk Threat (HJT): is used in aggression directed outside the brood. The head is held level on a slightly curved neck and jabbed backwards and forwards to the accompaniment of loud harsh one-syllabled calls, delivered with the beak slightly open. The wrists of the wings are raised a little. As the birds get older the forward movement of the neck is increased until eventually it is thrown forward horizontally with the bill pointing up, in a posture very similar to the adult Trumpet (TRU), although the call remains monosyllabic.

The orientation of both IMP and HJT (= early TRU) may vary. The cygnet can stand face-on to the object of the threat, or it may stand side-on and draw its neck back to the side (Fig. 5.4). In this second form the bill and

head do not point directly at the object threatened. The second form is seen frequently if a cygnet is approached by a stranger and cannot retreat, and so seems defensive in nature, although I have found (see Poulson 1948) that adult swans in this side-on posture may attack if pressed too far.

(c) Pecking Lunge (PEL): commonly used in intra-brood aggression, and is the same as the adult attack (Ch. 3, 3.3.1). The bill is open and an attack may end in biting and pulling at the victim's feathers (Fig. 5.5).

(d) Charge: in the threats directed at a cat, there was a change with age from the original IMP (plus hiss) through a display similar to the adult THR_{10} (Table 5.5) (seen in intra-brood aggression on Pukepuke Lagoon), to a charge with wings raised and half-open, body upright, neck curved back, and hissing with an open bill (Fig. 5.6). The charging birds usually approached rapidly by hopping on both feet at once (c.f. propulsion of adult THR_{hi} , on water).

(e) Slow-Wing-Flap (SWF): seen once, directed at a strange human. The same as the adult display (Ch. 3, 3.3.1).

The lower half to two-thirds of neck plumage is fluffed during both aggression and greeting.

Responses to sibling aggression varied, depending on the form of threat used (Table 5.6). "No reaction" i.e. continuation of whatever the victim was doing, was the most frequent response to IMP (10/18), while PEL usually (16/27) resulted in immediate avoidance. A cygnet avoiding PEL would draw its body slightly away, while its neck was pulled away quite markedly from the aggressor (Fig. 5.7). Usually the victim stood at an angle to the aggressor, and movement away from the aggressor could follow.

When young the cygnets showed the usual response to aerial predators i.e. when a hawk passed overhead they froze, crouched close to the ground with their necks twisted round

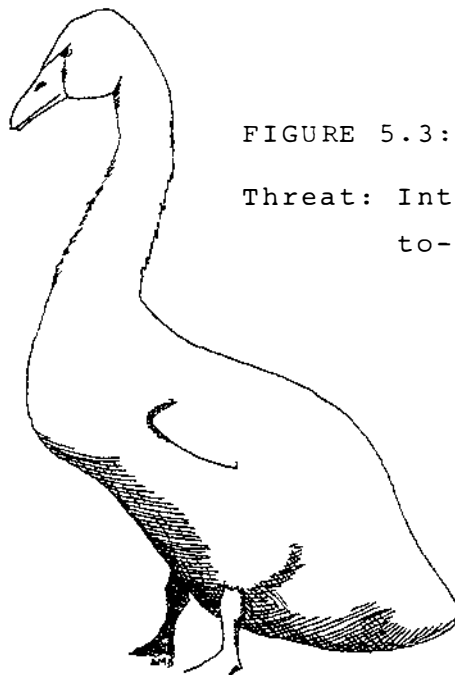


FIGURE 5.3:

Threat: Intention-Movement-
to-Peck (IMP)

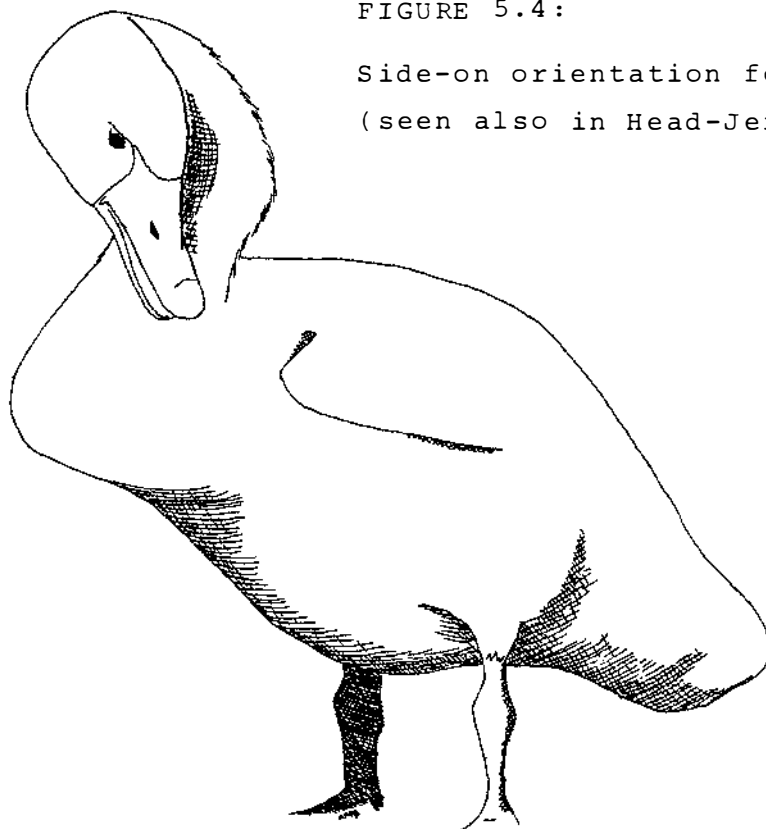


FIGURE 5.4:

Side-on orientation for IMP
(seen also in Head-Jerk Threat)

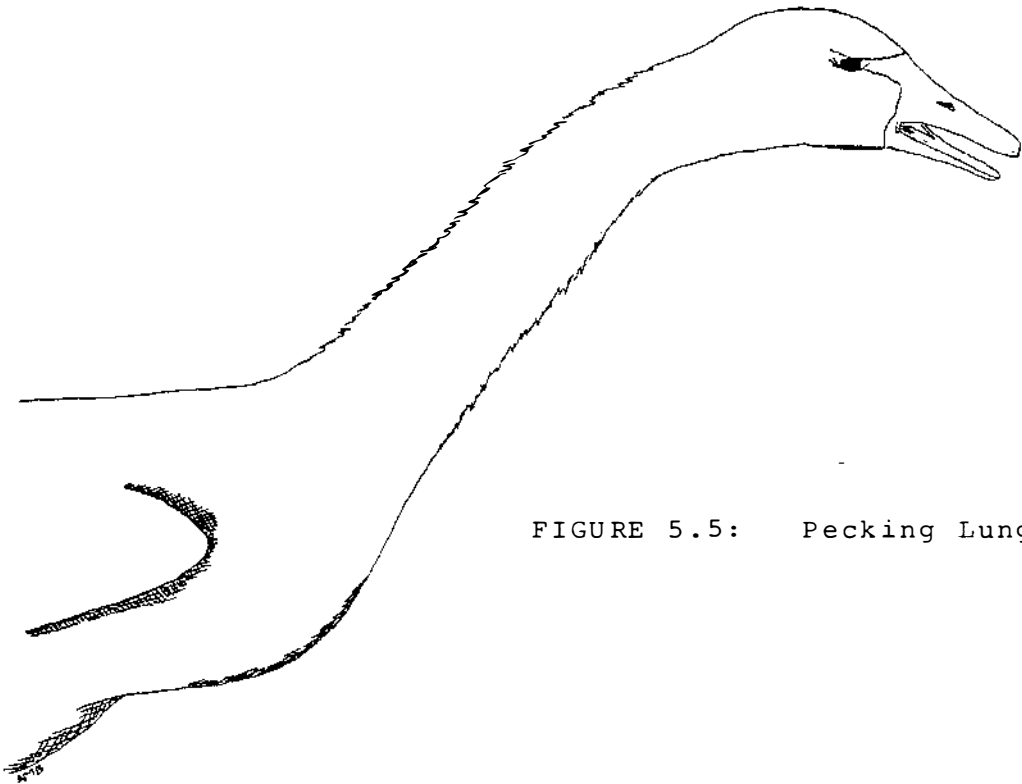


FIGURE 5.5: Pecking Lunge

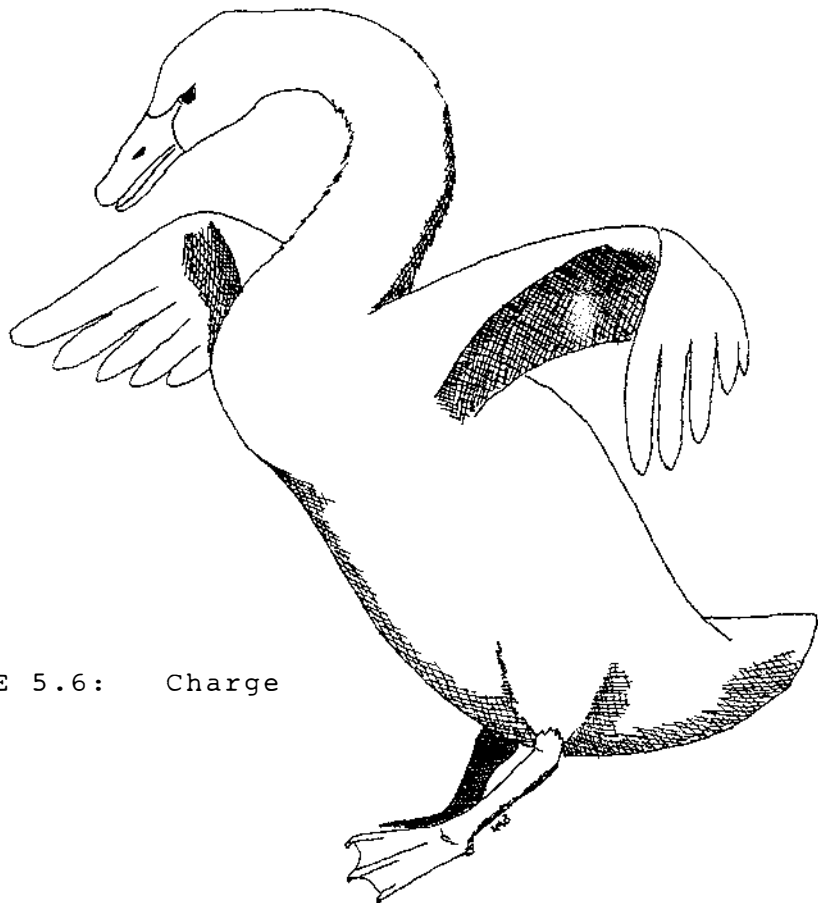


FIGURE 5.6: Charge

PLATE 5.1: Preening of one cygnet by another

PLATE 5.2: Crouch and sideways-stare



TABLE 5.5: EXPANSION OF ABBREVIATIONS USED IN TEXT

Abbreviation	Expansion
IMP	Intention-Movement-to-Peck. Common cygnet threat; used also by adults.
THR _{lo,me,hi}	Low-, medium-, and high-intensity threat display; described in Chapter 3.
HJT	Head-Jerk-Threat. Juvenile precursor of adult TRU display.
SWF	Slow-Wing-Flap. Long distance threat, with call; described in Chapter 3.
TRU	Trumpet threat; described in Chapter 3.
TRI	} reinforce social bonds; adult forms described in Ch. 4.
GRE	

TABLE 5.6: SIBLING AGGRESSION: FORM OF THREAT OR ATTACK AND FORM OF RESPONSE

Threat form	No reaction	Avoid with distress call	Brief Avoid precedes other act (n x greet)	Greets immediately	Retaliate	Preen	thr
hiss only	1			1			2
IMP	10		3 (1x)	5			18
PEL	4	3	13 (3x)	4	2	1	27
Total responses	15	3	16 (4x) *	10 *	2	1	47

* These are only those greetings which followed aggressive incidents; see also Table 5.14 a&b

to stare up with one eye (Plate 5.2). Small aeroplanes, having a "hawk-like" silhouette, also elicited this response. Sudden loud noises, such as that produced by a low-flying jet aircraft, were reacted to more strongly, in that the cygnets would run to shelter round and under me before crouching and peering up. This reaction to noise continued after they became habituated to "hawks" passing over.

(C) Behaviour influencing social relationships

(a) Imprinting: the process whereby young animals develop a preference for some conspicuous environmental object (usually the parents) and react positively to it by following, huddling and pecking (filial imprinting: Immelmann 1975), while at the same time developing a fear of novel objects (e.g. Hinde 1970). In Black Swans the "end" of imprinting is signalled by the development of a Greeting ceremony shared with siblings and the parents (or foster-parent), a strong tendency to follow the parents (Plate 5.3), and an avoidance of, and possibly fearful or defensive reactions to, other swans.

(b) Greeting and Triumph ceremonies: the movements of head and neck during a Greeting ceremony (GRE) are the same as those of adult swans (Plate 5.4), and this is also true of the Triumph ceremony (TRI), although cygnets do not show the characteristic Neck-Curved-Over posture until they are nearly fledged. Prior to this they Greet while their parents give the TRI display. For both displays, the accompanying vocalisations are much higher-pitched than those of the adults. (Adult ceremony pp104-105)

A cygnet initiating a GRE stands either at an angle to, or directly facing, the recipient and directs its head and bill movements to the other bird, which almost always responds by joining in. Thus it is possible to recognise initiator and respondent in most Greeting ceremonies.

(c) Climbing: when they were picked up and placed in my lap, the cygnets were not content to remain there but

climbed to settle on my shoulder (see Johnsgard & Kear 1968). This continued until they began to develop feathers (late Cl. II), although two birds, Ebony and Squeaker, continued to climb from the ground to sit in my lap long after it was impossible for them to sit at my shoulder.

In the wild, carrying of downy cygnets on the back of an adult is a behaviour pattern that the Black Swan shares with the Mute and Black-necked (*C. melanocoryphus*) Swans (Johnsgard & Kear 1968). However, carrying seems to be initiated by the cygnets, as adults make no effort to help them mount beyond staying still in the water while the young climb aboard. Young cygnets get cold and tired quickly and this behaviour pattern would provide them with a warm resting place while the family is on the water. Kear (1970) suggests that both carrying and creching may serve to reduce predation on the young (5.4.2).

(d) Vocalisations: these are important in maintaining family unity and also aid individual recognition (5.4.2). The cygnet begins calling while still in the egg (Kear 1972). About 2d. before hatching, the chick's breathing produces a clicking sound. Actual calling begins soon after this, especially if the egg is tapped or cooled. These pre-hatching vocalisations are probably similar to those described in the Greylag Goose by Fischer (1965), who distinguished three calls:

- (1) crying, or distress squeaking, when the egg is cooled or shaken;
- (2) the "wi" call, which seems homologous with the hatchling's contact call and is given in response to warming the egg (thus they would be stimulated by the parent resuming incubation after an absence), tapping the egg, and to noises e.g. parental calls, and sounds from other chicks;
- (3) the sleepy call, which often follows the wi-call and is the same as that given by tired hatchlings.

A number of the calls used by young cygnets are

variations on the wi-call. The basic call is the "contact" call (Kear 1972: "pleasure" call), a 4-6 syllable cheeping heard when the bird is feeding, preening, or moving in the company of siblings and parents. It probably serves to maintain group cohesion, until the greeting ceremony takes over this function.

The Greeting call consists of notes similar to the contact call but it is louder, delivered on a rising and falling cadence, and usually has fewer notes in each utterance. The characteristic posture of Greeting is not used by the cygnets until they are 5 - 7 days old, and the calls are infrequent before this age. When the cygnets are alarmed, 1-2 harsher calls precede a general Greeting ceremony.

"Sleepy" calls are given by cygnets huddled together and almost asleep. If still-active cygnets give these calls they will soon be huddling to doze or be brooded. The use of sleepy calls may lead to synchronisation of rest periods and facilitate parental brooding. They consist of a series of low soft trills, or slurred contact notes (Kear 1972).

Isolated, cold or hungry cygnets give characteristic distress calls. A deserted or threatened cygnet holds its neck stretched out obliquely, with all the down on its head erected, and gives one cry per breath (Fig. 5.8). The notes are high-pitched, slow and regular, and loud, and can be elicited from captive cygnets simply by disappearing from view. Hunger and cold calls are similar to the distress call (Kear 1972). All usually attract the parent and elicit the appropriate response. When hurt, cygnets give a loud, high-pitched shriek.

I have noted two threatening vocalisations. The first is a hiss; the second is a harsh single-syllabled call occurring together with the Head-Jerk Threat which appears to be a precursor of the adults' TRU display (Table 5.5).

PLATE 5.3: Cygnets following their
foster mother
(Photograph: B.A. Campbell)

PLATE 5.4: Greeting ceremony by
older (class V) cygnets



FIGURE 5.8: Distress posture of downy cygnet

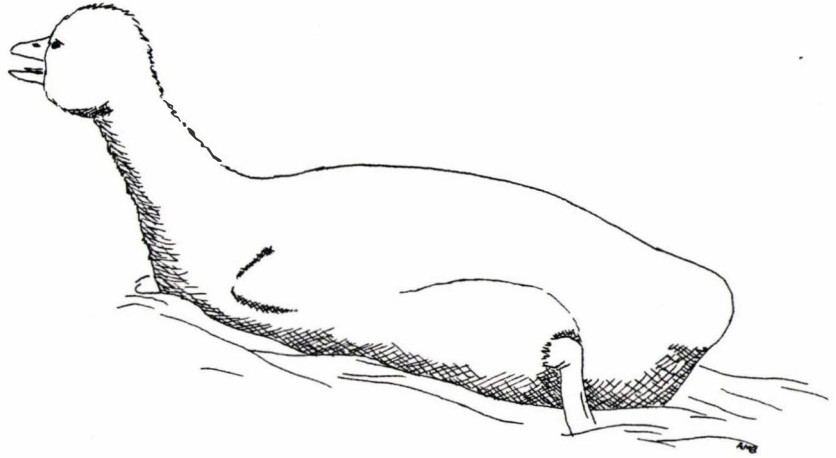
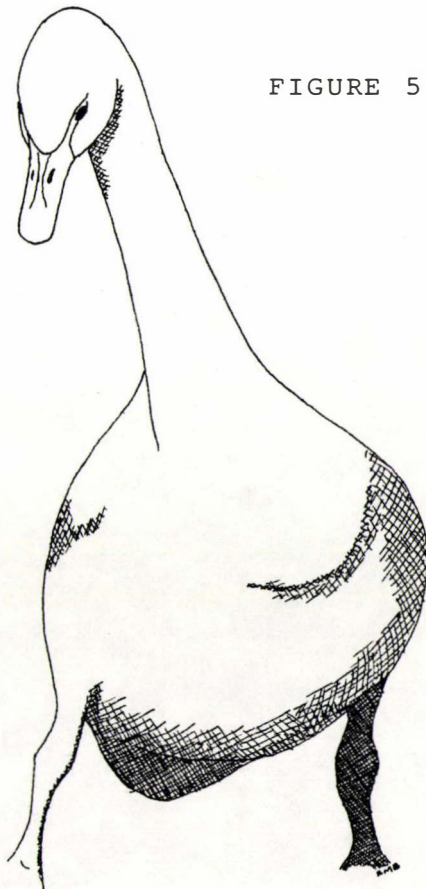


FIGURE 5.7: Avoidance of threat (from right)



5.3.2b Time of development of different behaviour patterns

The ages at which the cygnets' comfort, agonistic and social patterns first occur are presented in Tables 5.7, 5.8 and 5.9. Some points require elaboration.

The cygnets' growth, reflected in the gradual acquisition of feeding modes adapted to deeper water (Table 5.7), may have important effects on the use of an area by wild swans, as it means families are no longer restricted to feeding in shallow (shoreline) waters. Thus, by 8 - 10d., families on Pukepuke were moving widely and impinging on areas used by other swans (5.4.3).

Comfort movements (Table 5.7) such as standing on one leg and either stretching the other or using it to head-scratch only occurred in the first 5 - 6 days. Presumably after this period rapid weight gains made the birds ungainly and their balance for such acts was lost. These comfort movements are frequently seen again once birds are grown.

Intra-brood aggression (Table 5.8) on Pukepuke Lagoon, involving IMP, was first seen when those cygnets were 54 - 58d. old. A second scuffle, involving PEL and beating with the wings, was seen at 89 - 93d. However, it was difficult to observe the broods closely and many incidents would have gone unseen.

Once imprinted, my cygnets followed me readily (Table 5.9), staying very close (Plate 5.3) and becoming very distressed if left alone, although they quietened quickly if in their run. By 23d. they would go off alone, but would return if called, and were no longer upset when left alone. Their following distance by this time had increased from less than 1m between me and the lead bird to greater than 2m. By 48d. of age it was impossible to induce them to follow me until they themselves were ready to move. They could be left alone outside for 60 - 90 minutes and although they moved freely about the garden at such times they never left the property (of about 0.2ha), implying

recognition of a home range. By this stage they ranged widely and separately, no longer maintaining close physical contact with each other (see 5.3.3e).

5.3.3 Examination of social behaviour

5.3.3a Peck order within the group

I first saw intrabrood aggression when the aggressor was 14d. old, involving an IMP. The number of observed aggressive incidents (involving either threat or actual attack) over the entire rearing period was only 47 (Table 5.10; Fig. 5.9), so that it is not possible to draw many firm conclusions about the presence or development of a peck order within the group. However, the data suggest that two males, A and C, were the most aggressive while the two females, D and P, showed least aggression. There seems to be some relationship between a bird's putative rank and its physical development, particularly its acquisition of adult bill colour (Table 5.4; 5.4.3). The forms of aggression used in disputes within the brood are presented in Table 5.11. The most common of these was PEL, with or without holding and tugging at the victim's plumage, followed by IMP. There were few calls during these incidents. This may be compared with data collected during a brief period at Western Springs Park in Auckland, in December 1980 (Appendix V). A large (100 - 200) population of Black Swans exists there year-round, with 12 - 15 pairs breeding on the lake. The most common intraspecific aggressive act was again PEL (15/36), followed by THR_{me} and THR_{hi} (Table 5.5; descriptions Ch. 3, 3.3.1). IMP, always with a hiss, was used in all 8 interspecific threats. The only intraspecific threats accompanied by a vocalisation were 3 IMP during feeding squabbles and 2 THR_{hi} during boundary disputes.

A cygnet's response to aggression depended on the form of threat used by its sibling (Table 5.6).

TABLE 5.7: AGE OF FIRST APPEARANCE OF COMFORT AND
MAINTENANCE BEHAVIOUR PATTERNS

Age of cygnets (days)	Behaviour patterns
1-2	<p>Dabbling and sieving when feeding.</p> <p>Bill-clean, wing-flap, yawn (= jaw-stretch), foot-stretch, foot-nibble, head-scratch, head-flick and head-shake, body shake, general but skimpy oiling preening, in preening bouts.</p> <p>Climbing to adult's back (Pukepuke) or my lap and shoulder.</p>
3	<p>Grazing ashore (16d. for 1979 cygnet; 8+d. on Pukepuke).</p> <p>Neck-dips during bathing.</p>
4	<p>Wing-shuffle, wing-stretch, tucking one foot up into flank feathers.</p>
5	<p>Feed-Neck-Down in shallow water.</p> <p>Bathing with neck-dips, wing-thrash, swimming shake and incomplete somersaults.</p>
9-10	<p>Feed-Up-Ended in deeper water (11+d. on Pukepuke).</p> <p>Lengthy bouts of oiling preening.</p> <p>(End of parental carrying on Pukepuke).</p>
11-12	<p>Complete somersaults during bathing (14d. on Pukepuke).</p> <p>Bills tucked under wings to sleep.</p>
19	<p>Both-legs-stretch while lying on belly.</p>
33	<p>Foot paddling during feeding.</p>

TABLE 5.8: AGE OF FIRST APPEARANCE OF AGONISTIC
BEHAVIOUR PATTERNS

Age of cygnets (days)	Behaviour patterns
2	Threatening hiss from side-on position at human. (c.f. 8d. in Mute Swan, 24d. in Trumpeter: Kear 1972)
9	Hiss at cat.
12	Pecking Lunge (PEL); Intention-Movement-to-Peck (IMP) with hiss then lunge; both in interspecific aggression.
14	IMP - first intrabrood aggression.
20	PEL in intrabrood aggression.
28	Hiss and PEL at cat. Head-Jerk-Threat (HJT - early Trumpet) at human.
29	PEL and tugging feathers in intrabrood aggression.
36	Running charge at cat.
38	Hopping on both feet while charging.
47	Capable of pulling feathers out in fights. Full adult Trumpet (TRU).

TABLE 5.9: FIRST APPEARANCE OF BEHAVIOUR PATTERNS
INFLUENCING SOCIAL RELATIONSHIPS

Age of cygnets (days)	Behaviour patterns
-2	Distress squeak, wi-call (= contact call) and sleepy call, all while in egg (Fischer 1965).
0-1	Contact, sleepy, distress and pain calls.
5	Greeting call and posture used in sib:sib greetings. Following of parents established.
6-7	Brood greets parents and shares parental Greeting ceremony (8+d. on Pukepuke Lagoon).
23	Beginning to move independently of parents.
100	Join parental Triumph ceremony fully, rather than with just greeting calls (Western Springs, Auckland).

TABLE 5.10: TOTAL AGGRESSIVE INTERACTIONS
WITHIN A CRECHE

	Receiver of threat or attack						total threats given
	A	D	C	L	S	P	
A	-	5	2	2	3	6	18
D	1	-	0	0	1	0	2
C	1	2	-	2	4	8	17
L	0	1	0	-	0	2	3
S	0	2	0	2	-	0	4
P	0	0	1	1	1	-	3
total threats received	2	10	3	7	9	16	47

TABLE 5.11: INTRA-BROOD AGGRESSION: FORM,
CONTEXT, AND VOCALISATIONS

		Context				Total, each form
		Not recorded	Feeding ²	Preening/ Huddling ²	Moving	
form of aggression	Hiss only	0	0	1	1	2
	IMP	0	5 (1xhiss)	9 (2xcall) ¹	4 (1xgreet)	18
	PEL	2	13	8 (1xhiss)	4 (1xhiss)	27
Total incidents by context		2	18	18	9	47
Total vocalisations		0	1	4	3	8

1: call usually associated with Head-Jerk-Threat.

2: major activity, but with individuals moving about.

Number of threat/attack forms: 3

Number of overt attacks: 27 (PEL)

Number of threats: 20

FIGURE 5.9: Comparison of overall intrabrood aggression with greeting ceremonies from first and final observation periods (Direction of arrows indicate aggressor or initiator of greeting.)

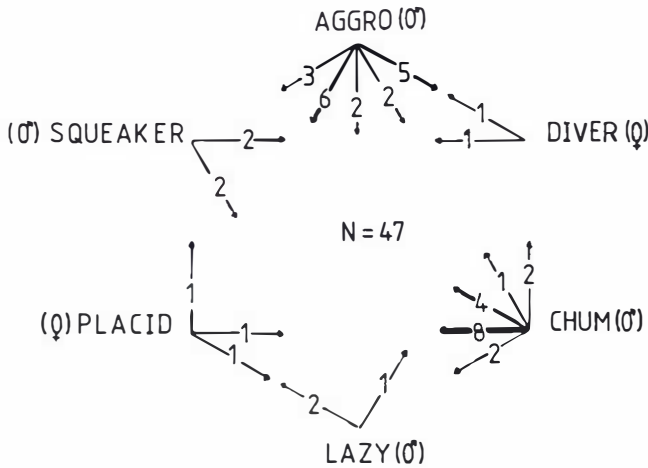


FIGURE 5.9a: Aggression within the group 26/9/80-23/11/80 (First incident 5/10/80).

FIGURE 5.9b: Greeting ceremonies within the group 6/10-12/10/80 (Group not settled in until 5/10/80).

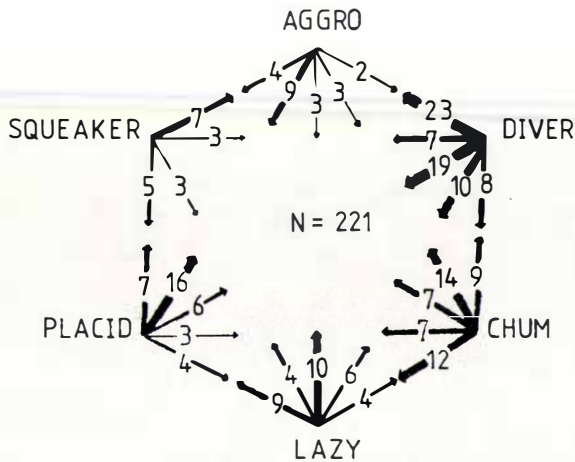
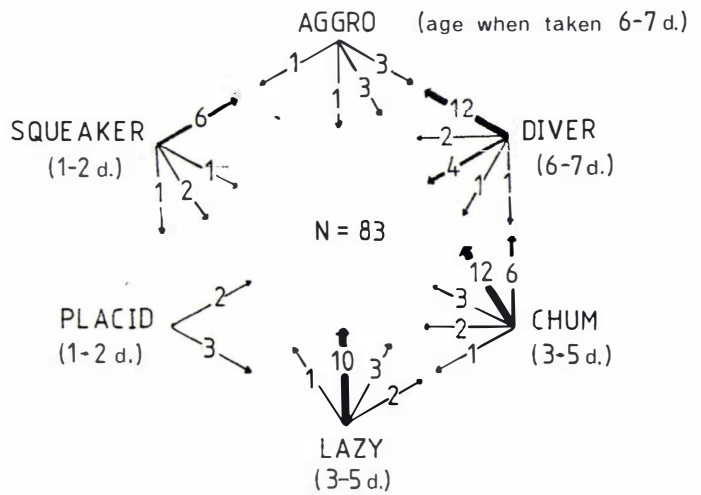


FIGURE 5.9c: Greeting ceremonies within the group 10/11-23/11/80.

5.3.3b Aggression directed outside the brood

The total number of observed aggressive incidents directed outside the brood, most involving other humans or a cat, is small ($N = 46$). However, an examination of the number of acts performed by each cygnet, and the separation of these into threats performed by one individual alone or as part of a group, supports the finding in 5.3.3a that A and C were the most aggressive birds in the group (Table 5.12).

Extra-brood aggression involved a greater number of threat forms than did disputes with siblings, ranging from a hiss alone to a full charge, and was accompanied by a greater number of vocalisations (Table 5.13). The sound most frequently used was a hiss (30 of 40 calls).

Intra- and extra-brood aggressive behaviour observed in captive cypnests also differed in the proportion of actual attack involved. Thus only 14/46 extra-brood acts included a charge or PEL, while 27/47 PELs were recorded in sibling aggression. The emphasis on physical attack in sibling aggression may have some bearing on the development of a peck order (5.4.3).

5.3.3c Development and delivery of Greeting ceremonies

The development of the Greeting ceremony is described in 5.3.2. Once the group as a whole had developed a mutual Greeting ceremony, greetings were given very frequently ($N = 682$ in 142.5h. detailed observation) and in a variety of contexts (Table 14a). Of 478 greetings examined by context (more than one individual might initiate a greeting at one time in a given context), 251 occurred while the group was moving, probably in response to the disturbance and mixing caused by movement i.e. greetings were delivered to "new" individuals. Aggression-related greetings were surprisingly uncommon (20/478), although their frequency increased with age, as did that of aggressive incidents. This may indicate the relatively late development of a rank order (5.4.3). Most such greetings were from victim

to aggressor and followed the incident (Table 5.14b).

It is difficult to distinguish any pattern in the frequency with which given individuals initiated and responded to greetings, or to relate the results to position in a social hierarchy, as has been done for geese (Stahlberg 1974). The bird found to be most aggressive, and so presumably at the head of a hierarchy, was A, who received the most greetings and gave very few (Table 5.15; Fig. 5.9). However, no clear relationship emerges for the rest of the creche. For example, D, perhaps one of the lowest-ranking cygnets, initiated greetings more than any of the others except C, who on the evidence from 5.3.3 a&b was next to A in the hierarchy.

5.3.3d Order when following

The captive brood almost always moved from place to place in single file. Analysis of the positions which they assumed in the file shows distinct differences between individuals (Fig. 5.10). Thus A or S tended to lead while C came last and D took a central position. These inter-individual differences are significantly different in both first and fourth observation periods (Friedmann 2-way analysis-of-variance; Siegel 1956: 166-172). For the first period, individual differences are significant at the 95% level (d.f. = 5, $\chi_r^2 = 11.1384$, $0.05 < p < 0.01$).

There was some change in preferred position with age, so that A and S, especially, tended to lead less often in the last 14 days of observation. This may be due to the fact that in the first 14 days almost all moves were begun by me, while cygnets initiated most shifts during the last 14 days. This would give those cygnets least attached to me an opportunity to lead off. However, a Spearman rank correlation (Siegel 1956: 202-213) indicates a strong positive correlation ($N = 6$, $r_s = 0.95$, $p < 0.01$) between the file positions of the cygnets in the first and final observation periods.

This same test, used to examine the relationship

between position in the file and greetings initiated or received in the same two periods, indicates a slight (non-significant) positive correlation between the number of greetings received and file position ($N = 6$, $I_{r_s} = 0.4928$, $IV_{r_s} = 0.4857$), and a slight (non-significant) negative correlation between position and greetings initiated ($N = 6$, $I_{r_s} = -0.3929$, $IV_{r_s} = -0.6858$) (5.4.3).

5.3.3e Group cohesion

Once the cygnets had begun settling in and developing a Greeting ceremony, I noticed that some individuals appeared to prefer the company of certain others. To examine this more closely I used a Single-Link-Cluster-Analysis (SLCA) proposed by Morgan *et al.* (1976) to show up subgroups within the brood and also to provide a measure (albeit an arbitrary one) of brood cohesion. This measure is a function of the number of counts in which individual cygnets were seen as part of a group rather than alone.

The results of this analysis are presented in Figure 5.11 (drawn from data tabulated in Appendix VI). This shows that for the first 4 weeks (up to about 32d. old) the creche was more close-knit than in the second half of the study, when the cygnets began to spend more time apart from each other. On Pukepuke Lagoon, both male and female parents were tending to leave the broods alone by this age, without the cygnets showing any distress. Similarly, the study group was frequently moving independently of me by the second half of the study (approx. 33-64d. old). By the time the Pukepuke broods reached 66d. they were splitting into subgroups and remaining in them for lengthy periods, quite independently of their parents' movements. This tendency to separate and spend time apart from the parents culminated in family and brood disintegration at 90-100d., with little or no intra-familial aggression being apparent.

Little can be said about subgroupings within the study creche, mainly because the data are not spread out

TABLE 5.12: FREQUENCY OF LONE AND GROUP ACTS SEEN
DURING EXTRA-BROOD AGGRESSION

Individual	number of involvements	single acts	group acts	group composition
A	20	13	7	4x in ADCLSP 1x ADC, AS, AL
D	6	1	5	4x ADCLSP, 1x ADC
C	18	10	8	4x ADCLSP 2x CS 1x CS, ADC
L	9	1	8	4x ADCLSP 1x LPS, LS, CL AL
S	16	6	10	4x ADCLSP 2x CS 1x LPS, SP, LS AS
P	8	2	6	4x ADCLSP 1x LPS, SP
Total involvement	77	33	44	group composition varied

There were: 46 separate incidents directed at objects outside the brood;
77 individual threats
33 incidents involving only one individual, while 13 involved two or more cygnets acting together

TABLE 5.13: AGGRESSIVE INCIDENTS DIRECTED OUTSIDE THE BROOD: OBJECT OF THREAT/ATTACK, THREAT FORM, AND VOCALISATIONS

	Object of threat/attack					Total each form
	Human "mother"	other	Cat	Passerine birds	Inanimate objects	
Hiss only	1	1	4	-	-	6
Defensive IMP	1	1	1(1xhiss)	-	-	3
IMP	-	1	7(7xhiss)	1(1xhiss)	2(2xhiss)	11
Defensive HJT	-	2(2xcall)	-	-	-	2
HJT/TRU	-	7(7xcall)	1(silent)	-	1(1xcall)	9
PEL	-	-	2(2xhiss)	-	-	2
SWF	-	1	-	-	-	1
Charge	-	-	9(9xhiss)	1(1xhiss)	2(2xhiss)	12
Total threats	2	13	24	2	5	46
Total vocalisations	1	10	22	2	5	40

Number of threat/attack forms = 6

Number of overt attacks = 14 (PEL, charge)

Number of threats = 32

1 e.g. washing flapping on line; blowing leaves

TABLE 5.14a: CONTEXTS IN WHICH GREETING CEREMONIES OCCURRED

Observation period	Context						Total for period
	bathing	feeding	preening/ huddling	alarm	aggression	moving	
I (6/10-12/10/80) ¹	3	12	12	4	0	28	59
II (13/10-26/10/80)	3	26	10	7	0	77	123
III (27/10-9/11/80)	5	36	16	3	5 ²	73	138
IV (10/11-23/11/80)	4	35	27	4	15 ³	73	158
Total over study	15	109	65	18	20	251	478

1: Number of ~~intra-brood aggressive incidents over~~ period III = 17.

2: Number of intra-brood aggressive incidents over period IV = 30.

3: Behaviour observed from 29/10/80 on, but imprinting not complete until 2/11/80.

Greetings given in an agonistic context subdivide as follows:

TABLE 5.14b: AGGRESSION-RELATED GREETINGS DIVIDED BY DIRECTION AND TIMING

	Direction		total greetings
	aggressor greets victim	victim greets aggressor	
Greeting precedes incident	2	3	5
Greeting follows incident	2	13	15
Total, each direction	4	16	20

TABLE 5.15: SUMMED GREETINGS FROM ENTIRE STUDY PERIOD

Individual initiating greeting	Individual receiving greeting						Total given
	A	D	C	L	S	P	
A	-	10	11	12	10	18	61
D	71	-	16	20	18	37	162
C	58	34	-	32	18	21	163
L	45	26	15	-	12	28	126
S	24	10	3	10	-	11	58
P	44	22	14	20	12	-	112
Total received	242	102	59	94	70	115	682

FIGURE 5.10: Preferred positions in moving file, for first and final observation periods

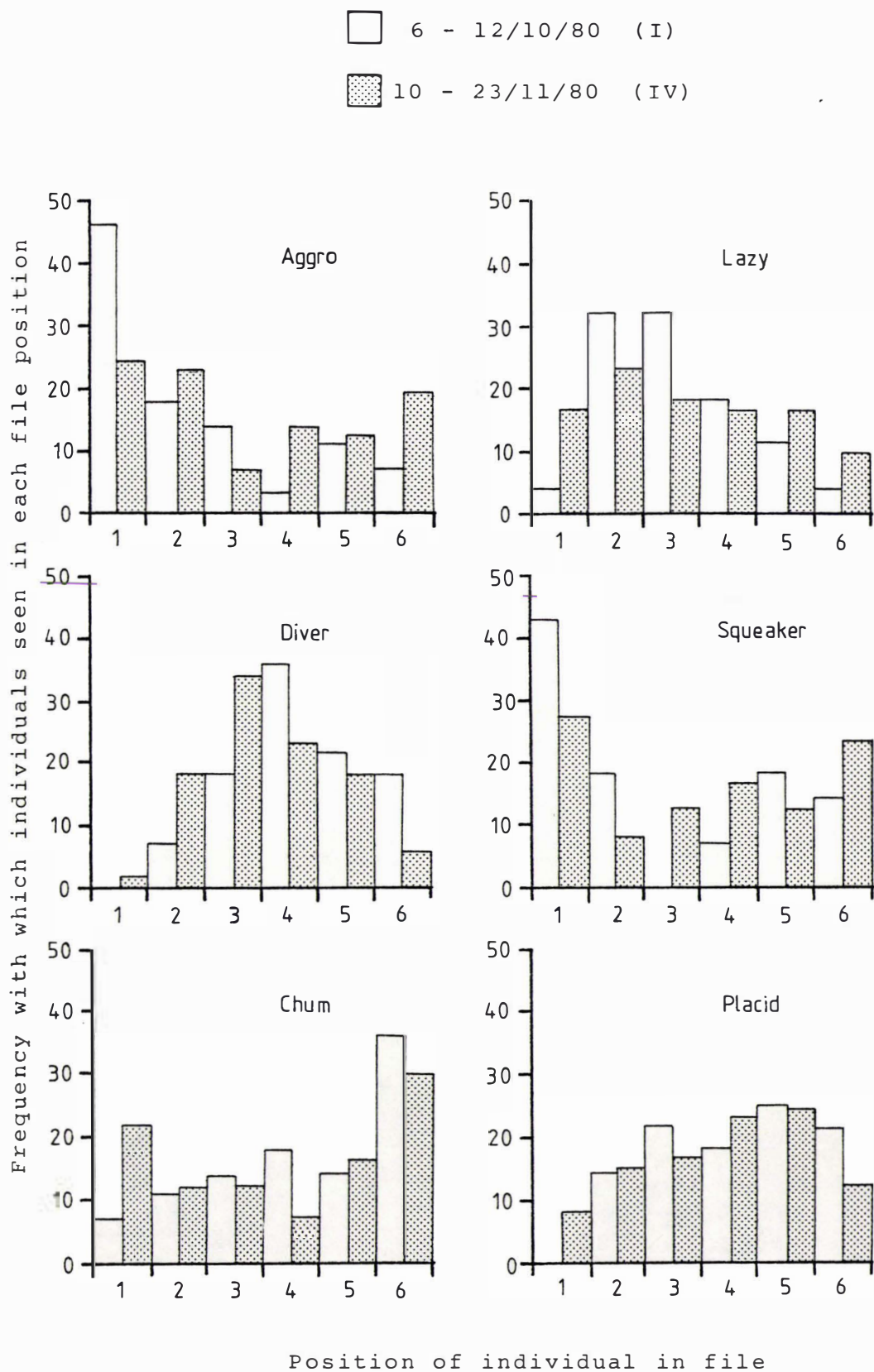
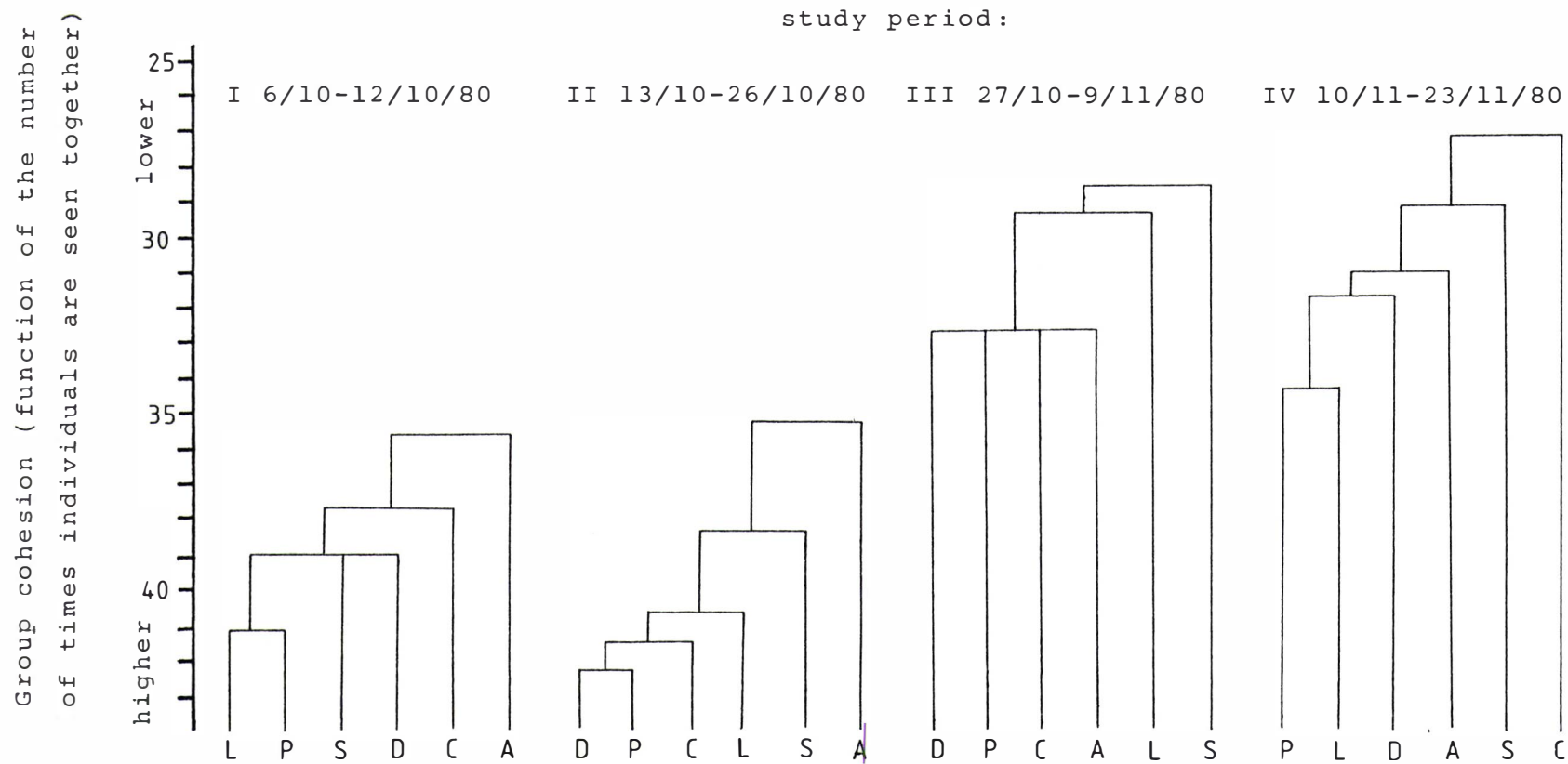


FIGURE 5.11: Dendrogram derived from SLCA (Appendix VII), giving a measure of changes in group cohesion



sufficiently along the vertical axis (group cohesion) for clear divisions to be drawn (Fig. 5.11). Generally, P tended to associate fairly closely with D, and to a lesser extent with L and C. This may explain P's fairly random placing in a moving file (5.3.3d; Fig. 5.10), with a tendency to avoid the leading position occupied by A or S. Squeaker tended to wander more widely than the rest as he got older, which would help to explain his lower cohesion values in periods III and IV, while at the same time to mix more with the others when moving (Fig. 5.10), and to spend more time grouped with them.

5.4 DISCUSSION

5.4.1 Matters relating to the use of captive birds

The birds used in this study were reared in captivity and it may be argued that data obtained from them are ~~inaccurate or irrelevant~~. ~~Certainly, their physical development~~, to the age of 60 - 70d., was faster than that of wild cygnets, particularly in the later stages of feathering (Tables 5.2, 5.3 a&b). This may be attributed to the constant supply of high-quality food that was available and to lack of harassment by other (adult) swans, and it probably affected the ontogeny of those behaviour patterns, such as deep-water feeding, which are limited by size and strength.

The frequency of performance of some acts may also have been influenced by the conditions of captivity, but the form of behaviour patterns should not have been much affected (Dilger 1962), and comparison with data obtained from wild birds should in any case show up any gross abnormalities. An example here is the finding that, given the opportunity, captive birds continued to climb onto and be carried by their "parent", long after increasing cygnet size made such behaviour impossible for the wild broods.

Some of the cygnets' behaviour may have been affected

by the age at which I obtained them. The fact that Ebony (1979) did not graze until she was 16d. old (Table 5.7) may be due to her being taken when only 1d. old, so that she probably never observed adults grazing. (She came from Western Springs, Auckland, where birds seldom graze ashore.) This theory requires that some learning be involved in choice of feeding method (5.4.2). Ebony was also small for her age (still less than the average hatching weight, at 9d.) and may have been physically unable to tear at the grass.

Also of relevance here is the fact that the cygnets reared in 1980 were taken from several family groups, and thus could be viewed as an artificial creche (5.4.2). They were of different ages and may or may not have been related, and these factors probably influenced the time of development of an intra-brood Greeting ceremony and also their recognition of me as a parent. Thus, although Pukepuke broods had developed Greeting ceremonies, including their parents, by 7d. old, the oldest birds of my creche were 10 - 12d. old before I was included in their shared Greeting ceremony. This implies that there is a lengthy sensitive period in which filial imprinting may take place (5.4.2). Sexual imprinting takes considerably longer. Hand-reared cygnets released at 60 - 70d. old may later mate successfully with other swans: Ebony mated and produced a clutch when 14 months old. Thus sexual imprinting is not finalised by the time of fledging.

5.4.2 The processes and implications of imprinting and individual recognition

The process of imprinting and the development of individual recognition are basic to the development of many, if not all, of the social behaviour patterns examined in this study.

Imprinting is a learning process which is generally viewed (Bateson 1966; Hinde 1970; Immelmann 1975) as being restricted to a "sensitive period" (*ibid.*) ranging in

length from the first few hours to the first few days of a young animal's life. Strictly speaking, this describes filial imprinting (Immelmann 1975); sexual imprinting, affecting mate choice, may take up to several months (5.4.1; Immelmann 1972).

The sensitive period is held to be relatively short in nidifugous young, such as Black Swan cygnets, which are capable of moving about very soon after hatching i.e. its lower limit must be related to the hatchling's ability to follow the imprinted object. The course of imprinting is marked by the rapid acquisition of a following response directed at some conspicuous and specific mobile object, generally the parent. Initially, the readiness with which neonates follow the stimulus increases with age. After a variable length of time (but generally less than or equal to 7d. after hatching: Hinde 1970; Vidal 1980) readiness to follow a novel stimulus decreases and strange objects may instead be actively avoided. Thus imprinting on an object, and the learning of that object's individual characteristics, overlap. The appearance of the avoidance response is usually seen as marking the end of the imprinting process. However, it has recently been found that, depending on previous experience, following responses may be elicited in chicks more than a month old (Vidal 1980). Two cygnets (A and D) which were approximately 7d. old when captured soon acquired a following response directed at myself.

Both auditory and visual stimuli are important in imprinting on and recognition of family members. It has been found that, for some species at least, "the most effective auditory stimuli resemble the calls of the natural parent" (Bateson 1966: 210), and I discovered that my hand-reared cygnets responded by greeting to my voice alone, even when I was out of sight. In fact, Bateson *et al.* (1980) conclude that although visual cues are of importance in individual recognition by Bewick's Swans, auditory cues are probably basic. Braithwaite (1981b) reaches the same

conclusion for *C. atratus*. However, the presence of a large, conspicuous moving object, which may or may not vocalise, is central to imprinting *per se* in neonates (Vidal 1980).

Thus, imprinting involves a following response directed to some conspicuous object, while at the same time the young animal learns the specific individual characteristics of the imprinted object. There is temporal overlap of the two processes.

It is logical to assume that the speed with which imprinting is completed would be related to the degree of mobility of the new family and the likelihood, and consequences of, their mixing and interacting with other family groups. Immelmann (1975: 24) states that "...under natural conditions the duration of sensitive periods is adapted very accurately to the biology and the specific ecological demands of a species". Thus in those species where the young are kept apart from others, either through direct parental interference or by restriction to a nest site (more relevant to altricial species e.g. Beecher *et al.* 1981 a&b: Bank Swallows *Riparia riparia*), the sensitive period for imprinting could reasonably be a lengthy one. It should be noted at this point that the accompanying learning process is a two-way one, so that the brood's characteristics are learned by the parents (Brown & Urban 1969; Prevett & MacInnes 1980). This has bearing upon the age of occurrence of some behaviours e.g. creching, or adoption of orphaned strange young.

The development of imprinting and family relationships have been well-studied in geese, swans' close relatives, but data for swans themselves are few. Braithwaite (1981b) states that imprinting in *C. atratus* is complete within 48h. of hatching, and that separation of parents and young within the first 30 - 40 days of cygnet life generally results in serious rearing difficulties, or death of the young. However, I experienced no problems in rearing cygnets whose ages when captured varied from 1 to 7 days. Assuming that recognition of parents and siblings is signalled by the

development of a Greeting ceremony and a strong following response, I suggest that the "sensitive period" in Black Swans covers at least 7 days, and recognition may take still longer to be finalised. Kear (1972) provides similar and supportive information for the Arctic-breeding northern swans, whose cygnets will follow humans instead of their parents at 7d. of age, but at 14d. have developed a fear reaction to novel stimuli. Thus imprinting in these swans must take some intermediate period. Such a lengthy sensitive period for learning parental characteristics is possible because these swans are strongly territorial and keep others far from the nest, so that cygnets have no opportunity to follow non-parents and immediate and precise imprinting and recognition become unnecessary. This is probably true for the strongly territorial Mute Swan as well.

The implications of the Black Swan's relatively long sensitive period for imprinting are many.

A conclusion of some importance with respect to the geographical and behavioural history of the Black Swan is that it was originally territorial, and has only recently developed the colonial nesting habit, probably in response to the transient nature of suitable breeding habitat in Australia. This would explain the presence of a lengthy imprinting period, whereas if colonial nesting were an evolutionarily ancient habit one would expect that, since the young are nidifugous, imprinting would have tended to take place over a shorter period, preventing brood mixing and the undue loading of some parents with more than their usual quota of young to defend. Some Black Swan populations do breed territorially (Braithwaite 1970; Williams 1980; this study) and in these cases usually fiercely defend their young from other birds. Furthermore, on the basis of evidence relating time of breeding to photoperiod, Murton & Kear (1973, 1978) suggest that the ancestor of the Black Swan may have evolved at higher latitudes than those covered by the species' present range. Breeding conditions then could have been similar to those affecting the extant

northern swans: a shorter breeding season, bringing with it a need for rapid growth of young and thus a need for a plentiful food supply, so leading to territorial breeding.

A lengthy imprinting period, coupled with the now-usual breeding habit of colonial nesting, permits the formation of creches of young in some situations. In many different species which nest colonially, nesting and hatching are generally fairly synchronous, if not for a colony as a whole then at least for subgroups within it (Nelson 1966; Brown & Urban 1969: Great White Pelican *Pelecanus onocrotalus roseus*). Thus large numbers of similarly aged young become available at one time and in a close-packed colony, especially if parental defence is weak and chicks are mobile, some mixing of broods would be inevitable. If imprinting were a very rapid process then brood-coalescence would soon become impossible, due to the rejection of strange young by both parents and offspring (e.g. Prevett & MacInnes 1980). However, in Black Swans the 7+d. learning period allows brood mixing and creche formation and creches have been observed to form from many different broods (Williams 1980) up till the class II stage of approximately 14d. (I. Buchanan pers. comm.). Also, given that some swans are poor parents in that their care and defence of the young is inadequate (I. Buchanan pers. comm.; pers. obs.), imprinting could theoretically take longer in such families as the cygnets would not be subject to constant parental presence and care (Hinde 1970). This could further extend the period in which creche formation is possible. Logically, once imprinting and recognition are finalised, composition of creches would remain constant.

The function of creching in the Black Swan is unclear. Kear (1970) suggests that both creching and carrying of young may reduce predation on the brood. Munro & Bédard (1977) have drawn a similar conclusion on the function of creching in the Eider Duck *Somateria mollissima*. However, *C. atratus* has few natural predators and their effects are

not held to be great (Guiler 1966; Lavery 1965; Lickers 1977). An alternative possibility for carrying is that it provides a warm resting place for the young cygnets, whose thermoregulatory ability is poor (Ricklefs 1968), while the family is on the water. Creching may serve a similar function when the group is on the land, as many young birds huddled together would be expected to conserve heat more efficiently than individuals (Brown & Urban 1969). A further suggestion (M. Williams pers. comm.) is that creches develop in locations where food supplies are concentrated in large discrete areas (e.g. *Ruppia* beds on Lake Ellesmere), and may promote more efficient feeding. Creching of young may also free some pairs to renest and produce second clutches (I. Buchanan pers. comm.), but although swans may produce a second clutch if the first is destroyed during incubation (pers. obs.), it is not clear whether they can do so once the first brood has been reared. Norman (1971) mentions second clutches, laid in nests already used once in the season, but does not say whether both clutches were produced by the same pair. The apparent costs and benefits of creching will be further discussed in Chapter 7.

Braithwaite (1981b) suggests that there is a close relationship between imprinting and a cygnet's ability to find and utilise food material. There is probably some relationship between close following of the parents and learning of food sources. De Jong & Bacon (1979) found that for Mute Swans, when the brood is very young the parents, particularly the female, initiate feeding activities and movements between feeding areas, in which they are invariably followed by the young. This pattern may be reversed later in development. Thus it is possible that the young learn where to feed and what to eat through observing their parents. Supporting this theory is my finding that a cygnet taken very soon after hatching and so with little, if any, experience of feeding with other swans did not begin grazing on dry land for several days, while the group captured while feeding on land with their parents were grazing even at 2d. old. Kear (1972) notes that adult swans with

young broods will pull vegetation up to the surface more frequently than when alone. This undoubtedly assists the young in feeding, especially in deep water, and they may again be learning what and where to eat. Parents with young also foot-paddle frequently, an act which stirs up detritus from the bottom and provides the young with another food source. Hence the development of a following response, ensuring close contact with the parents, is of great advantage to young cygnets.

5.4.3 Brood cohesion and social relationships

When following their parents, cygnets usually assume a single-file pattern. Although positions in the file may change, individuals seem to have preferred places in it (de Jong & Bacon 1979; 5.3.3d). It is possible that the frequency of leading the file is an indication of attachment to the parent. Thus decreasing attachment, together with increasing independence and decreasing brood cohesion (5.3.3e) would lead to more variation in the file position taken by each bird. De Jong & Bacon (1979) found that the order of following was also influenced by the development of a peck order, a process which took several weeks in their Mute Swans, and that those cygnets presumed to be dominant stayed closer to the parents and attained better growth rates than those left to follow. (This relationship was not apparent in my study.) This may be related to D. Scott's (1980) finding that Bewick's Swan cygnets which stay closer to the parents are better protected from harassment by other swans and are able to feed with less interruption. As cygnets get larger they tend to follow their parents less and to range more widely (5.3.3d, 5.3.3e). By this time, however, they are more capable of opposing strange swans and may win aggressive interactions with them, especially if they are still on their parents' territory (pers. obs. on Western Springs; see also D. Scott 1980).

Increasing cygnet mobility, which allows the whole family to range more widely, will lead to increased contact

with other swans. It has been suggested (K. Potts pers. comm.) that on Pukepuke Lagoon this may result in a drop in the number of flock birds through harassment by parents once the cygnets become mobile. I have no evidence for this; however, the areas used by flock birds are restricted once cygnets come out onto the main lake (Ch. 2, Ch. 3).

Of equal importance to following in the maintenance of family cohesion is the use first of contact calls (5.3.2a; Kear 1972) and later of a shared family Greeting ceremony. The Greeting ceremony does not develop in Black Swans until imprinting is at least partially completed. This implies that it entails individual recognition of family members, and indeed, vocal characteristics are held to be very important in this respect (Bateson et al. 1980; Braithwaite 1981b). In geese it has been found that the delivery and form of the greeting ceremony is related to the rapid and early formation of a stable peck order within the brood (Fischer 1965; Kalas 1977; Radesäter 1974b; Stahlberg 1974). I found that no definite peck order had developed in my captive brood by the end of an 8-week period, while greetings were very frequent once the shared ceremony had appeared at about 5d. of age. No evidence of aggressive motivation could be found in the majority of greetings and it seems likely that they are related, in the Black Swan at least, to some other facet(s) of social behaviour. It should be noted, however, that development of a peck order may be quite slow, as the number of greetings definitely associated with aggression, although small, increased towards the end of the study. The frequency of intrabrood aggression showed a similar age-related increase (Table 5.14a). Braithwaite (1981b) found a social hierarchy to be apparent when Black Swans were 70 - 80d. old, while de Jong & Bacon (1979) state that peck order development takes several weeks in Mute Swans.

Stahlberg (1974) found the frequency of greeting in Greylag Geese to be related to the group's peck order. She cites unpublished work by Radesäter, who found this to

be an inverse relationship, such that the most dominant bird received the most greetings and delivered least. Stahlberg's own data show an opposite trend. Radesäter (1974b), Stahlberg (1974) and Kalas (1977) also found that the greeting ceremony had the effect of reducing intrabrood aggression (see also Fischer 1965), by the development and increasing use of a submissive posture during the ceremony ("Facing Away": Radesäter 1974b). Actual rank in the peck order was decided by the outcome of fights occurring in the first 40d. of life (Stahlberg 1974); thereafter Facing Away during greeting ceremonies replaced actual fighting.

In this study data pertaining to peck order development were few (N=47) and no obvious hierarchy had developed by the end of the study (cygnet age 60 - 70d.), although two clearly dominant individuals, A and C, could be recognised (Table 5.10). Greeting ceremonies were very common once imprinting and recognition were finalised but of the 682 greetings analysed only 20 showed any temporal relationship to aggression. No postural differences similar to those described by Radesäter (1974b) and Kalas (1977) for dominant and subordinate birds were apparent in my group, although it is possible that the avoidance postures seen in response to attack (Fig. 5.7) could be similar in nature to Radesäter's Facing Away. (However, this posture could be simply a consequence of flinching away from the aggressor. I have not observed a similar posture in Greeting ceremonies between adult swans.) Nor was the frequency of giving and receiving greetings clearly related to the tentative peck order (Fig. 5.9), although the highest-ranking cygnet (on the basis of both intra- and extrabrood aggression) received the most and gave very few. No such relationship emerged for the next most aggressive swan.

Greetings were initiated most frequently when the brood was moving about *en masse*. They also occurred, at a lower frequency, during feeding or loafing bouts (Table 5.14a), although in the latter contexts they were usually the result of an individual coming up to or pushing in against one or more others, thus causing a minor disturbance.

General group Greetings (not analysed here) always followed a disturbance due to animals, other humans, or "hawks", and those recorded during bathing usually followed bursts of dashing-and-diving play, which could also be viewed as a disturbance. In all these cases greeting may be regarded as aiding individual recognition (Bateson *et al.* 1980; Braithwaite 1981b; Fischer 1965; Kear 1972) and as functioning to ensure family unity after disturbance and while travelling. Prior to the development of a full Greeting ceremony these functions are fulfilled by the use of more generalised "contact" calls (Kear 1972; pers. obs.). Any approach and/or suitable vocalisation on my part almost always resulted in a Greeting ceremony, but this was first directed to me although cygnet-cygnet ceremonies might follow. In the wild cygnets and parents generally respond to each other's greetings.

Greeting frequency does show some small relationship to the cygnets' preferred order when moving around, such that there is a slight positive correlation between the position in line and the ranking of greetings received. The bird(s) leading the file tended to receive more greetings than the trailing individual, while those with a central position were intermediate in the number of greetings received. One interpretation of this result is that the first bird to move disturbs or alarms the others, or perhaps presents them with a "new" individual requiring recognition, and so is greeted by them, while the one at the end initiates many greetings with those passing him/her as the group moves off but receives few because he is not presenting the same "alarming" stimulus. It must be noted that the brood never rose as one to move anywhere, and also that the first and last to rise usually stayed in those positions, while there was some shuffling of intermediate positions.

Imprinting was fairly complete, as indicated by the use of the shared Greeting ceremony, before any intrabrood aggression was observed. This is to be expected since

any peck order could not be sorted out until siblings could recognise each other. No clear peck order could be discerned as the total number of aggressive incidents was small. However, since they increased in frequency as the birds grew older it is possible that, as suggested earlier, the development of a social hierarchy within Black Swan broods is a slower process than has been found for other species studied. It could be expected that the frequency of aggression-related Greeting ceremonies would also increase with age.

A number of physical and behavioural variables could have an effect on the position of any given individual in a social hierarchy, in addition to the social behaviour patterns already considered. Those given some attention here are sex, physical size and growth rate, bill colour, and individual idiosyncracies in behaviour.

With regard to sex, both high-ranking birds, A and C, were male, while the two seemingly lowest, D and P, were female. However, the number of cygnets available was too small for any firm conclusions to be drawn (a criticism which can reasonably be extended to many hypotheses offered here). Nor did physical size and growth rate bear any apparent relation to rank, with males and females having very similar rates of weight increase (Table 5.1), while D was the next heaviest bird, after A, for much of the study. Aggro and Diver were oldest and heaviest at the time of capture and maintained their lead in weight over most of the rearing period.

Changes in bill colour may be important in rank-order development among young swans. The bright red adult bill is prominent in many threats, particularly the male territorial Parade but also those lower-intensity threat displays in which head and bill are pointed towards the opponent at close range. Cygnets avoiding (c.f. Facing Away) or adults fleeing from an attack turn the bill away from the aggressor. The two most dominant birds of my brood, A and

C, began developing adult bill colour some time before the lower-ranking cygnets, while D and S were the slowest to begin development (Table 5.4). Also the 1979 cygnet, E, directed several threats towards red objects.

It should also be recognised that individual differences in behaviour may be important in determining the development of dominant/submissive behaviour. Thus A and C were highly aggressive, tending to thrust in among or over the others most often as well as threatening them, and frequently using solo threats directed outside the brood (Table 5.12). Together with S, they were the most confident in human company, coming readily to be shut away in the evenings and offering no resistance to handling. Squeaker in particular would frequently approach me of his own accord and attempt to climb onto my lap if I was sitting down. This "climbing-to-be-carried" behaviour persisted in S until the end of the study, as it did in the lone cygnet E in the previous year, and was probably indicative of a high degree of attachment to the parent. Conversely D, L and P were noticeably more reluctant to approach me closely or to be handled; they actively resisted handling by running off or dodging among the others. When unable to escape these three would cower aside or flatten themselves to the ground; very occasionally they threatened me.

The performance of allopreening by the downy cygnets may also have had some agonistic significance. Unfortunately my records are insufficient to determine the truth of this.

Finally it is necessary to discuss observed differences in the form of intra- and extra-brood aggression found in this study (Tables 5.11 and 5.13). These differences are summarised by the statement that intrabrood aggression involved few threat/attack forms, with infrequent vocalisations and a high (>50%) frequency of actual attack, with the reverse being true for extra-brood incidents. They become easier to understand by making the reasonable assumption that the cygnets, being imprinted on one human,

would tend to view others as conspecifics. Thus, while the number of displays used in extra-brood aggression was high, several of them were directed at humans and were those forms used in long-distance threat by adult swans (TRU and HJT, SWF: 12/46) or were the close-quarters threats (IMP and PEL) used by both adults and cygnets. Physical attack in these incidents was limited to "non-conspecifics" - primarily a cat, which was probably seen as a potential predator. More calls were used in threat at non-conspecifics (29 of 40 calls) and most of these were hisses, while TRU or its predecessor HJT were frequent in conspecific threats (9 of 11 calls). The frequent use of a hiss directed at other species may be explained by the statement that "this is one of the most widespread aggressive or defensive patterns in vertebrates" (Kear 1972: 112) which implies that it would be equally widely understood.

The high frequency of physical attack in intra-brood disputes has been earlier discussed, and suggested to be due to the fact that a definite stable social hierarchy had not formed by the end of the study. Most incidents occurred while the cygnets were feeding or preening (Table 5.11) and may have involved disputes over access to food or loafing areas, or defended individual distance. No attacks were directed at "conspecific" humans, nor do wild cygnets attack, or indeed offer much threat to, strange swans until they are considerably older than my brood. Prior to this strong parental defence may preclude mixing with strangers (Ch. 6), but by the time of brood breakdown, when cygnets do threaten others, they more closely resemble adults in physical indicators of dominance such as bill colour, and possibly size.

Chapter 6

PARENTAL CARE AND FAMILY RELATIONSHIPS

6.1 INTRODUCTION

Extended parental care is generally seen in K-selection species (Brown 1975; Horn 1978): those with a long life-span, delayed maturity and repeated breeding, a lengthy period of dependence in the young, relatively large adults and young, and a stable environment. Clutch size, which limits the amount of care potentially available to each individual young, is relatively small. Brown (1975) notes that precocial species tend to have larger clutch sizes than altricial species, and comparatively less parental care. This tendency does not seem pronounced in the Anserinae, where adult investment in the care of young is high in both sexes.

Some degree of parental care occurs throughout the family Anatidae. The extent of the sexes' involvement is reflected by the nature of the pair bond. In the smaller members of the family the pair bond often extends only until the onset of incubation and care is provided by the female alone. In swans, geese and many tadornines the bond may last for more than one season (Ch. 4) and care is given by both sexes, although there is some division of labour (Kear 1970).

"Parental care" is a broad term, including incubation as well as brooding and carrying of young, feeding, defence of nest site and brood, young-parent recognition, and strength and duration of the family bond (Pettingill 1970). Not all of these behaviour patterns are common in waterfowl. Nest sanitation does not occur; the removal of broken eggshells as an anti-predator device has occasionally been recorded but is not widespread (Johnsgard & Kear 1968; Kear 1972). Carrying of young is largely restricted

to the swans, especially non-migratory species (Johnsgard & Kear 1968; but see Bailey et al. 1980; Hammer 1970). The other facets of care listed above are present to some extent in all Anatidae.

The male-female division of labour in Anserinae extends throughout all aspects of parental care. It begins with nesting, where the female selects the site (perhaps out of several prospected by the male) and does most of the building (Kear 1970). Incubation is primarily or wholly the female's task, so that defence of the nest devolves on the male. Time spent by the male in defence remains high once the brood has hatched, although female participation in this activity increases as the brood grows and becomes more independent. Brooding and, where present, carrying of the young, are performed mainly by the female, and it is usually the female who leads the young to food sources (de Jong & Bacon 1979).

Close contact between parents and young is facilitated by the process of imprinting and by the development of individual recognition, which is in turn further reinforced by the family cohesion it assists. Recognition is probably based largely on vocal characteristics (Bateson et al. 1980; Beecher et al. 1981 a & b; Cowan 1973, 1974; Rowley 1980), although physical appearance may also be a cue. Imprinting and the development of adult-young recognition appear to extend over several days in swans (Ch. 5; Kear 1972). In strongly territorial swans, as in hole-nesting altricial colonial species (Beecher et al. 1981 a & b: Bank Swallows; Rowley 1980: Galahs *Cacatua roseicapilla*), this is of little importance as families do not intermingle until the sensitive period for development of individual recognition is past. However, where Black Swans nest colonially with little inter-family aggression, broods can mix soon after hatching and creches may form of young from several families (Ch. 5, 5.4.2) (M. Williams 1980 and pers. comm.; see also Bédard & Munro 1977; Gorman & Milne 1972; Munro & Bédard 1977; Williams 1974; for creching in Shelduck and

Eider Duck).

Duration of the family bond varies. In migratory swans, as in geese, it continues through at least the first winter (e.g. D. Scott 1980). In the sedentary Mute Swan too the family may remain together over the first winter (MacSwiney 1966; Schulberg 1975), although juveniles are forcefully rejected at the start of the next breeding season. On Pukepuke Lagoon, Black Swan family bonds appear to break down at the start of the parents' moult, when cygnets are about 4 months old (Ch. 2, 2.4.1).

A decrease in parental care over the period when the young are present must be viewed in terms of parental investment. Thus at some time "the benefit [to young] from a given parental investment must decrease ... or else the species would not tend to produce any fixed number of offspring per season" (Trivers 1972: 139). The period of lessening attachment between parent(s) and young may be viewed as a time when there is conflict between their respective interests (Trivers 1974). Adults must terminate their investment at some stage to reduce as far as possible its cost to themselves; young may in turn wish to prolong the relationship to get the utmost possible benefit from it. The breakup of the family will probably be accompanied by agonistic interactions, when young attempt to elicit further parental investment while adults work on denying it altogether, often forcibly (MacSwiney 1966).

6.2 METHODS

Collection of data followed the methods outlined in Chapter 1. Casual notes on family relationships and interactions were also collected, where they related to birds already under observation.

This method provides descriptive data, in addition to some information on time-activity budgets (largely for a single pair) the roles of ♂ and ♀ in brood care, the

development of young (Ch. 5), and interactions between family groups and between families and flock birds. Changes in the degree and kind of care given over the period when broods are present can also be examined e.g. changes in proximity of parents and brood.

6.3. RESULTS

6.3.1 Description of relevant behaviour patterns

6.3.1a Incubation: this was not directly observed on Pukepuke Lagoon. General notes on incubation are given by Pettingill (1970), and the incubation behaviour of other swans is described by Cooper (1979: Trumpeter Swan *C. buccinator*), M. Evans (1975: Bewick's Swan; 1977a: Whistling Swan), and D. Scott (1977: Whistling Swan).

6.3.1b Brooding: was not observed on Pukepuke Lagoon.

6.3.1c Carrying: is characteristic of the sedentary Black, Mute and Black-necked Swans (Johnsgard & Kear 1968).

To be carried, young downy cygnets climb onto a parent's back, almost always at the ankle, behind the folded wings. A variant of this was seen at Western Springs, when a cygnet mounted with difficulty at the shoulder. The adult may raise its wings slightly to accomodate the cygnets but does not assist them to board, other than possibly making a "step" with its ankle. It does not always stay still. Carrying is initiated by the cygnets, often while the family is crossing open water too deep for them to feed, and may indicate a need for rest or brooding. It is generally terminated by adult actions, such as upending to feed, which tip the young off. (Fig. 6.1)

6.3.1d Attendance: is defined here as the presence of one or both parents with the brood, regardless of their activity. (Plate 6.1)

6.3.1e Feeding: in the Anatidae active feeding of the young is recorded only in the Magpie Goose (*Anseranas semipalmata*) and the Musk Duck (*Bizuria lobata*) (Kear 1970). Other members of the family will lead their young to suitable food sources, so that the young learn what to eat (Ch. 5, 5.4.2). On Pukepuke adult Black Swans remain with their young (< 14d.) broods to do much of their feeding in the shallows, as the young cannot reach food in deeper water (Ch. 5). The feeding habits of the adults may also indirectly provide food for the young: they tear up bottom vegetation more often when cygnets are present (Kear 1970), and also foot-paddle more frequently, stirring up detritus, plant matter and small invertebrates. Kear (1970) suggests that this latter behaviour pattern may have been ritualised as a display to attract cygnets to food sources.

6.3.1f Defence: the behaviour patterns used in the defence of young are the same as those for defence of territory (Ch. 3, 3.3.1). Interactions with flock birds and with the adults (and sometimes young) of other families are generally agonistic. Adults may attempt to drown strange undefended cygnets, seizing them by head or neck and forcing them under water. (Fig. 6.2)

6.3.1g Individual recognition: behaviour patterns relating to parent-young recognition are the following response (filial imprinting: Ch. 5, 5.4.2), which leads to recognition of specific individuals; continued close attendance by the parents, and their activities in keeping others away; and the development, at about 7d. old, of shared Greeting ceremonies (Chs. 4 & 5), whose continued use reinforces individual recognition. (Fig. 6.3)

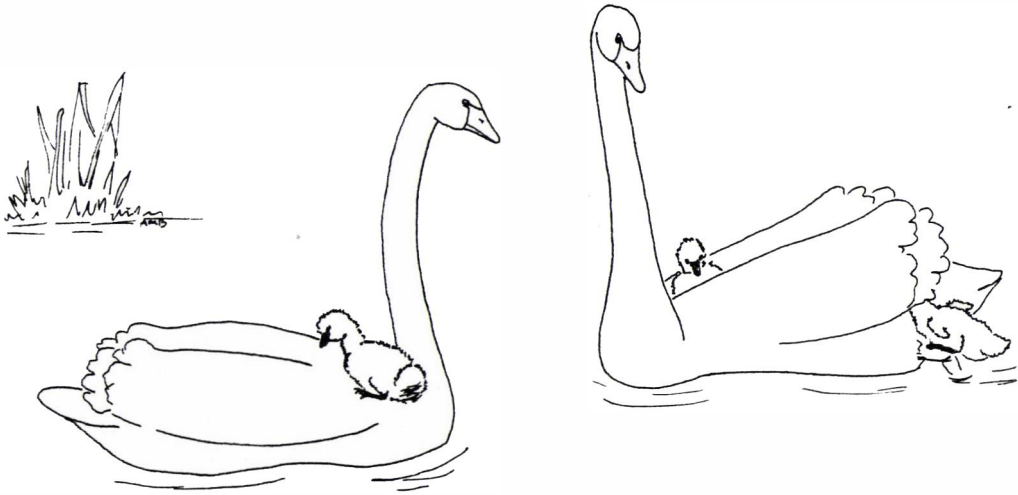


FIGURE 6.1: Adults carrying downy cygnets: ♀ (to right) is making a "step" with her ankle; the cygnet on the ♂'s back is in an unusual position

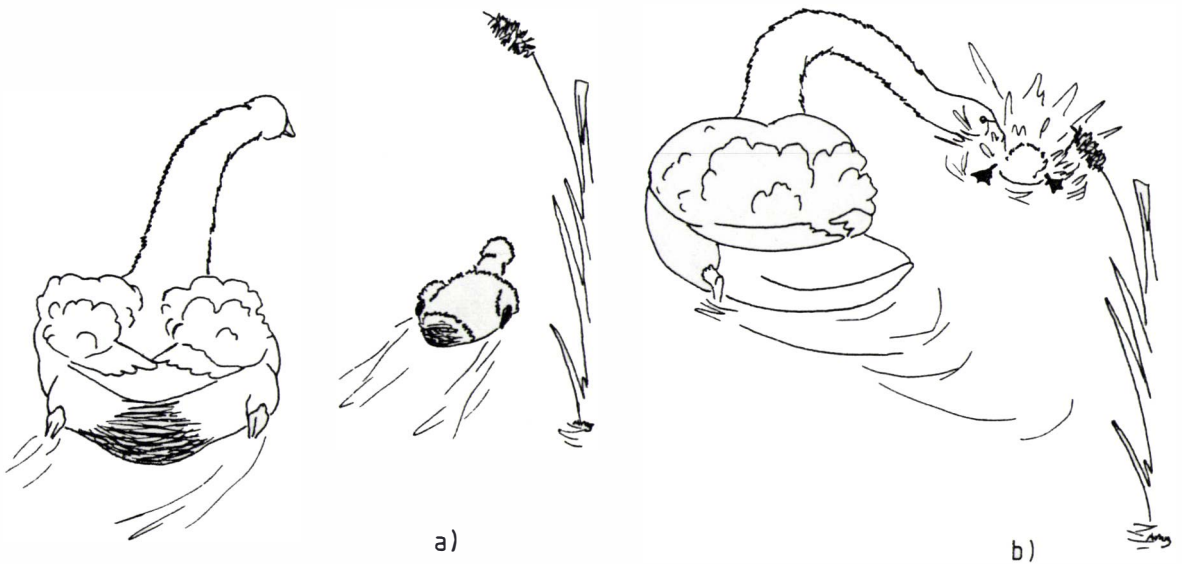


FIGURE 6.2: Male attempting to drown a strange cygnet
 a) ♂ preparing to lunge at cygnet
 b) ♂ holding the cygnet's head under water

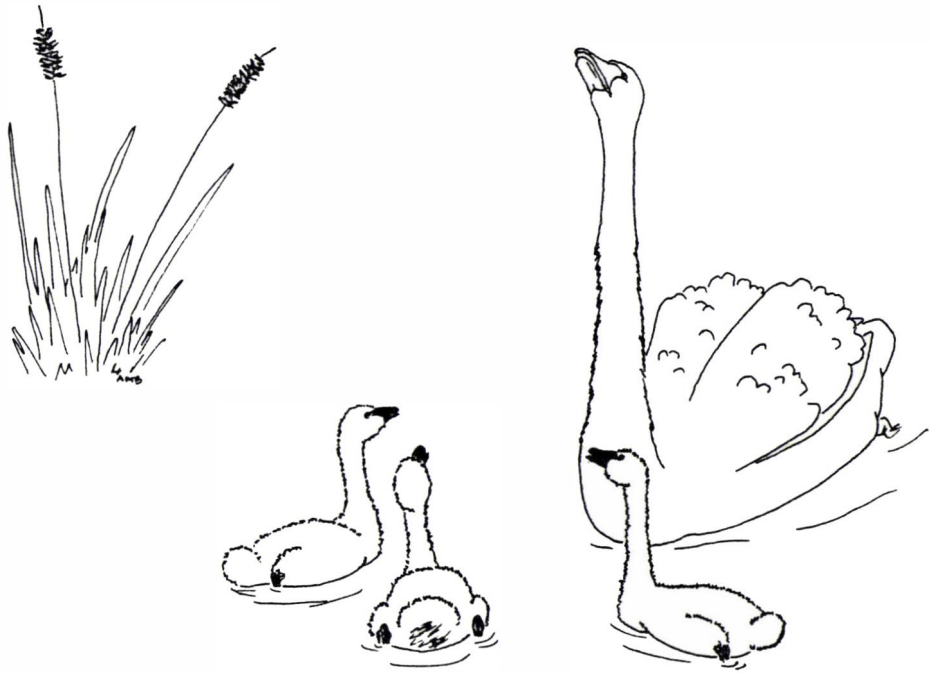


FIGURE 6.3: Greeting ceremony by adult ♀ and young brood

PLATE 6.1: Female in close attendance on
class I brood



6.3.2 Duration and frequency of behaviour patterns

6.3.2a Incubation: in New Zealand the incubation period of Black Swans averages 36.4d. (Miers & Williams 1969). On Pukepuke Lagoon it can only be estimated, taking as the start of the period the date when the proportion of time for which the female is visible decreases rapidly (Appendix I). This gives a figure of 5-6 weeks, part of which will be occupied in laying the clutch.

The degree of constancy of Black Swan incubation is uncertain. Soper (1960) recorded an extremely long period of 44-45d. The nest was left unattended for periods of 1-1.5h. and cooling of the eggs during this time may well have lengthened the time required for embryonic development. Incubation constancy in the other swans ranges from 70% of the day in the female Whistling Swan (M. Evans 1977a) to 95% for a female Trumpeter (Cooper 1979), and it is probable that, since both sexes incubate in the Black Swan, its overall constancy lies within this range.

6.3.2b Brooding: should only occur in the first 2-3 weeks of life, when the small downy cygnets have poor thermoregulatory ability. Young birds of this age were rarely seen in the open unless actively feeding or moving about; rest periods were taken in the shoreline raupo and so brooding could not be observed.

A creche of 6 captive cygnets (Ch. 5) spent their first 4 nights asleep or at least on shore. There was no nocturnal activity on the water. Their ages at the end of this period ranged from 7-12 days. At this stage at least some parental brooding would normally occur over the night. For the first 14d. of captivity daytime active periods of 1-1.5h. were separated by loafing (preening and dozing) bouts of similar length. In very young cygnets, especially, some dozing spells would involve brooding by a parent, particularly in adverse weather conditions.

6.3.2c Carrying: this is seen only in Class I cygnets (i.e. those less than 20-24d.: Table 6.1). After this time the cygnets are probably too large for adults to carry them comfortably. Also, since they are older, stronger, and have better temperature control, the cygnets' need for carrying will be reduced. However, the tendency to climb on and up was still present in some captive cygnets of about 70d. old.

Parental carrying of cygnets was observed 10 times in the 1978 breeding season, but only 3 times in 1979 although more broods were about. Families crossed open water, where most carrying occurred, less often in 1979. The duration of carrying, the number of cygnets carried, and the identity of the adults involved, are presented in Table 6.2.

6.3.2d Attendance: one or both parents accompany the cygnets constantly, and spend much time in their defence, until the brood enters Class III (at about 48-50d. wild, 41-48d. captive). At this stage parents begin to leave their young alone for varying periods of time. At the same time captive and wild cygnets show an increasing tendency to move independently of the parent(s).

Table 6.3 shows the number of times in each breeding season that broods of each age class were noted alone or accompanied by one or both parents during checks on their position and activity. It is clear from these data that the proportion of counts for which broods and one or both parents were apart increases rapidly with cygnet age. An accurate measure of the duration of "lone" periods is not available for all broods, but data for families 1, 6 and GC2 (Table 6.4) show that parents and young were separated only briefly (< 60 secs.) for Class I cygnets, but stayed apart for 60+ minutes by Class V-VI (about 100d.). In 1978 family U had already broken up and entered the flock by this age.

TABLE 6.1 CYGNET AGE-CLASS CLASSIFICATION

Class	Physical characteristics
I	Downy, newly hatched. Down pale grey, darker above; bill and legs dark grey/black; egg-tooth may be visible for first 3-4d.; nail of bill white. From 0 to 20-24d., in wild birds.
II	No contour feathers visible. Neck and tail becoming prominent, body shape becoming oval and long. Patches of down may protrude where feathers are developing underneath. From 20-24 to 48-52d. old.
III	Contour feathers developing on shoulders and flanks. Tail feathers quite obvious and facial feathers appearing. Still predominantly downy. Pink patches may be appearing on bill. From 48-52 to 70d. old.
IV	Face and upper neck well feathered; scapular, flank & tail feathers prominent and secondaries visible; belly feathered. Down patchy but persisting from rump to nape. From 70 to 89d.
V	Almost fully-feathered with primaries and secondaries well developed (a flapper). Patches of down on nape and rump. Bill pink, & white stripe may be obvious above nail. From 89 to 100d.
VI	Fully feathered & just able to fly; plumage much paler than that of adults, & has a brownish tinge. All flight feathers tipped black. Bill reddish-pink with white tip & nail. May have separated from parents. 100d.+.

TABLE 6.2 CARRYING: IDENTITY OF FAMILY, NUMBER OF CYGNETS CARRIED, DURATION OF CARRYING (All cygnets in age class I)

identity of parent	number carried ¹	duration (minutes) ²
♀6 3	4	6
	2	4
	1	1
♂6 3	1	4
♀1 4	1	1
	2	4
	5	1
	1	5
	4	3
	1	1
	1	1
♀8 5	2	1
	2	1

1: mean number carried = 2

2: mean duration = 2.54 minutes

3: maximum possible = 4

4: maximum possible = 6 in 1978, 7 in 1979

5: maximum possible = 5

TABLE 6.3 ATTENDANCE ON BROOD BY MALE, FEMALE, OR BOTH,
AS A PROPORTION OF TOTAL POSITION CHECKS

A. 1978

brood age	alone	with ♂	with ♀	with ♀	total checks	number of broods
Cl. I	(N) 1	1	30	42	74	2
	(f) 1.35	1.35	40.54	56.76		
Cl. II	3	9	18	24	54	2
	3.56	16.67	33.33	44.44		
Cl. III	35	26	88	92	241	3
	14.52	10.79	36.51	38.17		
Cl. V-VI	39	16	20	42	117	3
	34.29	14.29	17.14	35.71		

B. 1979

brood age	alone	with ♂	with ♀	with ♀	total checks	number of broods
Cl. I	4	8	32	67	111	11
	3.60	7.21	28.83	60.36		
Cl. II	2	6	34	34	76	5
	2.63	7.89	44.74	44.74		
Cl. III	18	2	28	29	77	3
	23.38	2.60	36.36	37.66		

TABLE 6.4 PAIR IDENTITIES: EXPANSION OF CODES USED
THROUGHOUT TEXT FOR RECOGNISED PAIRS

Code for pair	Derivation of title
1	first recognised pair, 1978
6	territory near maimai 6
GC	"Green collar": ♀ wore green neck collar
MM1-2	in the area of maimais 1 - 2
Dh	arrived from nearby pond, "Death Hole", when brood in Class III
U	"Unknown": also a Death Hole family
Y	"Young" pair, observed courting
SE	present in "southeast" corner
A?	uncertain identification of pairs on opposite shore from hide, 1978 - 1979 summer
B?	
Lge	both members of pair unusually large
Ra	pair at raupo arm between maimais 5 - 6
GC2	one of 3 pairs with one member collared; collared bird here was a ♀
A	first brood out in 1979
T	pair at tussock, far side of lagoon
R7	territory to right of maimai 7
8	eighth pair recognised in 1979
Ph	territory included pumphouse raupo
Uk	1979 pair of unknown origin

NOTE: pairs distinguished on the basis of physical (mainly plumage) characteristics

Where it occurs, separation of most families with Class I-II cygnets is entirely due to adult aggressive activity, but by Class III independent movements by the cygnets may also bring about family separation. At this stage the brood may also split, some cygnets moving with one parent and some with the other or quite alone.

6.3.2d Feeding: the duration and frequency of feeding bouts, wherein young learn from or are assisted by their parents, are unknown. Leading to food sources is necessary only until cygnets are capable of recognising these for themselves, after which the young may lead their parents instead (de Jong & Bacon 1979). Tearing of excess food from the bottom will probably last at least until the cygnets develop the ability to feed under water for lengthy periods: upending to 'feed first' appears at 11d. in the wild.

6.3.2f Defence: continues throughout cygnet development, until they fledge at about 4 months of age. It may - depending on the individual pair and on pressure from other families - decrease in frequency towards the end of the fledging period. However, using the number of position checks where ♂ and ♀ aggression were recorded, there is no significant difference in the overall proportion of aggression, with the exception of 1978 ♂s over the Class I-II interval (χ^2 2x2 tables, $\alpha = 0.01$, d.f. = 1, $p < 0.01$). An examination of the proportion of total visible time spent in threat or attack by ♂1 and ♀1 does show a decrease in male and an increase in female activity, over the rearing period (Appendix I).

During the field study, it appeared that most of the ♂ or ♀ defensive behaviour occurred while the parents were apart from their broods. Table 6.5 shows that both ♂ and ♀ aggressive acts occur considerably more often away from the cygnets, but also that the ♂ is more likely to threaten while with the brood. In addition, the data show that the ♂ is away from the brood more than the ♀, regardless of his behaviour. Overall, he spends more time in active defence than the female.

TABLE 6.5 NUMBER OF SIGHTINGS WHERE ♂ OR ♀ INVOLVED IN AGGRESSIVE ACTIVITY, WHILE ACCOMPANYING OR AWAY FROM BROOD

A. 1978

brood age	Female					
	aggression	with brood other ¹	brood total	away from brood aggression	brood other	total
Cl. I	(N) 9 (f) 12.50	63 87.50	72	1 50.00	1 50.00	2
Cl. II	1 2.38	41 97.62	42	8 50.00	8 50.00	16
Cl. III	19 10.56	161 89.44	180	61 66.30	31 33.70	92
Cl. V-VI	2 5.41	35 94.59	37	21 63.64	12 36.36	33

Male

brood age	Male					
	aggression	with brood other	brood total	away from brood aggression	brood other	total
Cl. I	11 25.58	32 74.42	43	39 55.71	31 44.29	70
Cl. II	2 6.06	31 93.94	33	12 41.38	17 58.62	29
Cl. III	12 10.17	106 89.93	118	91 54.17	77 45.83	168
Cl. V-VI	4 11.43	31 88.57	35	19 50.00	19 50.00	38

B. 1979

brood age	Female					
	aggression	with brood other	brood total	away from brood aggression	brood other	total
Cl. I	12 12.12	87 87.88	99	5 50.00	5 50.00	10
Cl. II	10 14.71	58 85.29	68	5 71.43	2 28.57	7
Cl. III	4 7.02	53 92.98	57	20 48.78	21 51.22	41

TABLE 6.5 cont'd.

B. 1979 brood age	Male					
	aggression	with brood other ¹	total	away from aggression	brood other	total
Cl. I	(N) 19 (f) 25.33	56 74.67	75	58 69.05	26 30.95	84
Cl. II	9 22.59	31 77.50	40	20 47.62	22 52.38	42
Cl. III	2 6.45	29 93.55	31	28 41.79	39 58.21	67

1: "other" includes feeding, loafing, greeting, carrying, and vigilance

It was apparent that some pairs were much more aggressive in defence of their breeding areas and young than others: this is reflected to some extent by the size of their territories (Ch. 3). Two pairs, A and Ra, were weak in defence of their broods and areas (Q¹Ra defended no apparent territory), and left their young unattended earlier than the others.

6.3.2g Recognition: the development of individual recognition takes at least 7 days (Ch. 5, 5.4.2), and is signalled by the shared performance of Greeting ceremonies, which previously had involved only the parents. Its development is a two-way process. Participation in family Greeting and Triumph ceremonies then continues until family members separate and cygnets enter the flock. Greeting ceremonies between siblings continue beyond this point.

Recognition of parents appears to last at least 6 months. A hand-reared cygnet recognised and greeted me after 6 months' separation, but not after a further 6 months had elapsed.

6.3.3 Sex roles in parental care

6.3.3a Incubation: an estimate of sex roles during incubation may be gained by examining the amount of time that male and female are visible over the period, and their activities. For pairs 1, 6, GC, and GC2 (the only pairs for which much data are available), female visibility declined sharply from the nest-building stage, and when they were present they spent much time feeding. Females 6 and GC2 appeared to sit throughout the day, Q¹ had definite nest recesses in the morning and evening, and Q¹GC left the nest towards the middle of the day. Although ♂ and ♀ of these pairs were seen together for part of most presumed nest recesses, the ♀s were also seen alone for lengthy (30-40 min.) periods; the absent ♂s are assumed to have been sitting or incubating for part of this time.

Thus, the ♂ Black Swan shares in incubation duties to a minor degree (see also Delacour 1954).

6.3.3b Brooding: the roles of ♂ and ♀ in brooding are unknown. However, since the young broods are frequently out of sight for much of the day while the ♂ is visible and active, it is likely that most brooding is by the attendant female.

6.3.3c Carrying: it is clear from Table 6.3 that the carrying parent is almost always (12 of 13 sightings) the female. Since there is a slightly greater chance of seeing the Class I brood with both parents than with the ♀ alone, this sex difference cannot be entirely explained by different availability of one parent.

6.3.3d Attendance: in both 1978 and 1979 the Class I broods were most likely to be seen with the pair, but after this attendance by both parents together decreased rapidly. When seen with one parent only, this was most likely to be the female, throughout both rearing periods. Male attendance on the brood fell off more rapidly in 1979, probably because there were more families present and so a greater need for aggressive behaviour away from his family, to keep the groups separated. Thus attendance on (i.e. close association with) the growing brood is primarily a ♀ duty.

6.3.3e Feeding: since there is a tendency for the ♀ to lead the family about, and since she spends overall more time with the young, she is more likely to lead them to food, to draw their attention to it, and perhaps to tear vegetation for them.

6.3.3f Defence: there is no significant difference between ♂ and ♀ in the proportion of aggression occurring with and away from the brood. Both parents move away from the cygnets in threat or attack. However, overall the ♂ is more visible than the ♀ and spends more time in

territorial defence. Appendix I provides this data for ♀1, the most visible and most aggressive of breeding pairs on the lagoon. In all pairs, the ♂ is the prime mover in brood defence.

6.3.4 Interactions with others

6.3.4a With other families: broods were never seen to approach closely on Pukepuke until after they had fledged and left their parents. Other families were either left alone, especially if not encroaching deeply on the family's space, or else attacked. Some pairs showed a definite tendency to threaten or attack (pairs 1, 6, GC2, R7), while others did not initiate confrontations frequently. If the response to approach was threatening one or both parents (but usually the ♂) moved out from the cygnets, so that they were separated from any dispute. Inter-family disputes primarily involved males, though ♀s might attend their mates, especially once broods were becoming independent.

Most threats or attacks reach broods only if they are alone. On Pukepuke this situation is unusual until broods enter Class III, and even then their parents are still in the vicinity. On Western Springs, cygnets and adults become separated more easily, as families mingle at feeding sites, and cygnets may then be attacked by males of other families. Parents respond to their cygnets' distress calls if in the area, but if they have moved off they may not hear and do not appear to notice the absence of a family member. On one occasion in Auckland I observed a Class III cygnet being harassed by adults and juveniles (Class VI), while its parents did nothing to protect it but moved away rapidly, leaving it to follow.

6.3.4b With flock birds: again, differences are apparent in the behaviour of individual pairs (see also Ch. 3, 3.3.4c). Thus pairs A, Ph, Ra and sometimes T and 8 (Table 6.4) tolerated the close (<5m) presence of flock birds. They

might enter a low-intensity threat posture but otherwise left the flock members alone. Pairs 1, GC2, 6 (in 1978), R7 and 7 were highly aggressive towards flock birds once the brood hatched and did not tolerate any intrusions into the family area. In the case of ♂1 this extended for at least 30-50m around the brood.

The responses of flock birds to unaccompanied cygnets are varied. When family Dh first appeared on the lagoon (5-6/12/78) one of the Class III brood became separated from its family and spent 2h. wandering alone among flock members. Its parents apparently did not hear its frequent distress calls. Generally other swans tolerated its presence and allowed it to approach to within 1m of them, but the ♂ of a non-breeding pair was hostile, threatening the cygnet 3 times and following through to a Pecking Lunge on one occasion.

Cygnets appear to enter the flock as whole or part broods, although these groups may then break down. They mingle readily with flock members, once fledged, and are not threatened or attacked, apart from minor disputes over feeding or loafing sites. I did not observe any harassment of juveniles in the flock.

6.4 DISCUSSION

6.4.1 Individual recognition

Recognition of individual parents and young must be central to prolonged parental care, especially in precocial birds. If this were not so, parents would tend to incur large costs in the support of strange offspring. Miller & Emlen (1975: 142) state that "To achieve maximal relative fitness for its genes, a parent ... must not only care for and provision its offspring efficiently but must refrain from contributing to the survival of competing-gene carriers at the expense of its own reproductive output". Consequently colonial species would be expected to possess

mechanisms preventing the mingling of broods, unless such mingling was beneficial. Lazarus & Inglis (1978) found that Pink-footed Goose parents would tolerate additional strange goslings, although they did not say of what age. They found that all components of the parents' time budget were independent of brood size, so that extra investment was not required, and suggested that a potential benefit of adoption could be a reduced risk of predation, through the dilution effect (Krebs & Davies 1981). Greater brood size might also enhance family dominance status (Hanson 1953).

The development of recognition does not follow immediately upon hatching of the young, but may extend over a period of days. The development of parental recognition of chicks, at least, "has become geared through natural selection to the rate of development of chick mobility, to territory size and nest congestion, and to other social and ecological conditions characterising the nesting habits of a particular species" (Miller & Emlen 1975:140).

Filial imprinting is basic to the development of recognition in precocial chicks. The process is described in Ch. 5 but, briefly, is the rapid acquisition of a following response to some fairly generalised object(s) and a fear or flight response to other, different objects. Thus, in the Coot (*Fulica atra*) filial imprinting is complete in about 24h. (Alley & Boyd 1950), after which the young cannot be tamed or hand-reared. However, the authors also found that the adoption of strange chicks, of similar age to the brood, might occur for up to 14d., implying that recognition of young as individuals was not completed until then. In the Common Eider of the Saint Lawrence estuary, broods may mingle throughout the fledging period, but permanent creches are usually formed from such mixing only in the first days after hatching (Munro & Bédard 1977). It is not clear whether this is the result of fairly specific imprinting or of early recognition of the "mother's" characteristics. Prevet & MacInnes (1980)

found that the rare adoptions occurring in Snow Geese were seen only in broods less than 7-10d. old, after which recognition of the strangers, by goslings and parents, led to their rejection. Emperor Geese (*Anser indicus*) with "newly hatched" young may adopt orphaned young of similar age (Eisenhauer & Kirkpatrick 1977). Similarly, under colonial-nesting conditions Black Swan cygnets may enter creches until about 14d. old. This last point is important when considering the ancestral nesting habit of *C. atratus* (Chs. 5 & 7).

Although there are minor physical differences in facial appearance in most waterfowl - and major differences in the Bewick's Swan (M. Evans 1977b; D. Scott 1978) - recognition on the basis of vocal characteristics is widespread and probably of major importance. This is true for other groups as well: both Rowley (1980: Galahs) and Beecher et al. (1981 a & b: Bank Swallows) found that adult-young recognition centred on "signature" calls peculiar to each individual nestling. Cowan (1973, 1974) showed that individual recognition of parents by young Canada Geese depended on auditory and visual cues, and that auditory cues were of most importance. Similarly Collias & Collias (1956) found that specific contact and distress calls maintained family cohesion in Canvasbacks (*Aythya valisineria*) and Blue-wing Teal (*Anas discors*), and could presumably be used to identify individuals (see also Kear 1972). In Black Swans also auditory cues are important, given the general similarity of appearance, and individual differences in calls may be detected by the human ear. The highly vocal Greeting and Triumph ceremonies are central to cohesion of pair and family. (Ceremonies described pp 104-105)

6.4.2 Significance of family behaviour

The maintenance of family cohesion has important survival value. Prevett & MacInnes (1980) list a number of factors relating to the survival value of family behaviour in Snow Geese: protection from predators;

increased feeding time for juveniles, through parental protection and intervention in disputes; increased access to food and other resources, since families have higher dominance status than non-family birds; learning of migration routes and wintering sites. De Jong & Bacon (1979) and D. Scott (1980) arrived at similar conclusions in their respective studies of Mute and Bewick's Swans. Brooding and carrying by parents are also of value, since very young cygnets tire easily and cannot cope with cold or wet conditions (Lickers 1977). Carrying is common only in the non-migratory Mute, Black and Black-necked Swans (Johnsgard & Kear 1968). It is thought that young of the other species are less exposed to predators and grow too rapidly for carrying to be of much benefit.

Although parents gain from care-giving, through ensuring successful reproduction of their genes, they must also incur considerable costs in terms of the time and energy invested in brood care. D. Scott (1980) found that the costs to Bewick's Swan parents were greatest early in the winter, once families had reached their wintering grounds. Compared to non-family pairs, parents spent more time in threat postures (see also Lazarus & Inglis 1978), had higher frequencies of aggression, and spent less time feeding; males, but not females, gained weight more slowly. Care, and therefore costs, declined in the second half of the winter.

Male and female parents have different investments and costs over the breeding season (Trivers 1972). Lazarus & Inglis (1978) found that only the female Pink-footed Goose incubates, losing 30% of her body weight over the incubation period. She must spend much time feeding once incubation is over. A male loses only 17% of body weight over the same period, and so has lower feeding requirements. Once the brood has hatched he spends much more time than his mate in vigilant postures, watching mainly for predators. The authors found that the gander's greater investment and costs during the fledging period complement the female's

investment during incubation, and allow her to recover from it.

The costs of care to territorial Black Swans on Pukepuke Lagoon are not clear. The amount of time spent in agonistic behaviour, before and while broods are present, is more than for flock birds (Ch. 3). The proportion of visible time spent feeding is considerably less, but this estimate does not allow for time spent feeding while hidden in the raupo. Apparent investment in aggression does not decline until brood disintegration begins, about 4 months after hatching (Appendix I), and territories are maintained until this time (Ch. 3), although their size may decrease markedly.

The Pukepuke birds show a distinct division of labour in family care. Although the sexes share incubation to some extent, the female has the greater investment (6.3.3a). Once the brood hatches the female spends more time with the cygnets than the male, often feeding, while the male continues active in defence (6.3.3 d & f). Brooding and carrying are largely the female's responsibility, and overall her investment in the young is probably slightly greater than that of the male (Trivers 1972).

Much of the post-hatching investment on Pukepuke goes into keeping families separate from each other and to some extent from flock birds (Ch. 3). While cygnets are young (Class I-II) the benefits of separation are clear: a reduction of feeding competition, since suitable food sources for young chicks (especially those yet incapable of feeding in deep water) are discrete and relatively finite. Older broods, apparently utilising the same food sources as adults, may be less in need of this investment, although keeping same-aged cygnets apart would reduce peer-group competition. Wide separation of broods would also reduce the likelihood and effects of harassment by other breeders. Such a reduction would also result from the observed tendency for adults to move away from their young in order to meet or prevent threats.

6.4.3 Effects of parental status

Parental dominance may affect the degree and nature of social encounters and of breeding success, in and out of flocks. Hanson (1953) stated that family status in a Canada Goose flock was dependent on family size, such that larger families generally dominated smaller (see also Raveling 1970). Lazarus & Inglis (1978) agreed, finding also that families dominated pairs and pairs dominated single birds. Size and personality of individual ganders were of lesser importance. However, individual characteristics are important in dominance relationships in the pre-family (pair only) stage and in those species where juveniles do not join the parents' disputes. Collias & Jahn (1959) found that the more dominant male Canada Geese had a better chance of pairing and breeding successfully. For Black Swans Braithwaite (1981b) noted that captive birds of stable associations were dominant to other associations and had a greater rearing success. Their territories were avoided and their attacks went unanswered, even if the victims' offspring were involved. On Pukepuke, if territory size and frequency of aggressive display, both before and during brood presence, are used as indicators of dominance, then $\phi 1$ was the dominant pair in both years under study. They successfully reared larger-than-average broods in 1978 and 1979 (6 & 7, c.f. $\bar{x} = 4.0$ & 3.5). Conversely, all brood A and Ra cygnets died in 1979; their parents spent little or no time defending them from flock and territorial birds, avoiding confrontations if possible. Pair Ra had no apparent defended area. Both competition and harassment may have contributed to the cygnets' deaths. Families T, 8, and R7 also disappeared from the lake, but as units; they may have left the area, died, or simply become more retiring, probably as a result of interactions with other, more dominant pairs.

Considering waterfowl in general, Patterson (1976: 140) suggested that "Social interaction within a population can be considered as an intermediate variable relating

population size or output to some ultimate variable, such as food supply, and an alternative to direct competition for the resource itself". Aggressive interactions between breeders could set up a dominance hierarchy among them, serving to limit production because dominant birds force others to less favourable locales. This apparently occurred on Pukepuke, in 1979, where ♂1 defended a large territory and other breeders were restricted in where they could nest, but still bred successfully on their smaller areas. It is likely that more pairs could be supported on the large site now claimed by a single aggressive pair (Ch. 7). In addition, aggressive interactions between parents could decrease the rearing success of subordinate pairs through harassment or competition. Interactions between the broods themselves, mingling during parental disputes, might also affect cygnet mortality (Patterson 1976).

6.4.4 Duration of family behaviour

The duration of family behaviour varies. In most Anserinae (e.g. Elder & Elder 1949; Hanson 1953; Prevett & MacInnes 1980; D. Scott 1980) adults and young remain together for at least the first winter, migrating together to the wintering grounds. Even in the sedentary Mute Swan families may winter as a unit. As discussed earlier (6.4.2) there are obvious advantages to this prolonged cohesion.

Elder & Elder (1949) suggested that small flocks of Canada Geese were single family units, and larger groups an amalgamation of these. The situation in Black Swans is not as clear-cut (Ch. 2, 2.4.1). I observed groups joining the Pukepuke flock that were obviously family units, of two adults and 3-6 recently-fledged juveniles. However, of the broods originating on or around Pukepuke Lagoon, brood 1 and possibly brood 6 entered the flock independently of their parents, who remained to moult on the lake. Family Dh also appeared to break up before entering the flock, the 4 juveniles travelling together but apart from

any adults. Thus family cohesion lasts until the cygnets fledge, at about 100d. old. Recognition of family members may persist for much longer (6.3.2g). There was no harassment of newly-joined juveniles by adult flock members.

There is no obvious behaviour precipitating termination of the parent-cygnet bond in Pukepuke families (c.f. MacSwiney 1966). Parental aggression towards the brood was not seen, although intra-brood disputes were recorded (Ch. 5) and may have contributed to observed brood-member separation prior to the adult-young break. Sibling conflicts may, through determining rank order, have an effect on the amount of care received from parents. This could be reflected in order when following (Ch. 5) and proximity to parent(s), since cygnets on the outskirts of the group would be more exposed to harassment by others (de Jong & Bacon 1979; D. Scott 1980).

Final family disintegration may be due to a combination of increasing cygnet independence, indicated by a growing tendency on their part to travel alone, uninfluenced by parental movements, and a similarly increasing tendency (Table 6.3) for both parents to leave older juveniles alone for lengthy periods of time. The ultimate result is a relatively peaceful family separation.

Chapter 7

SYNTHESIS

7.1 INTRODUCTION

A number of major points arise from the data and discussions of the previous chapters. These relate to

(1) the observation, description and interpretation of previously unknown, or poorly described, behaviour patterns;

(2) the use of behavioural data in affirming taxonomic relationships within the genus *Cygnus*;

(3) determination of the likely ancestral breeding mode of *Cygnus atratus*;

(4) discussion of the separation into colonial and territorial breeding modes in New Zealand and Australia, how these differences are maintained, and some of the likely behavioural differences between the two forms;

(5) the annual cycles of behaviour, particularly breeding activities, seen in the Black Swan;

(6) consequences of the territorial breeding mode operating on Pukepuke Lagoon, and suggestions for management of the population there.

7.2 BEHAVIOUR PATTERNS OF THE BLACK SWAN

7.2.1 Achievements of this study

Although some work has been done by other authors on the ethology of *C. atratus* (Braithwaite 1970, 1981b; Braithwaite & Frith 1969b; Delacour 1954; Frith 1967; Johnsgard 1965; Poulson 1948; Tingay 1974), a full description of its behaviour patterns has not been given.

My research has provided descriptions and preliminary analyses of the behaviour patterns exhibited by both flock birds and breeders in a situation where breeding pairs occupy relatively large, discrete territories. Courtship,

pair-bonding and breeding behaviour; aggression and territoriality; cygnet growth and development; and family relationships are examined, as well as basic time-activity budgets and flock activities. The only acts which could not be directly observed were those of nest-building, incubation and brooding, and any related displays, which occurred within and were hidden by the shoreline vegetation.

An obvious application of these data is their use as a basis for comparison with colonial-nesting swans, to indicate quantitative and qualitative similarities and differences in their behaviour. Dissimilarities in environments must also be considered.

7.2.2 Description and interpretation

The existing descriptive work is not always complete. This criticism extends to sexual, agonistic, and pre-flight behaviour patterns.

A. Pair-related behaviour

Black Swan copulatory activity is described in the literature as a simple display sequence when compared to that of the Mute Swan (Braithwaite 1981b; Johnsgard 1965), consisting solely of mutual head- and neck-dipping, with a post-copulatory call and single display following treading. I have found it to be more complex and much closer to *C. olor*'s display. The latter contains the following elements: dipping of the head only (= Head-Dip in *C. atratus*), and of both head and neck (= Neck-Dip); head-shaking on raising the head from the water (= Head-Shake); mutual neck erection (= Facing Together); occasional ritualised preening - form not stated; more frequent ritualised rubbing of the head against flank or back (= Cheek-Rub-Lateral-Preen); ritualised dabbling or bottom feeding (which I have never observed in *C. atratus* although Lind (1959) suggested a feeding-movement origin for some swan displays); and a post-treading call and postural display (Boase 1959; Huxley 1947; Johnsgard 1965). Comparison with data presented in Ch. 4 (4.3.3) will show that this series of acts is indeed very similar to that of the Black Swan. In addition, I have seen some displays in Black

Swan copulations which were previously not recorded at all in either species: crossing of ♂ neck over ♀, and vice versa, during Head- and Neck-Dipping, and Nibble-Preening of the ♀'s neck by her partner.

Both of these newly-described displays are likely to be derived from Mounting and to signal the ♂'s intention to do so. The display component ♂/♀ pushes the ♀ down into the water and may stimulate her to enter the prone position prior to Mounting. In the form ♂/♀ during the Neck-Dip display, it has a significant effect on the subsequent performance of ♀PRO, although other ♀ acts may also follow (Table 4.8a). The occasional performance of ♀/♂ is less easy to explain; it may be an accidental occurrence. Nibble-Preen-Partner is also a Mounting-derived display, similar to the action of grasping at the ♀'s neck feathers during Mounting and Treading. However, it is linked only with Neck-Dip by the ♀ (Table 4.8a) and does not lead immediately to the ♀ copulatory position.

Precopulatory displays arising from preening and bathing are universal in the Anserinae, although differences exist in their finer details and in the post-treading posture and call. Thus Collias & Jahn (1959) describe what are basically bathing movements in Canada Geese, initiated by ♂ or ♀. They emphasise that the pair is least likely to be disturbed if mating on their own territory, indicating the importance of a territory for successful breeding in this species at least. (I found that Black Swan copulations, both on territories and in the flock, might sometimes be closely observed but not interfered with, although Braithwaite (1981b) asserts that nearby swans are strongly attracted to mating pairs.) Bewick's Swan (M. Evans 1975), Mute Swan (Boase 1959; Cross 1947; Huxley 1947; Johnsgard 1965), and Trumpeter Swan (de Vos 1964) also use preening- and bathing-derived displays. All displays have in common Head-Dip, Neck-Dip and Head-Shake components, with varying additions. The Black Swan's display is closer to *C. olor*'s than to that of any other swan species for which data are

available. The "northern" swans - Trumpeter, Whistling, Whooper and Bewick's Swans - fall into a separate group which in some ways more closely resembles the geese.

Mute and Black Swans also show similarities in the pair-related Greeting and Triumph ceremonies. The Black Swan's ceremonies are described in Ch. 4 (4.3.1). Boase (1959) describes *C. olor*'s triumph ceremony as follows: the ♂ returns to the ♀ in the "busking" posture (= high-intensity Threat in *C. atratus*) after an aggressive incident, making a dull snoring sound. The birds then face each other with neck bases touching, secondaries raised, necks erect and slightly curved and bills level. They perform a mutual head-turning ceremony and then continue with "false-preening". Johnsgard (1965) notes that the Mute Swan's triumph display is performed by strongly bonded birds, and I found that it developed relatively late in Black Swan courtship. Johnsgard also recognises a close temporal link between aggressive behaviour and triumph display in the Mute Swan. The Black Swan shares this link between aggression and the Triumph ceremony (Ch. 3: 3.3.2; Fig. 7.1), and the high-intensity Threat which may precede the ceremony is posturally very similar to Mute Swan "busking".

The Triumph ceremony of *C. atratus* is related to a Greeting ceremony, differing in its apparent aggressive motivation and in the characteristic Necks-Curved-Over (NCO) end-posture. This differs from Braithwaite's (1981b) description of a Triumph ceremony as a high-intensity Greeting display. A similar NCO posture, but one lacking the raised-wing (threatening) component, occurs after some copulations and is linked to the close presence of others (Ch. 4: 4.3.3; Table 4.7) and perhaps to aggressive tendencies in the ♂ or pair.

A shared Greeting ceremony develops relatively early in pair-bond formation in Black Swans, while a Triumph ceremony is seen between firmly mated birds engaged in defending some resource.

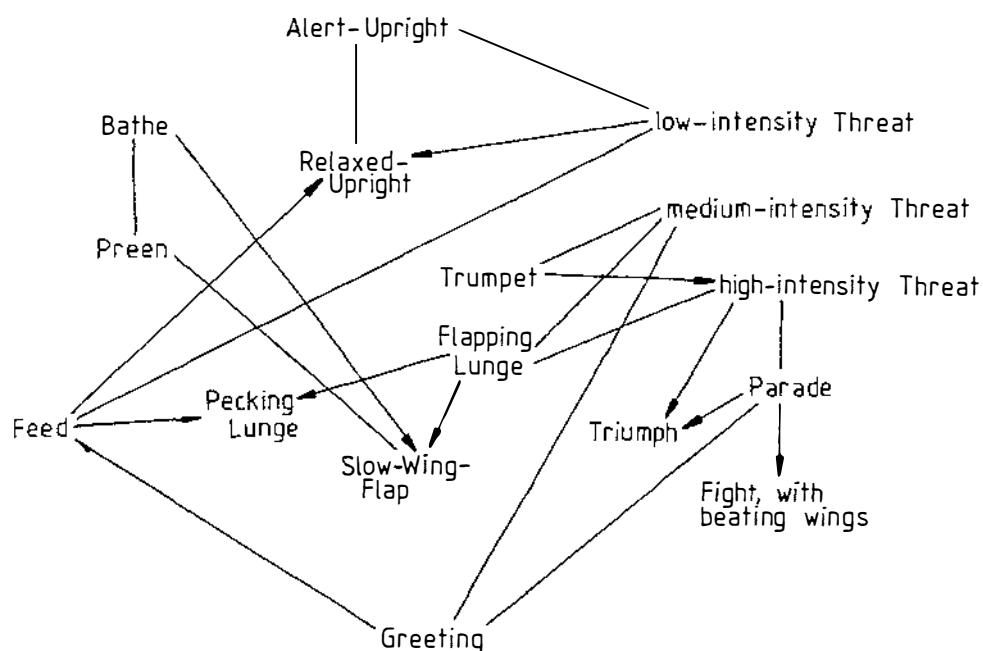


FIGURE 7.1: Behaviour-pattern transitions occurring significantly more often ($p < 0.01$) than expected in aggressive sequences (Derived from Ch. 3: Table 3.2)

—— transition occurs significantly more often than expected, in both directions

→ transition occurs significantly more often than expected, in one direction only

— transition occurs significantly more often than expected in one direction, and significantly less often in the other

B. Aggression

Some threat displays are also alike in form in the two species. High-intensity threat and "busking" are very similar; charges by Mute Swans may end in a Flapping Lunge (Wilmore 1974; c.f. Ch. 3: 3.3.1); and fights (Fight, with Beating Wings) sometimes occur. However, both the Slow-Wing-Flap (SWF) and Trumpet (TRU) displays appear peculiar to the Black Swan, although wing-flapping is ritualised in triumph ceremonies by the "northern" swans (Johnsgard 1961, 1965) and geese (Lorenz 1965).

Braithwaite (1981b) links SWF with the end of the Triumph (TRI) ceremony. Following my definition of the ceremony, this linkage is not apparent (Fig. 7.1), nor are SWF and the Greeting ceremony closely associated. If the TRI-SWF link did exist it would make *C. atratus*'s Triumph ceremony more similar to that of the northern swans. Slow-Wing-Flap, probably derived from "ordinary" or comfort-behaviour wing-flapping (McKinney 1965), occurs in conjunction with the preening that follows many aggressive incidents, and is also significantly linked with the Flapping Lunge that terminates many chases (Fig. 7.1; c.f. Braithwaite & Frith 1969b).

Similarly, I believe that the Trumpet display has also been misinterpreted. Rather than a stationary threat by the ♂ and an "incitement" by the ♀ to further ♂ aggression (Braithwaite 1981b), I have found that its performance, by either sex, is often a prelude to active chasing or further threat, by the performing swan (Fig. 7.1). In form it appears to be a "stationary Flapping or Pecking Lunge" at a distant adversary.

C. Preflight

The preflight display of the Black Swan comprises a "slim" and erect body posture (Anxiety-Upright) and a particular call involving jerking movements of the head and neck. Johnsgard (1961) did not recognise any definite pre-flight activities, and noted that this lack was shared

by the Mute and Black-necked Swans, while Braithwaite (1981b) described the calling as involving only chin-lifting, not movement of the neck. In this respect his display description more closely resembles the Greeting calls given in alarming situations (Ch. 4: 4.3.1). It is possible that the head-jerking and neck movements of the pre-flight display are similar in signal value to the "pumping", with emphasis on the up-beat, observed by Lorenz (1951) in mallards intending to fly off.

The numerous behavioural similarities apparent between the Mute and Black Swans (A-C above) serve to reaffirm the close relationship ascribed to these species by Johnsgard (1961, 1965), and to separate them from the more "goose-like" northern species. *Cygnus olor* and *C. atratus* have a shared evolutionary history of behaviour patterns; their breeding habits may show a similar relationship.

7.3 DERIVATION AND MAINTENANCE OF BREEDING HABITS

It is now recognised that the Australian and New Zealand populations of the Black Swan exhibit both territorial and colonial breeding habits. The presence of the two breeding modes in a single species raises two interesting questions:

(1) which is likely to have been the "ancestral" breeding habit?

(2) are the two breeding modes likely to represent two different "strains" of swan, or is some other factor involved in their separation?

7.3.1 Ancestral breeding habits

The first question can be answered by examining comparative studies on imprinting (Ch. 5) and the photoperiodic controls of breeding (Kear & Murton 1976; Murton & Kear 1973, 1978; Lofts & Murton 1968). All other swan species are ancestrally and presently territorial, although under certain naturally-occurring conditions (on the islands of the Baltic: Kear 1972; M. Williams pers. comm.) the Mute Swan shows a tendency to colonial nesting.

Differences in the sensitive periods for imprinting and the development of individual recognition in many bird species are clearly related to their nesting habits (Immelmann 1975). Where broods are immediately mobile, a rapid completion of these processes is predicted unless broods are kept strictly apart or unless mixing of broods is not disadvantageous. Otherwise young of several different families would intermingle and parents could well find themselves rearing other adults' young, to the possible detriment of their own. Thus, if colonial nesting were ancestral in Black Swans, the imprinting period should be extremely short to prevent undesirable mixing and adoption of young, unless creching has always been advantageous (but see 7.4).

However, in Black Swans, as in the other swans and also geese, the sensitive period for imprinting and learning of individual characteristics (a two-way process) extends for several days (Ch. 5; Kear 1972). The other swan species are strongly territorial and broods do not mingle until fledging: a short imprinting period is not necessary. A similarly lengthy imprinting period is seen in colonial-nesting altricial species where young remain in nest holes until fledging (Beecher *et al.* 1981 a & b; Rowley 1980). It is probable that, like its relatives, the Black Swan was originally a territorial breeder and that its colonial nesting habit is a more recent adaptation to a particular set of environmental conditions. Kear & Murton (1976; Murton & Kear 1973, 1978) provide data on the effects of photoperiod which suggest that the genus *Cygnus* evolved in the southern hemisphere and that *C. atratus* may once have bred at a higher latitude than is now included in its range. In this case, environmental conditions then prevailing may have been similar to those relating to territoriality in the Arctic-breeding swans.

7.3.2 Maintenance of two breeding modes in the population

The second question relates to the likelihood of swans which breed on territories and those which nest colonially

possessing underlying genetic differences. Williams (1975, 1980) has demonstrated that the New Zealand population is divided into a number of geographically separate groups, with little evidence of intermingling. The majority of swans may move greater or lesser distances to traditional moulting sites but still return to a discrete geographical area for the breeding season, while a minority may remain on their home ponds to moult, as is the case for at least some pairs on Pukepuke Lagoon. Thus any genetic differences arising within a group could be perpetuated, although the selective pressures influencing their maintenance in the population are not clear. Since, within a locality both territorial and colonial nesting may occur (e.g. Lakes Ellesmere and Whangape), for the two "strains" to remain distinct each must possess phenotypic markers, presumably behavioural: particularly courtship and copulatory behaviour. This is another aspect of Black Swan behaviour which warrants investigation.

The alternative to the presence of genetic differences controlling breeding mode is that the choice of breeding method is mediated by learning. This requires recognition of characteristic environmental features. Environmental imprinting is a recognised process (Immelmann 1975) and Black Swans show some degree of philopatry, as do their relatives. Coleman & Minton (1979) found that, of 98 ♂ and 98 ♀ Mute Swans banded as pulli, "a total of 36 ♂s and 60 ♀s were [recaptured] within five miles of their natal site. Of these, 13 ♂s and 32 ♀s were within one mile of their hatching site, often on exactly the same territory on which they were reared". (This would generally be the case only if the original parents were no longer present.) Most of the birds concerned had first moved well beyond this range, usually to join flocks. The birds' first nests were often within five miles of their natal site, and this tendency was more pronounced in ♀s. Minton (1968) commented that, having once bred on a territory, swans tend to return to it in subsequent years after joining a flock to moult. Female Snow Geese show similar site tenacity (Finney & Cooke 1978), while "colony site tenacity after first breeding is

well developed" in Ring-billed Gulls *Larus delawarensis* (Southern 1977). Such strong site tenacity has not yet been demonstrated in Black Swans, but its presence to some degree is likely, and restriction to a given geographical area is apparent (see above). Learning the physical characteristics of the natal site would obviously affect the breeding mode into which the young swan settled.

Evidence for the resolution of this question could be collected through a simple but long-term and time-consuming experiment. Eggs collected from a colonial site would be substituted for those from a territorial site, and vice versa, and the histories of the fledglings followed. If genetic factors were more important in determining breeding mode, the exchange should not have a significant effect on the birds' breeding habits. However, if learning were the major determinant, the majority of young swans would enter the same breeding mode as their foster parents. The fortunes of a human-fostered group could also be studied. Obviously large numbers of eggs would be required and the experiment would span at least four years (until the majority of the swans had attained sexual maturity and bred), but the results would be fairly conclusive. Quicker methods, such as iso-electrical focusing of egg, feather or blood proteins, may well show biochemical differences but do not demonstrate that such differences are necessarily accompanied by behavioural variations.

7.4 KNOWN AND PROPOSED BEHAVIOURAL DIFFERENCES BETWEEN COLONIAL AND TERRITORIAL BREEDERS

It is assumed that the two breeding modes are a response to habitat differences (listed by Williams 1980). The concomitant behavioural adaptations are largely unknown, but some suggestions can be made.

7.4.1 Breeding behaviour

Territorial Black Swans are strongly monogamous. A single ♂ and ♀ will stay together for at least one breeding

season and quite possibly for several (Ch. 4). There are a number of reasons for this:

(1) If territories are large (in the order of a hectare), a single swan would probably be incapable of defending a territory as well as caring for clutch and brood.

(2) Territorial defence, shared by ♂ and ♀, may begin up to three months before laying and so represents a considerable investment of time and energy. A large pre-nesting input, by a parent of either sex, makes it likely that that parent will stay on to care for the young, in order to make good its investment (Trivers 1972, 1974).

(3) Short of setting up a ménage à trois on his existing territory the deserting partner (most probably ♂) may be unable to find and establish a new territory in the face of competition from other, already settled pairs (Ch. 4).

In contrast, the colonial situation is such that defended areas are small enough (the immediate vicinity of the nest) to be adequately defended by one member of a pair, although some losses to nest material or clutch may accrue during nest recesses; brood defence is not required and in fact the brood may coalesce with others to form a creche (see below), relieving at least one set of parents of any familial responsibility. With an extended breeding season a new mate, if available, may be attracted and provided for.

This raises the possibility that not all breeding in colonial areas is by monogamous pairs, and that other associations may also exist successfully (Braithwaite 1970, 1981b). Groups of two ♀s and one ♂ have been observed in the Mute Swan (Dewar 1936; Ellis 1936). Pair bonds may be brief, since the potential for re-mating exists (for the ♂: a gravid or incubating ♀ is not an attractive proposition to a new mate since his investment would be in some other ♂'s offspring) and one bird may care adequately for the young.

If this is the case, the implication (at least for serial monogamy) is that the time needed to develop a pair bond, and to synchronise ♂ and ♀ gonads, is less than expected. In the large flocks seen on colonial areas, the gonadal stimulation necessary to achieve physiological readiness to breed may be supplied by the close presence of numbers of displaying birds (Beer 1975). This effect would reduce the time required to synchronise ♂ and ♀ breeding systems. Similarly the duration of the pair bond may be shortened, when compared with that of territorial Black Swans and other Anserinae, since it is possible for one partner to raise the brood successfully. Male investment is considerably reduced since the costs of territorial defence (in which he plays the major role) are negligible; precopulatory and courtship costs may or may not be decreased. The ♀'s initial input (nest-building and egg-laying) remains constant, and incubation is primarily her concern (Ch. 6). This increases the likelihood of ♂ desertion and re-mating. In addition, promiscuous behaviour has been recorded in the males of other colonial-nesting species (Gladstone 1979; Mineau & Cooke 1979).

7.4.2 Aggressive behaviour and brood care

The nature of care given to the brood also differs between colonial and territorial Black Swans. On Pukepuke Lagoon broods are usually kept apart from each other and from adults until fledging, through the aggressive activities of their parents (Ch. 6). Poorly defended cygnets, or chicks separated from their parents, may be harassed by other swans: this may contribute to poor growth rates and/or increased mortality. In addition the potential food supply for very young cygnets is relatively restricted (see Williams 1980), and feeding competition may be reduced by defence of a territory and separation of broods (but see 7.6.2). However, at least some broods hatching in colonies enter creches (Williams 1980 & pers. comm.; I. Buchanan pers. comm.), when mixing of cygnets is permitted by the close and unrestricted proximity of

families. Thus creching is the result of differences in aggressive behaviour and also of the Black Swan's possession of a relatively long imprinting period (Ch. 5; 7.3.1). I predict that the frequency of all displays used in territorial defence, notably Parade and Flapping Lunge but perhaps also Slow-Wing-Flap and Trumpet, will be reduced in aggressive displays by colonial swans.

The benefits of creching are unclear; advantages and costs will show up in estimates of cygnet and fledgling production. Such data are few. Williams (1980) shows that on Lake Ellesmere (where creching occurs) 65% of cygnets which remain in family broods fledge, while for the colony 52.2% of cygnets hatched reach independence. Data from other colonial-nesting areas are similar. Figures for Pukepuke Lagoon show an overall fledging total of 87.5% (100% in 20 of 29 broods). A possible advantage of creching is that it may enhance cygnet feeding on the abundant but patchily distributed sources available (Williams 1980). A reduction of predation on individual chicks, through the dilution effect, is also a possibility. However, the benefits and losses to individual parents have yet to be examined.

Creching is frequent in the Eider Duck and in Shelducks, and the adoption of orphaned young has also been reported in some geese (e.g. Eisenhauer & Kirkpatrick 1977) and in gulls (Graves & Whiten 1980). Gorman & Milne (1972) suggest that creching in the Common Eider is of benefit to ducklings as an anti-predator device, and also frees Qs to feed (see also Munro & Bédard 1977). Williams (1974) found that creching *per se* was "a major proximate cause of mortality" to Shelduck, but that ducklings in creches had a greater probability of fledging, spending more time feeding than the young of single families. Creching was due to ducklings being more attracted to each other than to adults, and so tending to coalesce when young families were in close proximity to each other. Patterson *et al.* (1982) found no significant difference between donor and recipient parents

in *Tadorna tadorna* with respect to the number of their own offspring reared to fledging i.e. neither "giving" nor receiving another bird's offspring improved the chances of one's own chicks.

Decreased breeding success in colonial swans may also be affected by social interactions prior to hatching. Miers & Williams (1969) found that breeding success in the colony of Black Swans at Lake Ellesmere was lower at higher nest densities. (Similar data for several other species are offered by Coulson, 1971.) This may be due to intra-specific interference, especially agonistic interactions, although nest destruction, through the theft of nest material, and egg theft or breakage may also be important. Similarly Ewaschuk & Boag (1972), studying Canada Geese, found that high nesting density was accompanied by a high level of intraspecific interference, which could be effective in increasing the frequency of nest desertion and so of predation on the exposed eggs. Patterson (1976) also found that interference at the nest tended to increase the tendency to desert and so decreased breeding success. In addition, he suggested that aggressive interactions decreased the rearing success of subordinate birds in a population, through harassment and/or competition, based on his finding that only dominant Shelducks successfully reared broods. This situation may also prevail among territorial Black Swans (Ch. 6). Aggressive incidents between older broods, facilitated by their mixing during parental disputes, may also influence brood mortality.

Unfortunately, due to the scarcity of data, the effects of social interactions on the breeding success of Black Swans, the disadvantages and benefits of colonial and territorial breeding, and the behavioural differences between the two habits, remain largely conjectural and offer an interesting field for future research.

The preceding chapters have detailed and discussed flock behaviour, aggression and territoriality, mating, and brood care in the Pukepuke Lagoon Black Swan population. On this lake there is a distinct breeding cycle and the behaviour categories listed above form a series of inter-related cycles (Fig. 7.2). Such a clearly defined cycle is not always present in Black Swans.

Braithwaite (1970) states that Australian swans breed regularly in winter and early spring in the southern parts of their range. However, in the north and in arid regions, breeding appears to be more dependent on the timing of rainfall than on the photoperiod changes which must be basic to the cycle (Kear & Murton 1976; Short 1973). In Queensland the swans breed in the period February-May, following monsoon rains, while in arid zones birds will appear and breed whenever, and for as long as, suitable habitat is available (see also Lavery 1965). In the southern part of their range, Black Swans usually begin nesting in July-August. Timing varies to some degree between years and is affected by water levels in the breeding grounds. Braithwaite & Frith (1969b) concluded that the timing of breeding and associated activities in Black Swans is controlled primarily by rainfall although "reasonable evidence of a residual photoperiodic influence" was also noted. However, since breeding has a definite starting time in those parts of the species' range where suitable habitat is available for most of the year, the effects of photoperiod on physiological cycles are surely more than "residual". In addition, since it takes some time for the gonads to reach full breeding condition, photoperiod must be the ultimate controlling factor. Otherwise a considerable lag time would be obvious in breeding responses to rain-changed water levels. Where swans are maintained outside their normal habitat range, time of breeding is definitely controlled by photoperiod (Kear & Murton 1976; Murton & Kear 1973).

The New Zealand swan population also shows a definite start to its breeding season, even though, given suitable conditions, breeding may continue for six to eight months (Miers & Williams 1969). On Lake Ellesmere breeding is markedly seasonal, although affected by changing water levels: laying usually begins in early August and ends by December. On Lake Whangape, in the Waikato, breeding has a clearly defined start in June, but may continue for six months, again related to water levels (controlled by hydro-electric schemes) (Lickers 1977; Miers & Williams 1969; Williams 1980). Williams (1980) states that solitary (territorial) swans breeding in wetlands with stable winter and spring water levels show regular timing of nesting, starting in July and continuing into October. This is the case on Pukepuke Lagoon. He adds that colonial nesters tend to breed at irregular times, determined by changes in water level.

Figure 7.2 demonstrates the annual activity cycles seen on Pukepuke Lagoon. Breeding territories are first defined in May, although some pairs may begin defence a month or less before breeding begins. Defence continues until the broods fledge in January of the following year. Sexual activity occurs at a low level in spring and summer but builds up over the autumn to peak in late July, then drops off abruptly. The July high is when most fertilisations occur; the earlier activity may be regarded as "practice", serving to strengthen pair bonds, demonstrate sexual efficiency and synchronise ♂ and ♀ gonads. Most broods appear about five weeks later, in August, and remain with their parents until they fledge four to five months after hatching. Families then separate and territorial defence ceases.

However, the majority (75%: Ch. 1) of the Pukepuke Lagoon population (at the time of nesting) does not breed on the lake. Within this non-breeding flock, numbers, activity and use of the lagoon may fluctuate. Activity patterns are dependent on energy requirements, themselves influenced by physical and physiological features of the

environment and the individual (Ch. 2). Changes in population size, and in the observed patterns of area use, are to some extent affected by the presence and activities of the few territorial breeders and will be discussed in detail later (7.6). Excluding these factors, the other major recurring event in the flock's year is the annual moult, extending over late summer and early autumn and usually involving some sort of "moult migration" (T. Caithness, M. Williams pers. comm.). Where this occurs it is a movement over relatively short distances and should not be confused with the breeding migrations of geese and the northern swans. Although some breeders remain on their nesting territories for the moult (Ch. 3, 6), most probably enter the flock and leave it again once moulting is completed. Mute Swans may or may not rejoin the flock for the non-breeding season (Minton 1971); all migratory Anserinae do so. In the latter group the family usually remains together to join the flock (Elder & Elder 1949; Hewson 1964; Prevet & MacInnes 1980; Raveling 1969; D. Scott 1980). This is not always the case in Mute (MacSwiney 1966) or Black (pers. obs.) Swans.

The flock contains a large pool of birds which do not necessarily breed in any one year, although they are of an age to do so. Mute Swans may pair at two years old, but do not usually breed until the age of four, or more (Coleman & Minton 1979; Minton 1968); the younger birds remain in the flocks with the mature non-breeders. Both single birds and pairs with known breeding histories may enter the flock and remain there for one or more seasons. Similarly Williams (1980) has found that the majority (approximately 80%) of the New Zealand Black Swan population does not breed in any one year, although many swans are over four years old and the species may attempt breeding at two years (Braithwaite & Frith 1969b) or less (pers. obs.). Frith (1967) suggests that the very large numbers of non-breeders, seen in many Australian flocks during the breeding season, probably comprise immatures, or else adults unable to find nest sites. Birds which have bred and moulted earlier in the year may also be present.

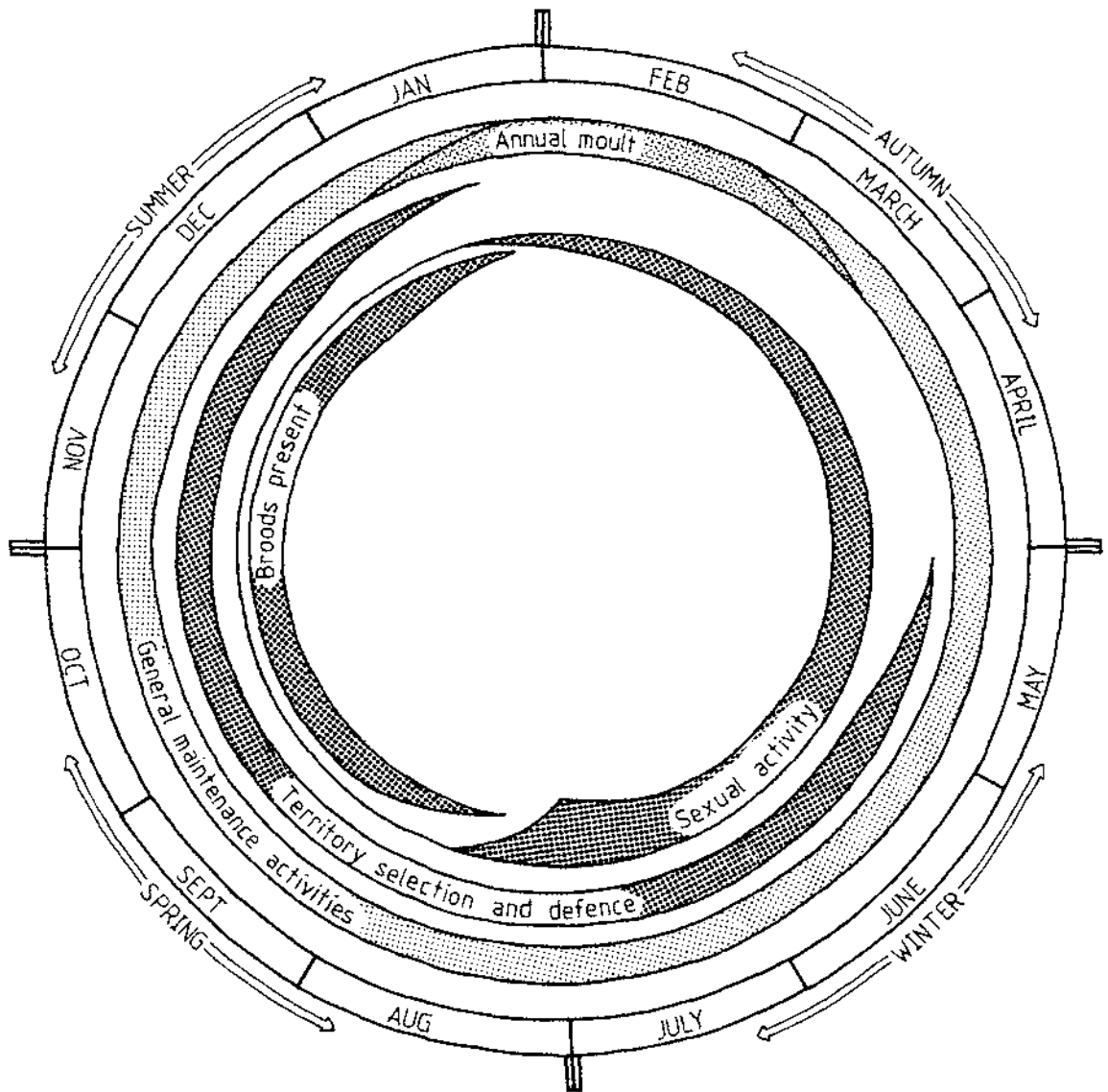


FIGURE 7.2: The annual cycle of activity of the Black Swan population of Pukepuke Lagoon

Other factors may also prevent birds from breeding: ill health, below-par physical condition, death of or divorce from a mate, or inability to find a compatible partner (Ch. 4). In localities where territorial breeding is the norm, a shortage of nest sites and suitable territories may restrict breeding, especially if swans are strongly philopatric and return to their natal area to nest: the original pairs may still be present.

7.6 THE RELATIONSHIP BETWEEN TERRITORIALITY AND USE OF THE LAGOON BY FLOCK AND BREEDING SWANS

7.6.1 Restrictions on flock use

On Pukepuke Lagoon breeding territories are held over the period May-January, although not all are defended for such a lengthy space of time (Ch. 3). It is apparent that the activities of at least some territorial pairs restrict flock use of the lagoon over some part of the breeding season (Fig. 7.3 a-c); they may also affect overall flock size (K. Potts pers. comm.).

When flock size and the feeding component of the flock's time budget are compared (Fig. 7.4), it is clear that flock numbers are at their lowest at that time when the proportion of time spent feeding is at its peak. This also coincides with a high degree of territorial activity. Thus, when flock feeding requirements are at their highest, the use of a considerable part of the lagoon is denied to it by the activities of one or two territorial pairs. (Other pairs tolerate the non-breeding flock members.) Both the reduction in feeding area and the behaviour of breeding pairs may contribute to the reduced flock size in spring, although some members will themselves be moving on to nesting sites. The spring flush in plant growth should provide an ample food supply.

It is possible that removal of the principal aggressors from the lagoon would increase its availability to flock

birds, given that a new dominant pair did not arise to take their place.

7.6.2 Management of the breeding population

A similar effect is seen with respect to the number of breeding pairs supported by the lagoon. With one or two exceptions, all nesting pairs defend a territory over the breeding season, but the size of these territories varies considerably (Table 7.1). The reasons for this variation are not completely understood but appear to depend in part on the aggressive tendencies of individual pairs (Ch. 3: 3.3.4). A dominance hierarchy of sorts is apparent, with ♂1 at the top with respect to territory size, duration of defence, and aggressive behaviour.

It is also possible that the area available for feeding by very young cygnets, which are incapable of feeding underwater for any length of time, influences the size of territory defended (Williams 1980). However, Table 7.1 shows that the amount of "cygnet-feeding-area" included in a territory also varied (only "visible" open-water areas may be measured). The total cygnet-feeding-area enclosed is dependent on the overall size of the territory.

The breeding success of a given pair may be partially dependent upon the amount of food available to the young brood. However, if this is the case, the lower limit of cygnet-feeding-area is not reached in the Pukepuke territories, since even the smallest area supported the cygnets beyond the class I (0-14 d.) stage (Fig. 7.5). The two broods which did not pass this stage were not protected by their parents and were exposed to harassment by and close competition with other breeders and flock members. It is probable that adequate parental attendance and defence (Ch. 6) are essential to rearing success in a territorial-breeding locality. (The loss of one cygnet from the GC2 brood of 1979 is attributed to predation or disease, since parental defence was such that harassment was never a problem.)

FIGURE 7.3: The relationship between territorial activity and flock use of Pukepuke Lagoon

- a) flock use during maximum territorial activity, 1978
- b) flock use during maximum territorial activity, 1979
- c) flock use of Pukepuke Lagoon when territorial activity is at a minimum

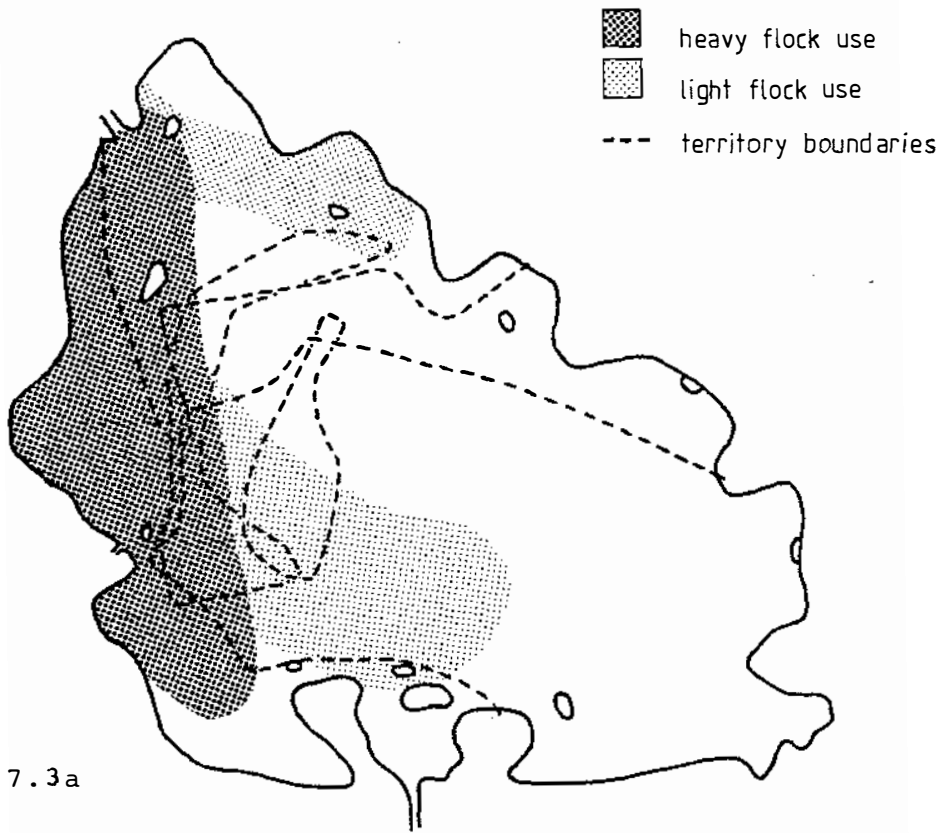


FIGURE 7.3a

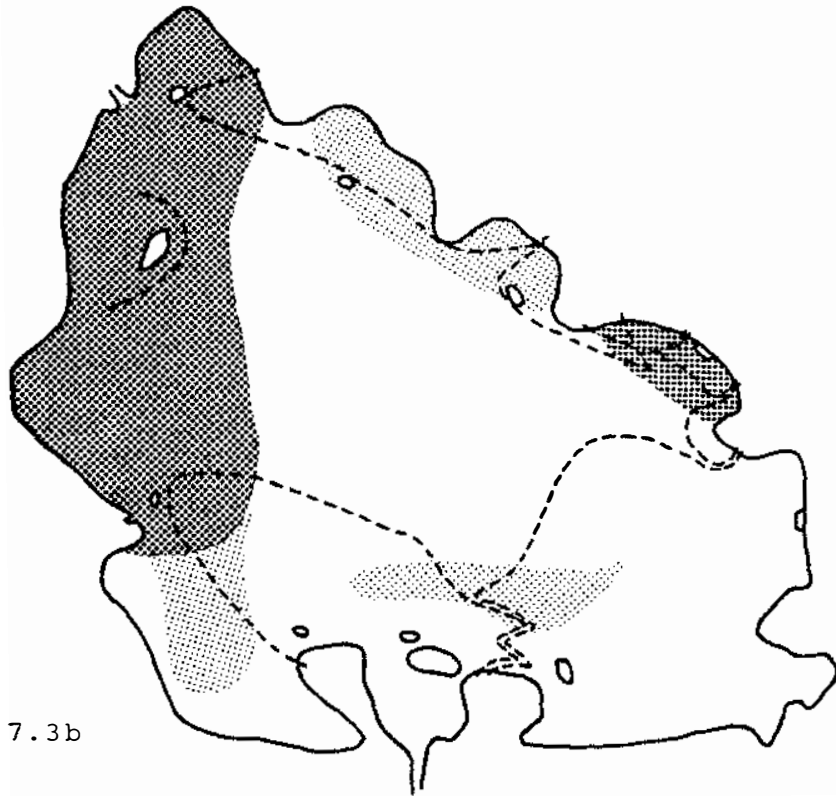


FIGURE 7.3b

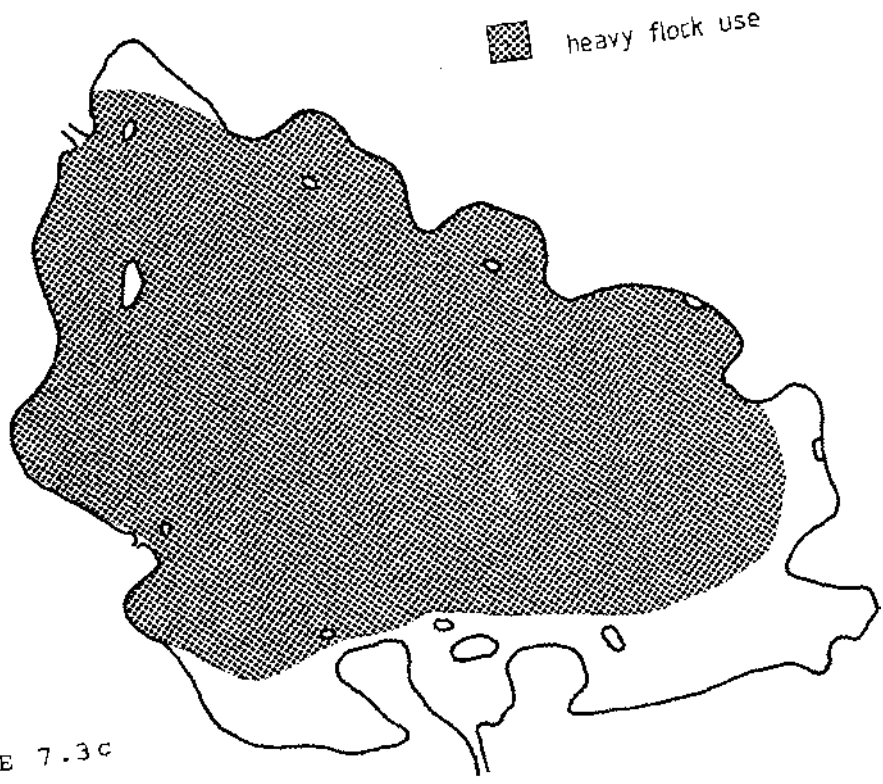


FIGURE 7.3c

FIGURE 7.4: Monthly and seasonal changes in population size and activity, Pukepuke Lagoon, 1978-1979

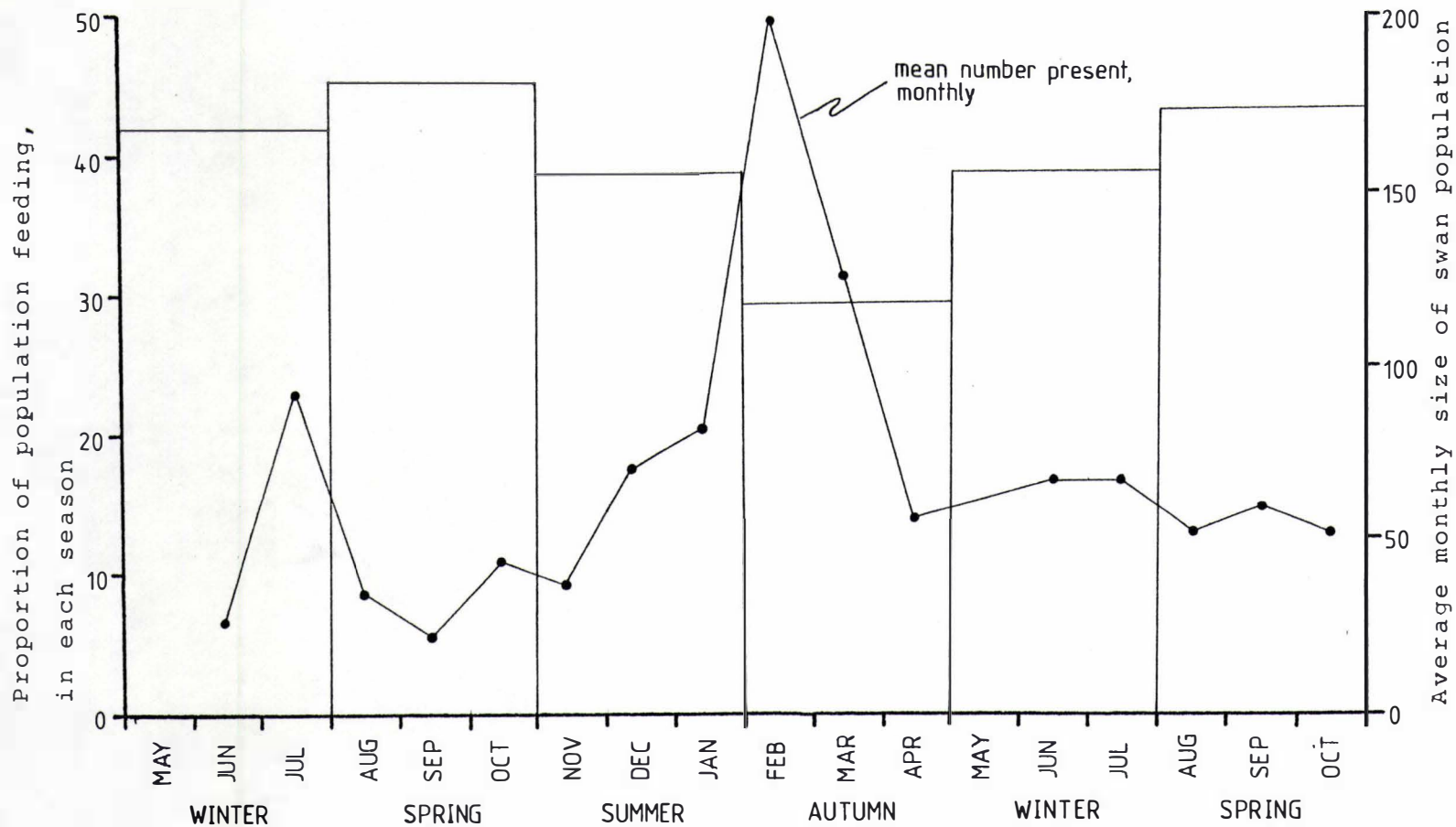


FIGURE 7.5: Enclosed cygnet-feeding-area versus relative breeding success for pairs with cygnets reared to at least class I (1979 broods)

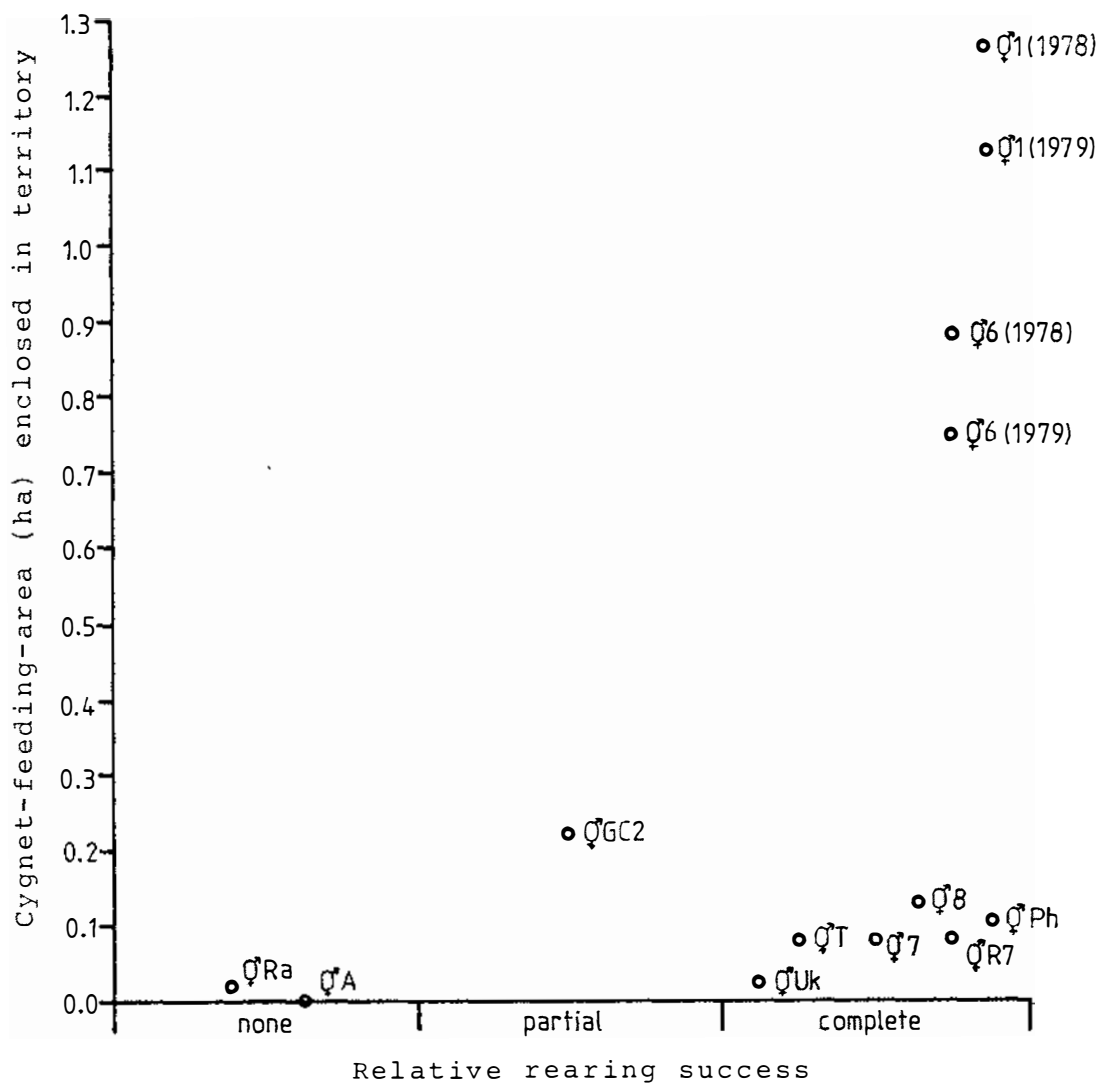


TABLE 7.1 THE SIZE (ha) OF DEFENDED AREAS AT THE TIME WHEN CLASS I CYGNETS WERE PRESENT ON THEM, AND THE AMOUNT OF CYGNET-FEEDING-AREA (c.f.a.) THEY ENCLOSED, 1978 AND 1979

pairs	breeding seasons			
	1978		1979	
	territory size (ha)	c.f.a. (ha)	territory size (ha)	c.f.a. (ha)
1	5.88	1.26	3.98	1.13
6	1.75	0.88	0.75	0.75
GC *	0.64	0.53		
GC2			0.97	0.22
7			0.08	0.08
A			0.03	0.02
T			0.08	0.08
Ph			0.25	0.10
R7			0.08	0.08
8			0.13	0.13
Uk			0.03	0.02
Ra			no defended area	

* : ♀GC had their clutch removed before hatching; this figure represents the maximum defended area and the amount of shallow-water feeding area it encompassed.

Since a cygnet-feeding area of approximately 0.03ha seems sufficient to rear a brood through the class I stage (although food quality and quantity were not measured), it is apparent that Pukepuke Lagoon could potentially support a greater number of breeding pairs than is currently the case, provided that most of them showed the relatively low aggressive tendencies seen in most 1979 pairs. Removal of the belligerent ♂1, and possibly ♀GC2, and culling of any strongly dominant pairs which arose to take their place, would free a large area for settlement by other breeders. The decrease in cygnet production brought about by the removal of the prolific ♂1 should be more than compensated for by the settlement of several pairs with an average (5.5 eggs) clutch size.

For both these proposals (7.6.1 & 7.6.2), the best time to perform such a removal experiment would be at the end of a breeding season i.e. in January, when most or all broods have fledged. This would maximise the preceding year's cygnet production, while allowing several months (laying does not occur until late July - early August) for newcomers to prospect for and settle on their own breeding territories. The situation would obviously have to be monitored each season, to guard against the appearance of a new, strongly-aggressive duo.

7.7 CONCLUDING REMARKS

In conclusion, the following are the main results and hypotheses offered by this thesis:

(1) The behaviour of both flock members and territorial breeders in a population of Black Swans is described as fully as possible (Chs 2, 3, 4, 5, 6), making a considerable contribution to the available data on this species.

In particular, new details and analyses of sexual and aggressive behaviour are presented and related to existing data. This provides further confirmation for existing

taxonomic divisions of the genus *Cygnus*. It also reveals several points on which I differ with earlier descriptions and analyses. These differences may lie in the nature of the populations studied: mine was territorial and free-ranging while Braithwaite's, at least, was captive and perhaps derived from colonial individuals. Captivity may affect the frequency of performance of some acts, but the form of the behaviour patterns should not be greatly altered. In any case comparison with wild birds would show up any gross abnormalities (Dilger 1962). One act certainly affected by the circumstances of captivity is the probably-aggressive Necks-Curved-Over end-posture of copulation, which is unlikely to occur if pairs are alone (e.g. single pairs in captive collections). This does not explain the absence from other descriptions of a number of precopulatory displays, nor the apparently erroneous linkages between aggressive acts and pair-bond maintenance displays (see 7.2.2).

(2) Time-activity budgets and cycles of behaviour are examined. This reveals definite cycling of breeding and related activities in territorial swans. Flock birds' patterns centre on major energy drains during the year, such as preparation for the moult and, for some, entering the breeding pool (Ch. 2). No diurnal activity rhythms are apparent; it is more likely that general maintenance behaviour follows polyphasic patterns. The timing of breeding is under photoperiodic control; water levels are usually stable during the Pukepuke breeding season and so are unlikely to affect the initiation of gonadal recrudescence. Sexual behaviour peaks in late winter and broods appear in early spring, in time for the spring flush in plant growth.

(3) The Black Swan population of Pukepuke Lagoon is clearly divided into territorial and flock swans. A number of behavioural cues may be used to distinguish potential breeders from the flock. Apart from the obvious defence of a particular area, differences in the frequency of some behaviour patterns, and the exclusive performance of others, indicate the identity of territorial birds.

The defence of relatively large areas, and in some cases the complete exclusion of others from them, is of definite significance to the management of this lagoon, and of other similar locales (7.6). Flock use is restricted at a time when its members' feeding needs are at their greatest, and the potential number of active breeding pairs is also reduced by the activities of a few belligerent birds. The removal of such birds, and monitoring changes in the breeding population, would indicate how much their individual behaviour affects the overall breeding potential of an area.

(4) On a wider scale this study also provides an information-base which may be used for comparison with colonial swans' behaviour patterns and activity cycles. Data obtained from studying the imprinting of cygnets on their parents (Ch. 5), combined with published information on breeding responses to photoperiod, indicate that Black Swans are ancestrally territorial. The colonial habit is a secondary adaptation to a specific set of currently prevailing conditions.

The factors underlying young swans' entry into a given breeding mode are uncertain. There may be some genetic control: this would necessitate some form of phenotypic marker, presumably behavioural, so that individuals of one "strain" could recognise each other. Since the swans are strongly philopatric, learning and ecological imprinting could equally well affect their choice. A long-term egg-exchange experiment would provide an answer.

The two breeding habits thus offer interesting fields for research. I predict differences in the use of those threat displays which are good identification criteria for territorial swans. The duration and strength of pair bonds and the length of the courtship period may also vary, and some differences in brood care have been shown to exist. The underlying environmental factors affecting the colonial/territorial dichotomy also require further examination.

SUMMARY

Chapter 1

The research methods appropriate to a primarily observational study are discussed, and the area (Pukepuke Lagoon - a Manawatu dune lake) and characteristics of its Black Swan population are described.

Chapter 2

The behaviour patterns, time-activity budgets and the manner of area utilisation by the large non-breeding flock are discussed. Feeding and loafing activity cycles are affected by major energy-expensive events during the year, such as the moult, or breeding preparations: feeding peaks over the spring, loafing around the time of the moult. The flock's use of the lagoon is restricted in winter and spring by the aggressive activities of a few breeding pairs.

Chapter 3

Aggressive behaviour and the mechanisms of territory selection and defence are described. Aggression by territorial swans makes up the greater part of the total aggressive incidents observed on the lagoon. The behaviour patterns Parade, Trumpet, Slow-Wing-Flap and Flapping Lunge occur at a much higher frequency in the displays of territory owners and are useful clues to the identity of prospective breeders.

Territory size varies from 0.03ha to 10.69ha (maximum values), but this variation does not appear to affect breeding success. The reasons for this extreme size differential, and for differences in duration and degree of defence activities are not clearly understood, but depend in part on the food resources available to young cygnets

and/or females, and also on the aggressive tendencies of individual pairs.

Chapter 4

Courtship, pair-bond maintenance, and copulatory acts and displays are listed. Pair-bond maintenance displays are briefer and less conspicuous than precopulatory activity, and may (31.5% of cases) involve only the male. Both ♂ and ♀ participate in copulatory activity, although the ♀ determines whether or not the sequence will continue. Other swans rarely interfere.

All sexual behaviour shows a diurnal (mid-day peak) and annual (mid-winter peak) rhythm.

The bases for pair formation, the cues used in mate selection, the strength and duration of the pair bond, and the function of this bond are discussed. Black Swans do not pair for life although the bonds generally last for at least one breeding season in territorial breeders. Mate choice depends on physical characteristics and behavioural cues, including the ability to defend a territory, and a strong bond enables division of labour over most breeding activities and, where it lasts for several seasons, enhances breeding success. These conclusions are valid only for territorial swans: comparison with colonial birds is necessary to obtain the full spectrum of bond strengths and functions, and of display frequencies and performances.

Chapter 5

Physical growth and behavioural development of cygnets are examined, using a captive brood for close observations. This provides data on growth rates, ontogeny of behaviour patterns, and development of social relationships. Captive swans grow faster than wild broods, but their behavioural development parallels that of the wild birds. Imprinting and individual recognition take one - two weeks to finalise:

this information suggests that the ancestral breeding mode of Black Swans was territorial. Brood and family cohesion is maintained by the use of Greeting ceremonies, and individual positions in a social hierarchy are still not determined after 70 days.

Chapter 6

The different behaviour patterns used by adults in brood care, and the relationships within the family, between families, and between families and flock, are described and discussed. Clear sex roles are apparent, the male being most prominent in defence while the ♀ carries the main burden of attendance on and care of the brood. Strong family behaviour is important in a territorial context, as otherwise harassment by and competition with other territorial swans may considerably reduce a pair's breeding success. Families break up once the broods have fledged.

Chapter 7

The main points arising from the preceding chapters are interrelated. Data on the swans' behaviour are discussed in relation to other authors' work: some new information on sexual and aggressive behaviour patterns is presented. The derivation and maintenance of breeding habits are discussed: whether the colonial and territorial breeding modes are maintained in the population by genetic or learned controls would be best determined by a long-term egg-removal experiment. These two breeding modes offer ample room for future comparative research into sexual, aggressive and brood-care behaviour.

On Pukepuke Lagoon, the activities of one or two belligerent pairs appear to restrict the activities and numbers of flock swans and other breeders. A closely-monitored culling experiment would be of considerable interest and could well increase the breeding output of the lagoon.

APPENDIX I TIME-ACTIVITY BUDGETS OVER THE
BREEDING SEASON, FOR A SINGLE PAIR

Sufficient data on time-activity budgets are available only for ♂1, the most aggressive, and probably dominant, pair on the lagoon.

The periods examined here are nest-building, incubation, and brood care, for 1978 and 1979. Activity classes are alert, feed, loaf (preen + doze), aggression, and sexual and pair-related behaviour. All these are considered as proportions of the total time, in each period, that ♂1 and ♀1 were visible on the lagoon (% visible time). The time spent in a given activity was compared, using χ^2 2x2 tables, for each period between years.

Of the activity classes studied, only aggression is likely to be accurately measured, since all aggressive activity appeared to occur on the open lagoon, in full view. Sexual activity occurred on the open water, but pair-bond maintenance displays are likely to go unnoticed (Ch. 4), while Greeting ceremonies may occur at the nest as well as on the lagoon. Similarly, alert behaviour, feeding and loafing behaviour may all be concealed to some degree by the shoreline vegetation.

A. Proportion of total observation time for which ♂1 visible.

	nest-building		incubation		brood care	
	1978	1979	1978	1979	1978	1979
♂ visible time	96	215	538	583	2146	636
% total observation	15.24	35.25	26.77	31.34	53.72	38.55
♀ visible time	86	133	126	260	1801	485
% total observation	13.65	21.80	6.27	13.98	45.08	29.39
total time in observation (minutes)	630	610	2010	1860	3995	1650

B. Proportion of visible time (%vt) spent in given activity classes by ♂ and ♀, 1978 and 1979 breeding seasons.

<u>Alert</u>	nest-building		incubation		brood care	
	1978	1979	1978	1979	1978	1979
♂ time	11	13	32	42	551	116
%vt	11.46	6.05	5.95	7.20	25.68	18.24
♀ time	13	4	21	42	368	111
%vt	15.52	3.01	16.67	16.15	20.43	22.89
<u>Feed</u>						
♂ time	33	23	330	107	893	259
%vt	34.37	10.70	61.34	18.35	41.61	40.72
♀ time	23	19	101	78	906	153
%vt	26.74	14.29	80.16	30.00	50.31	31.55
<u>Loaf</u>						
♂ time	50	109	112	287	383	67
%vt	52.08	50.96	18.96	49.22	17.84	10.53
♀ time	50	69	0	95	306	97
%vt	58.14	52.52	0.00	36.53	16.99	20.00
<u>Aggression</u>						
♂ time	2	60	75	126	303	183
%vt	2.08	27.91	13.94	21.61	14.12	18.77
♀ time	0	31	4	24	205	113
%vt	0.00	23.31	3.17	9.23	11.38	23.30
<u>Sexual</u>						
♂ time	0	10	0	21	16	11
%vt	0.00	4.65	0.00	3.60	0.75	1.73
♀ time	0	10	0	21	16	11
%vt	0.00	7.52	0.00	8.08	0.89	2.27

Sexual activity obviously involved both male and female for the same length of time. It occupied only a small proportion of time in both years and was not analysed further.

However, the proportion of visible time occupied by other activities showed significant differences between years for at least some behaviour patterns. These differences are indicated below.

Overall visibility

♂1 was visible for less time during nest-building and incubation during 1978 ($p < 0.001$, $p < 0.01$) in comparison to the same periods in 1979, but spent significantly more time in the open ($p < 0.001$) over the 1979 brood care period. For ♀1, overall visibility was less for nest-building and brood care in 1978 ($p < 0.001$ for both), but time spent in the open during incubation was significantly more in 1978 than in 1979 ($p < 0.001$).

Alert postures

♂1: no significant difference in time spent in alert postures during incubation for both years, but these occurred at a significantly higher frequency during nest-building and brood care in 1978 ($p < 0.01$, $p < 0.001$).

♀1: the only difference exists during nest-building, when time spent in vigilance was higher in 1978 than 1979 ($p < 0.01$).

Feeding

♂1: time spent feeding in the open was greater in 1978 than in 1979 for the periods nest-building and incubation ($p < 0.001$, $p < 0.001$), but there was no difference between the years for brood care.

♀1: spent considerably more time feeding in the incubation and brood care periods of 1978 ($p < 0.001$ for both); the decrease for 1979 incubation was most pronounced.

Loafing

♂1: less time spent loafing during incubation of 1978 than 1979 ($p < 0.001$), and more time during 1978 brood care ($p < 0.001$).

♀1: loafing occupied the same proportion of visible time in both years for nest-building and brood care, but occurred significantly more often during 1979 incubation.

Aggression

♂1: occurred at significantly higher levels in 1979, for all three periods ($p < 0.001$ for all).

♀1: was more frequent in 1979 than 1978, for nest-building and brood care ($p < 0.001$ for both).

In addition, aggression by Q1 during the 1979 brood care period rose over that time to occupy a greater proportion of total visible time than that of σ 1.

Aggression over the brood care period, as a proportion of total visible time:

1978			1979		
date	σ 1	Q1	date	σ 1	Q1
18-19/10	29.41	9.73	7/9	23.76	9.72
1-2/11	7.71	3.52	13/9	31.75	5.71
15-16/11	10.23	9.39	27/9	31.36	4.55
29-30/11	15.14	13.77	17-18/10	25.97	6.57
5-6/12	15.04	16.01	31/10-1/11	34.15	65.44
21/12	6.94	0.00			

APPENDIX II STATISTICS USED IN PRODUCING THE
MATRIX PRESENTED IN TABLE 3.2
(after Radesäter 1974a)

Only transitions from one act to a different one are considered. Thus the upper-left lower-right diagonal of the matrix is blank and must be corrected for in calculation of the expected (e) value of each cell. The correction is one proposed by Lemon & Chatfield (1971):

expected value in any cell =

$$\frac{\text{row total for cell} \times \text{column total for cell}}{\text{overall matrix total} - \text{column total for cell}}$$

e.g. for the transition ALU - THR₁₀

$$e = \frac{246 \times 502}{4135 - 502} = 33.99$$

To obtain a probability level for the difference between observed (o) and expected values in each cell, a 2x2 X² test is used (Brown et al. 1967). Instead of recalculating expected values, the corrected "e" value from the preceding equation is substituted into the cell in question, and the other "e" values are derived by subtraction of this from the marginal totals.

Thus, for the cell ALU - THR₁₀

	THR ₁₀	2nd act of pair other than THR ₁₀	marginal totals
ALU	"o" 50 "e" 33.99 X ² 7.54	196 212.01 1.21	246
1st member of pair other than ALU	"o" 452 "e" 468.01 X ² 0.55	3437 3420.99 0.07	3889
marginal totals	502	3633	4135

degrees of freedom = 1 X²_{total} = 9.37 α = 0.01 p < 0.01

The two behaviour patterns are not independent

APPENDIX III

TABULATION OF DATA USED IN SINGLE-LINK-CLUSTER-ANALYSIS OF AGGRESSIVE BEHAVIOUR, DERIVED FROM THE TRANSITION MATRIX OF TABLE 3.2^a

		second member of display pair																		
		ALU	IMP	THR _{lo}	PEL	THR _{me}	THR _{hi}	FL	FBE	PAR	SWF	TRU	TRI	GRE	REU	preen	feed	DR	B	FF
first member of display pair	ALU	-	5.6	32.2	11.6	23.2	6.0	9.1	7.1	3.0	6.6	5.7	1.7	14.5	24.6	14.5	20.5	7.9	7.7	*42.5
	IMP		-	11.1	0.0	0.2	0.0	0.0	0.0	17.4	0.6	0.0	1.7	10.7	13.9	10.5	*38.3	0.0	0.0	0.0
	THR _{lo}			-	6.1	36.4	10.1	14.0	3.3	6.3	18.9	6.0	5.6	25.3	30.3	30.4	*51.0	14.8	6.9	0.6
	PEL				-	12.3	11.2	8.0	0.0	3.2	7.5	0.9	3.8	12.3	9.1	14.3	*26.5	0.0	0.0	0.0
	THR _{me}					-	22.4	36.3	13.7	14.6	18.6	*38.0	23.7	*45.5	14.0	28.9	31.7	7.7	13.2	17.0
	THR _{hi}						-	*37.7	24.2	*31.8	6.4	18.4	16.9	24.5	5.2	15.5	15.0	0.4	5.0	0.2
	FL							-	7.2	7.5	15.3	11.2	6.9	6.9	3.0	7.8	2.9	0.0	3.2	0.3
	FBE								-	20.9	0.0	0.9	0.0	6.7	0.0	10.0	10.0	0.0	3.3	0.0
	PAR									-	4.5	1.4	12.9	22.6	0.5	11.9	8.0	0.0	1.6	8.9
	SWF										-	2.4	4.2	5.1	10.3	*44.5	10.3	0.0	*35.9	0.0
	TRU											-	3.5	17.2	3.1	1.8	8.8	0.0	2.0	0.0
	TRI												-	7.3	5.0	16.7	13.3	0.0	3.3	0.0
	GRE													-	9.3	14.7	23.1	0.4	7.4	25.7
	REU														-	23.9	25.2	*36.4	0.0	0.0
	preen															-	11.1	14.3	34.3	8.3
	feed																-	21.4	0.0	0.0
	DR																	-	0.0	0.0
	B																		-	0.0
	FF																			-

a: data corrected to one decimal place

*: cells used in dendrogram

APPENDIX IVa TRANSITION ANALYSIS OF MALE-FEMALE INTERACTIONS DURING COPULATORY-DISPLAY SEQUENCES

** p < 0.01

*** p < 0.001

†† "e" values too small to permit testing. However, "observed" values such that results are obviously of some significance

FOLLOWING ACTION (female)

	HD	HD/♂	ND	ND/♂	ND _{hi}	ND _{hi} /♂	REU	ALU	FT	CRLP	PP	PRO	♂CALL	♀CALL	NCO	NOS	other	row total
HD	41 7.20 ***	0 0.51 ns	76 65.31 ns	0 3.57 ns	17 15.42 ns	0 0.38 ns	34 13.13 ***	2 6.24 ns	7 55.31 ***	31 12.23 ***	0 6.50 **	7 13.95 ns	0 6.63 **	0 1.47 ns	0 1.34 ns	0 5.16 ns	1 1.66 ns	216
HD/Q	11 5.27 **	0 0.37 ns	111 47.77 ***	0 2.61 ns	13 11.28 ns	0 0.28 ns	10 9.60 ns	0 4.57 ns	3 40.46 ***	0 8.95 **	0 4.75 ns	10 10.21 ns	0 4.85 ns	0 1.07 ns	0 0.99 ns	0 3.78 ns	0 1.21 ns	158
ND	31 19.97 **	8 1.41 ns	341 181.11 ***	53 9.90 ***	24 42.76 ***	0 1.06 ns	37 36.40 ns	2 17.32 **	37 153.37 ***	53 33.93 **	0 18.02 **	9 38.70 ***	0 18.38 ***	0 4.06 ns	0 3.71 ns	0 14.31 ***	4 4.59 ns	599
ND/Q	4 12.27 ns	0 0.87 ns	262 111.27 ***	0 6.08 **	13 26.27 **	0 0.65 ns	33 22.36 ns	0 10.64 **	5 94.23 ***	0 20.84 ***	11.07 ***	51 23.77 ***	0 11.29 ***	0 2.50 ns	0 0.28 ns	0 8.79 **	0 2.82 ns	368
ND _{hi}	5 6.27 ns	0 0.44 ns	27 56.84 ***	1 3.12 ns	123 13.42 ***	6 0.33 ns	9 11.42 ns	1 5.43 ns	9 48.13 ***	2 10.65 **	0 5.66 ns	4 12.14 ns	0 5.77 ns	0 1.28 ns	0 1.16 ns	0 4.49 ns	1 1.44 ns	188
ND _{hi} /Q	0 1.10 ns	0 0.08 ns	1 9.98 ***	0 0.55 ns	29 2.34 **	0 0.06 ns	0 2.01 ns	0 0.95 ns	0 8.45 ***	0 1.87 ns	0 0.99 ns	3 2.13 ns	0 1.01 ns	0 0.22 ns	0 0.20 ns	0 0.79 ns	0 0.25 ns	33
REU	10 6.97 ns	0 0.49 ns	93 63.19 ***	2 3.45 ns	9 14.92 ns	0 0.37 ns	54 12.70 ***	3 6.04 ns	1 53.51 ***	11 11.84 ns	15 6.29 **	8 13.50 ns	0 6.41 **	0 1.42 ns	0 1.29 ns	0 4.99 ns	3 1.60 ns	209
ALU	0 2.60 ns	0 0.18 ns	0 23.58 ***	0 1.29 ns	0 5.57 ns	0 0.14 ns	1 4.74 ns	65 2.25 **	0 19.97 ***	1 4.42 ns	10 2.35 ns	0 5.04 ns	0 2.39 ns	0 0.53 ns	1 0.48 ns	0 1.86 ns	0 0.60 ns	78
FT	2 30.33 ***	0 2.15 ns	68 275.15 ***	0 15.03 ***	9 64.96 ***	0 1.61 ns	0 55.30 ***	0 26.31 ***	800 233.00 ***	5 51.54 ***	0 27.38 ***	25 58.79 ***	0 27.92 ***	0 6.17 **	0 5.64 **	0 21.74 ***	1 6.98 **	910
CRLP	7 4.33 ns	0 0.31 ns	13 39.31 ***	0 2.15 ns	2 9.28 ns	0 0.23 ns	15 7.90 **	3 3.76 ns	2 33.29 ***	86 7.36 **	0 3.91 ns	0 8.40 **	0 3.99 ns	0 0.88 ns	0 0.81 ns	0 3.11 ns	2 1.00 ns	130
PP	0 3.37 ns	0 0.24 ns	0 30.54 ***	0 1.67 ns	0 7.21 **	0 0.18 ns	10 6.14 ns	14 2.92 **	0 25.86 **	0 5.72 ns	76 3.04 **	0 6.52 **	0 3.10 ns	0 0.69 ns	0 0.63 ns	0 2.41 ns	1 0.77 ns	101
NPP	0 1.13 ns	0 0.08 ns	22 10.28 ***	0 0.56 ns	2 2.43 ns	0 0.06 ns	2 2.07 ns	1 0.98 ns	1 8.71 ***	2 1.93 ns	0 1.02 ns	3 2.20 ns	1 1.04 ns	0 0.23 ns	0 0.21 ns	0 0.81 ns	0 0.26 ns	34
MO	1 2.97 ns	0 0.21 ns	7 26.91 ***	0 1.47 ns	0 6.35 **	0 0.16 ns	0 5.41 ns	2 2.57 ns	1 22.79 ***	0 5.04 ns	0 2.68 ns	78 5.75 ***	0 2.73 ns	0 0.60 ns	0 0.55 ns	0 2.22 ns	0 0.68 ns	89
TRE	0 2.53 ns	0 0.18 ns	1 22.98 ***	0 1.26 ns	0 5.43 ns	0 0.13 ns	0 4.62 ns	0 2.20 ns	0 19.46 ***	0 4.30 ns	0 2.29 ns	21 4.91 **	53 2.33 **	0 0.52 ns	0 0.47 ns	0 1.81 ns	0 0.58 ns	76
♂CALL	0 1.77 ns	0 0.13 ns	0 16.03 ***	0 0.88 ns	0 3.78 ns	0 0.09 ns	0 3.22 ns	1 1.53 ns	0 13.57 ***	0 3.00 ns	0 1.59 ns	0 3.42 ns	50 1.63 **	0 0.36 ns	0 0.33 ns	2 1.27 ns	0 0.41 ns	53
♀CALL	0 0.77 ns	0 0.05 ns	0 6.95 **	0 0.38 ns	0 1.64 ns	0 0.04 ns	0 1.40 ns	0 0.66 ns	0 5.89 **	0 1.30 ns	0 0.69 ns	0 1.49 ns	0 0.71 ns	23 0.16 **	0 0.14 ns	0 0.55 ns	0 0.18 ns	23
NCO	0 1.00 ns	0 0.07 ns	0 9.07 ***	0 0.50 ns	0 2.14 ns	0 0.05 ns	0 1.82 ns	1 0.87 ns	0 7.68 **	0 1.70 ns	0 0.90 ns	0 1.94 ns	0 0.92 ns	0 0.20 ns	19 0.19 **	10 0.72 **	0 0.23 ns	30
NOS	0 2.37 ns	0 0.17 ns	0 21.47 ***	0 1.17 ns	0 5.07 ns	0 0.13 ns	0 4.31 ns	2 2.05 ns	0 18.18 ***	0 4.02 ns	0 2.14 ns	0 4.59 ns	0 2.18 ns	0 0.48 ns	0 0.44 ns	0 1.70 ns	0 0.54 ns	71
other	1 0.80 ns	0 0.06 ns	3 7.23 ns	0 0.40 ns	1 1.71 ns	0 0.04 ns	0 1.46 ns	1 0.69 ns	2 6.15 ns	1 1.36 ns	1 0.72 ns	0 1.55 ns	0 0.74 ns	0 0.16 ns	0 0.15 ns	0 0.57 ns	13 0.18 **	24
column total	113	8	1025	56	242	6	206	98	868	192	102	219	104	23	21	81	26	3390

PRECEDING ACTION (male)

APPENDIX IVb TRANSITION ANALYSIS OF FEMALE-MALE INTERACTIONS DURING COPULATORY-DISPLAY SEQUENCES

** $p < 0.01$

*** $p < 0.001$

†† "e" values too small to permit testing. However, "observed" values such that results are obviously of some significance

FOLLOWING ACTION (male)

	HD	HD/Q	ND	ND/Q	ND _{hi}	ND _{hi} /Q	REU	ALU	FT	CRLP	PP	NPP	MO	TRE	QCALL	QCALL	NCO	NOS	other	row total
HD	16 7.04 ***	4 5.36 ns	20 19.92 ns	8 12.36 ns	2 6.15 ns	1 1.06 ns	10 6.94 ns	3 2.56 ns	39 30.45 ns	8 4.24 ns	0 3.49 ns	1 1.13 ns	1 3.01 ns	0 2.60 ns	0 1.81 ns	0 0.79 ns	0 1.03 ns	0 1.03 ns	0 0.65 ns	113
HD/Q	2 0.50 ns	0 0.38 ns	3 1.41 ns	2 0.88 ns	0 0.44 ns	0 0.08 ns	0 0.49 ns	0 0.18 ns	1 2.16 ns	0 0.30 ns	0 0.25 ns	0 0.08 ns	0 0.21 ns	0 0.18 ns	0 0.13 ns	0 0.06 ns	0 0.07 ns	0 0.17 ns	0 0.05 ns	8
ND	52 63.85 ns	69 48.66 ***	182 180.70 ns	140 112.20 ***	24 55.79 ***	5 9.61 ns	63 62.92 ns	0 23.25 ***	453 276.16 ***	16 38.43 ***	0 31.61 ***	7 10.23 ns	5 27.28 ***	1 23.56 ***	0 16.43 ***	1 7.13 **	3 9.30 ns	0 22.01 ***	4 5.89 ns	1025
ND/Q	1 3.43 ns	3 2.61 ns	12 9.70 ns	8 6.02 ns	1 2.99 ns	0 0.52 ns	3 3.38 ns	0 1.25 ns	26 14.82 ***	0 2.06 ns	0 1.70 ns	1 0.55 ns	0 1.46 ns	0 1.26 ns	0 0.88 ns	0 0.38 ns	0 0.50 ns	0 1.18 ns	0 0.32 ns	55
ND _{hi}	12 14.89 ns	10 11.35 ns	15 42.13 ***	12 26.16 **	22 13.01 **	5 2.24 **	7 14.67 ns	1 5.42 ns	148 64.39 ***	1 8.96 **	0 7.37 **	1 2.38 ns	0 6.36 **	0 5.49 **	0 3.83 ns	0 1.66 ns	2 2.17 ns	1 5.13 ns	2 1.37 ns	239
ND _{hi} /Q	0 0.37 ns	0 0.28 ns	1 1.06 ns	0 0.66 ns	0 0.33 ns	0 0.06 ns	0 0.37 ns	0 0.14 ns	5 1.62 ns	0 2.23 ns	0 0.19 ns	0 0.06 ns	0 0.16 ns	0 0.14 ns	0 0.10 ns	0 0.04 ns	0 0.05 ns	0 0.13 ns	0 0.03 ns	6
REU	20 12.65 ns	8 9.64 ns	33 35.79 ns	20 22.22 ns	6 11.05 ns	1 1.90 ns	23 12.46 **	1 4.60 ns	40 54.69 ns	19 7.61 **	27 6.26 **	4 2.03 ns	0 5.40 ns	0 4.67 ns	0 3.25 ns	0 1.41 ns	0 1.84 ns	0 4.36 ns	1 1.17 ns	203
ALU	7 6.10 ns	0 4.65 ns	3 17.28 ***	0 10.73 ***	1 5.33 ns	0 0.92 ns	21 6.02 ***	10 [†] 2.22	2 26.40 ***	6 3.67 ns	44 [†] 3.02	0 0.98 ns	0 2.61 ns	0 2.25 ns	0 1.57 ns	0 0.68 ns	1 0.89 ns	1 2.10 ns	2 0.56 ns	98
FT	65 54.07 ns	56 41.21 **	260 153.02 ***	154 95.02 ***	108 47.25 ***	18 8.14 ***	29 53.28 ***	2 19.69 ***	113 233.86 ***	44 32.55 ns	0 26.77 ***	12 8.66 ns	5 23.10 ***	0 19.95 ***	0 13.91 **	0 6.04 **	1 7.87 **	0 18.64 ***	1 4.99 ns	868
CRLP	28 11.96 ***	1 9.12 **	41 33.85 ns	2 21.02 ***	13 10.45 ns	0 1.80 ns	28 11.79 ***	1 4.35 ns	45 51.73 ns	27 7.20 **	0 5.92 ns	3 1.92 ns	0 5.11 ns	0 4.41 ns	0 3.08 ns	0 1.34 ns	0 1.74 ns	0 4.12 ns	3 1.10 ns	192
PP	0 1.56 ns	0 1.19 ns	0 4.41 ns	0 2.74 ns	0 1.36 ns	0 0.23 ns	2 1.53 ns	0 0.57 ns	0 6.74 **	0 0.94 ns	22 [†] 0.77	0 0.25 ns	0 0.67 ns	0 0.57 ns	0 0.40 ns	0 0.17 ns	0 0.23 ns	0 0.54 ns	1 0.14 ns	25
PRO	2 13.64 ***	4 10.40 ns	9 38.61 ***	15 23.97 ns	1 11.92 ns	1 2.05 ns	2 13.44 ***	1 4.97 ns	8 59.00 ***	0 8.21 **	0 6.75 **	3 2.19 ns	77 5.83 ***	75 5.03 **	0 3.51 ns	21 [†] 1.52	0 1.99 ns	0 4.70 ns	0 1.26 ns	219
QCALL	0 6.48 **	0 4.94 ns	0 18.33 ***	0 11.38 ***	0 5.66 ns	0 0.97 ns	1 6.38 ns	0 2.36 ns	0 28.02 ***	0 3.90 ns	0 3.21 ns	0 1.04 ns	0 2.77 ns	0 2.39 ns	53 [†] 1.67	0 0.72 ns	16 [†] 0.94	34 [†] 2.23	0 0.60 ns	104
QCALL	0 1.43 ns	0 1.09 ns	0 4.05 ns	0 2.52 ns	0 1.25 ns	0 0.22 ns	0 1.41 ns	1 0.52 ns	0 6.20 **	0 0.86 ns	0 0.71 ns	0 0.23 ns	0 0.61 ns	0 0.53 ns	0 0.37 ns	0 0.16 ns	5 0.21 ns	17 [†] 0.49 ns	0 0.13 ns	23
NCO	1 1.31 ns	2 1.00 ns	0 3.70 ns	1 2.30 ns	0 1.14 ns	0 0.20 ns	0 1.29 ns	3 0.48 ns	2 5.66 ns	0 0.79 ns	0 0.65 ns	1 0.21 ns	0 0.56 ns	0 0.48 ns	0 0.34 ns	0 0.15 ns	0 0.19 ns	10 [†] 0.45 ns	0 0.12 ns	21
NOS	0 5.05 ns	0 3.85 ns	0 14.26 ***	0 8.87 **	0 4.41 ns	0 0.76 ns	12 4.97 ***	51 [†] 1.84	1 21.82 ***	0 3.04 ns	7 2.50 ns	0 0.81 ns	0 2.16 ns	0 1.86 ns	0 1.30 ns	0 0.56 ns	0 0.73 ns	8 1.74 ns	0 0.47 ns	81
other	0 1.68 ns	0 1.28 ns	4 4.76 ns	0 2.96 ns	2 1.47 ns	0 0.25 ns	2 1.66 ns	1 0.61 ns	8 7.27 ns	3 1.01 ns	2 0.83 ns	0 0.27 ns	0 0.72 ns	0 0.62 ns	0 0.43 ns	0 0.19 ns	0 0.24 ns	0 0.58 ns	5 0.16 ns	27
column total	206	157	583	362	180	31	203	75	891	124	102	33	88	76	53	23	30	71	19	3307

PRECEDING ACTION (female)

APPENDIX V LIST OF FOODS EATEN BY CAPTIVE CYGNETS

commercial chick-starter crumbs (up to three weeks)
and pellets
soaked whole wheat
sprouted Mung beans
egg yolk (first one - two days)
chopped lettuce
chopped cabbage
grated carrot

These foods were supplemented by grazing on

Dock (*Rumex obtusifolius*)
Sow thistle (Puha *Sonchus oleraceus*)
Clover (*Trifolium repens*, *T. subterraneus*)
Yorkshire fog (*Holcus lanatus*)
Ryegrass (*Lolium perenne*)
Dandelion (*Taraxacum officinale*)
Hawksbeard (*Crepis capillaris*)

APPENDIX VI AGGRESSIVE INCIDENTS AND ASSOCIATED
 VOCALISATIONS USED BY SWANS AT
 WESTERN SPRINGS, AUCKLAND
 (Data from 3h. observation)

Threat form	number	vocalisation	context
IMP	11	11 (hiss)	8 interspecific threats (human, goose as object); 3 during feeding, at other swans
THR _{lo}	3	-	feeding disputes
PEL (& hold)	15	-	feeding disputes
THR _{me}	8	-	feeding disputes
THR _{hi} /PAR	7	2 (hiss)	boundary or feeding disputes

Of 44 aggressive incidents, six involved geese and two humans i.e. eight were interspecific. Of 36 intraspecific incidents, 15 involved physical attack. Vocalisations occurred with 13 threats: all were hisses, and the threats were at close range (one - two body lengths). In comparison, the long-range threats TRU and SWF involve very loud calls.

APPENDIX VII "NORMALISED" DATA FOR SINGLE-LINK-
CLUSTER-ANALYSIS OF CYGNET GROUP-
COHESION

The data are "normalised" to correct for differing numbers of observations in each block.

The normalisation (Morgan et al. 1976):

$$d_n = \frac{100 \times \text{raw cell data}}{\text{total notations}}$$

e.g. for cell AD, block I, $d_n = \frac{100 \times 25.00}{36.5 + 36.5}$

* indicates cells used in dendrogram (Figure 5.11)

Block I (6/10 - 12/10/1980)

	A	D	C	L	S	P
A	-	34.25	32.19	32.88	35.62*	34.25
D		-	36.99	38.36	36.99	39.04*
C			-	37.67	36.99	37.67*
L				-	36.30	41.09*
S					-	39.04*
P						-

Block II (13/10 - 26/10/1980)

	A	D	C	L	S	P
A	-	35.16*	32.81	32.81	27.34	29.69
D		-	41.41*	32.28	37.50	42.19*
C			-	39.06	34.37	38.28
L				-	35.94	40.62*
S					-	38.28*
P						-

Block III (27/10 - 9/11/1980)

	A	D	C	L	S	P
A	-	32.64	26.39	28.47	25.00	32.64*
D		-	32.64*	29.17*	23.61	32.64*
C			-	27.78	22.92	27.08
L				-	28.47*	27.78
S					-	25.69
P						-

Block IV (10/11 - 23/11/1980)

	A	D	C	L	S	P
A	-	28.95	23.03	27.63	26.97	30.92*
D		-	26.32	31.58*	28.95*	30.92
C			-	23.68	23.68	26.97*
L				-	25.00	34.21*
S					-	24.34
P						-

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