SOCIAL BEHAVIOUR, PAIR FORMATION, AND THE
BEHAVIOURAL EFFECTS OF TESTOSTERONE IN THE MALLARD
(ANAS PLATYRHYNCHOS)

by

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CHAPTER I

INTRODUCTION

I.1. THE MALLARD: ANNUAL CYCLE AND SOCIAL ORGANISATION

Many of the aspects of social and reproductive behaviour mentioned in the following summary are described in detail in later sections, but additional information on general life style and behaviour may be found in WEIDMANN (1956), McKINNEY (1975b), BELLROSE (1976) and CRAMP & SIMMONS (1977).

The mallard, Anas platyrhynchos L., is one of the 'dabbling ducks' (Tribe Anatini) in the sub-family Anatinae, family Anatidae. Seven races are known, but the nominate A.p.platyrhynchos is the most widely distributed, occurring in both resident and migratory populations across the mid-latitudes of the northern hemisphere.

It is mainly a lowland species, but is adaptable to a wide range of habitats. The mallard prefers shallow water, and may be found in lakes, marshes, reservoirs, canals, mudflats, and also estuaries and sometimes sheltered coasts. The species is highly adaptable to man; mallards are commonly found in city parks, and breed well in captivity. Mallards require fresh water daily for drinking, bathing and feeding, but they are highly mobile and may breed some distance from water.

The diet varies with habitat and season, but mallards will eat almost anything. The commonest feeding method is surface dabbling, whereby a wide variety of aquatic animals and plants is taken. Other feeding methods include 'upending' to dredge the bottom sediment, occasionally diving, and also terrestrial feeding, consuming seeds, plants, worms and insects.

The sexes are dimorphic in plumage. The familiar nuptial plumage of the male is characterised by a bottle-green head, white collar and chestnut-brown breast, with a grey body and upturned tail feathers. The female is a cryptic mottled brown, and both sexes possess the blue speculum on the secondary flight feathers. The eclipse plumage, worn only for one

to two months during the summer, is basically similar to the female breeding plumage, as is the first juvenile feathering.

In common with most non-equatorial species, the mallard breeds in the spring. Outside the breeding season mallards are gregarious; large flocks of hundreds or even thousands of birds are common. Migration, if it occurs, is also undertaken in flocks.

The flocks are formed in late summer to early autumn, as the birds come together after the post-breeding moult. The social organisation in a wild flock does not extend to a rigid peck-order (WEIDMANN, 1956), but the behaviour of flock members is often synchronised. In autumn and winter flocks, periods of rest and of the major maintenance activities such as bathing, preening and feeding tend to be partially synchronised. The synchronisation of certain activities is achieved by displays and calls, such as the preflight head-pumping display and the alarm call and posture. Social facilitation is particularly characteristic of the 'diving play' or 'dashing-and-diving' (LEBRET, 1948; McKINNEY, 1965a), and of the 'social display'.

A polyphasic diurnal rhythm of activity is reported to occur in the wild (RAITASUO, 1964), and also in captivity (DESFORGES, 1974). RAITASUO studied a large residential population of mallard in Finland, and found that their day could be divided into periods of activity lasting 45 to 75 minutes, with intervening rest periods of 30 to 45 minutes. A similar polyphasic diurnal rhythm has also been found in the frequency of vocalisations (ABRAHAM, 1974).

Many flocks make regular flights to and from feeding areas in the early morning and evening (WINNER, 1959). This bimodal flight pattern is shown abortively by sedentary birds (WEIDMANN, 1956), and it may be based on an endogenous activity rhythm (WINNER, 1972).

The sex ratio in winter flocks is usually biassed in favour of males (many references are quoted by CRAMP & SIMMONS, 1977). This is

generally attributed to a greater mortality of females during the breeding season, but HOCHBAUM (1944) has also reported a slight preponderance of males in the secondary sex ratio, at hatching.

Courtship, mating and social display activities begin as soon as the flock is re-convened in the autumn. The formation of pair bonds begins immediately, and in many populations the majority of birds are paired by the end of October.

Residential flocks remain integrated until February or March, when pairs disperse to seek nest sites. Migrant populations usually disperse soon after arrival on the breeding grounds; females often home to the area in which they bred in previous years, and may even use the same nest site (SOWLS, 1955). Mallards breed in their first season and, exceptionally, females may nest in the same season in which they hatched (BOYD, 1957).

Nests are made on the ground in dense or light undergrowth, in hollow trees, sometimes in the open and occasionally up trees. Some mallards range a considerable distance from water to find suitable nesting cover, and distances of up to three to five miles have been reported (DUEBBERT, 1969).

Both members of the pair search together for a nest site, though the female usually takes the lead (SOWLS, 1955). Once a site has been chosen the pair uses a 'home range', which includes the nest, in which they pursue all their maintenance activities, but the home ranges of neighbouring pairs may overlap considerably.

Laying takes about two weeks, the duck laying one egg per day, with occasional missed days. Incubation begins as soon as the clutch is complete, and is accomplished by the female alone.

During the laying period the drake spends most of his time in one or more 'activity areas' or 'waiting areas' within the home range, where the female joins him when she comes off the nest. The pair bond usually

breaks during the first week of incubation (McKINNEY, 1965b); the drake spends less and less time at the waiting areas and soon departs from the home range completely (GILMER et al. 1975). Cases of a drake accompanying the brood have been occasionally reported (DZUBIN, 1955, 1969b; RAITASUO, 1964); this seems to be more frequent in very crowded populations (TITMAN & LOWTHER, 1975) and is more likely to occur in pairs which breed early in the season (McKINNEY, 1965b).

If her first clutch is lost or abandoned, a female may lay one or more replacement clutches. Re-nesting is apparently quite common in the mallard (e.g. SOWLS, 1955); the breeding season is long compared with other ducks, and in Britain eggs may be laid at any time between the end of February and the end of June, sometimes even later.

Social behaviour during the breeding period is characterised by aerial pursuits and attempted rape of females by drakes.

As the breeding season draws to a close, the birds begin to congregate for moulting. These post-breeding groups comprise mainly males and those females who were unsuccessful at breeding. Females with broods tend to keep their family apart from other birds and do not moult themselves until the young are independent.

The two moults follow closely upon one another. First the body feathers are shed, and the cryptic eclipse plumage is assumed. The wings are moulted when the eclipse plumage is almost complete; the primaries fall together and the bird is flightless for three to four weeks as the new flight feathers grow. After a brief period a second moult replaces the body feathers with the new nuptial plumage.

There is no temporal synchronisation of moulting in the flock, and it seems that the chronology of moult in males is related to age and breeding activity. Younger males tend to moult earlier than older males, both in the wild (BOYD, 1961) and in captivity (GOLDSMITH, unpublished observations). In a captive group of mallards HOCHBAUM (1944) reported

that the drakes which bred earliest also moulted earliest.

Groups of moulting, especially flightless, birds tend to remain in seclusion, and there is very little social activity at this time (RAITASUO, 1964). Soon after moulting, however, social activity is resumed and pair formation begins again.

Pair formation in the mallard, and the behaviour involved therein, is discussed more fully in section 3, but first the social behaviour of the mallard is described.

I.2. THE SOCIAL BEHAVIOUR OF THE MALLARD

The following account is based largely on the works of LORENZ (1941), WEIDMANN (1956), RAITASUO (1964), JOHNSGARD (1965) and McKINNEY (1975b). A comprehensive analysis of the vocalisations has recently been published by ABRAHAM (1974).

2.1. Social display

Social display or 'Gesselschaftsspiel', also sometimes called 'social play', 'social courtship' or 'communal courtship', is one of the most conspicuous activities of the mallard. The phenomenon of social display is widespread in the Anatinae (LORENZ, 1941; JOHNSGARD, 1965), and is particularly highly organised in the mallard.

The activity involves a number of birds, both males and females, swimming together in a fairly close group, constantly adjusting their positions and intermittently performing characteristic display movements and vocalisations. These behaviour patterns are referred to as social displays, whereas the term social display is used to denote the entire activity.

A typical display 'session' may last a few minutes, sometimes up to an hour or longer, and several such sessions may occur throughout the

day. Social display normally occurs only in water but captive birds may

display on land if no water is available (deLANNOY, 1967; DESFORGES &

WOOD-GUSH, 1976). All adult birds may partake, both paired and unpaired

individuals, with the exception of females who are brooding or leading

young.

Description of social display

The first visible indication of an imminent display session is

that the males assume the _intent_ posture, with the head drawn down beneath

the shoulders so that the white neck band disappears, and the head feathers

erected to present a rounded profile.

The males constantly adjust their relative positions by _swimming_

manoeuvres, and a number of _secondary displays_ or _introductory displays_ are

given. These movements, which may also occur in non-display situations,

are as follows:

tail-wag: lateral movements of the tail

head-shake: rapid lateral shaking of the head and bill

head-flick: shaking of the head as above, but the head is also stretched

forward and the head and neck are rotated at the same time as the lateral

head-shake.

introductory shake: a head-flick performed as the upper part of the body

is raised from the water, with an accompanying tail-wag. This display has

been variously designated as preliminary shake (LORENZ, 1941), introductory

shake (WEIDMANN, 1956) and swimming shake (McKINNEY, 1965a).

Every so often there will be a 'burst', interspersed amongst the

secondary displays, when one or more usually several males give one or more

major displays in rapid succession. There are three so-called major dis-

plays, the _grunt-whistle_, the _head-up-tail-up_ and the _down-up_.

Grunt-whistle

This display, named after the accompanying vocalisations, is also

termed the <u>water-flick</u> by CRAMP & SIMMONS (1977). The male dips his bill
in the water and rapidly raises his body, leaving his head hanging down so
that his body forms an arch.   The bill shakes rapidly, and lifts a spray
of water droplets to one side.   At the peak of the arch the drake utters
the two vocalisations, a clear fluted whistle followed by a low-pitched
grunt.   The water spray, which may reach a distance of several feet
across the water, is usually directed towards another bird.   When a paired
male performs the display the spray is usually directed towards his mate,
if she is present (WEIDMANN, 1956).

The evolutionary origin of the grunt-whistle has received much
attention.   LORENZ (1941) considered that the display was a ritualised
introductory shake, and he cited other species, such as the mandarin duck/,
in which the display apparently occurs in a less exaggerated form.

McKINNEY (1965a) believed that the grunt-whistle was derived from
the belly-preen display, whilst SIMMONS & WEIDMANN (1973) considered that
its evolutionary origin was a directionally-biassed head-shake (see later).

<u>Head-up-tail-up</u>

This display is in fact a sequence of three separate movements.
(a) <u>Head-up-tail-up proper</u>.   The drake abruptly raises his head, tail and
wings (which remain closed), so that the body appears abnormally short and
high.   He holds this posture briefly and gives a whistle call, whilst
looking towards another bird.   A paired male usually faces his own mate.
(b) <u>Nodswimming</u>.   The drake then lowers his head and neck onto the sur-
face of the water, stretches out his body, and maintains this flattened
posture as he swims in a wide arc.   The duration and spatial pattern of
the nodswimming is variable depending on the positions and movements of
nearby birds, but the drake will sometimes swim around the female to whom
he directed the head movement mentioned above (WEIDMANN, 1956; RAITASUO,
1964).

/ The latin names of species mentioned in the text are listed in Appendix 1.

(c) <u>Turn-back-of-head</u>. After completing his nodswim the drake sits back up in the water and moves in front of the female, and holding his head high, turns the back of his head towards the female. The head feathers are flattened laterally, so that a dark band down the back of the head is presented to the female. The drake then swims slowly away, maintaining the head posture, and trying to <u>lead</u> the female, who may or may not follow him. This phase is very variable in duration, depending on the response of the female.

Nodswimming and turn-back-of-head do not always follow the head-up-tail-up. Of a total of 665 head-up-tail-ups recorded by JOHNSGARD (1960a), 94.3 per cent were followed by nodswimming, but turn-back-of-head is more often omitted if the male is not in a suitable position on completion of nodswimming.

The turn-back-of-head movement also occurs on its own, independently of the head-up-tail-up and nodswimming. Lone turn-back-of-head may occur during social display and also at other times.

Down-up

In this display the male first holds his head erect (this phase may be omitted), then tips his body forwards and downwards so that the breast lies deep in the water and the tail is raised. The bill is dipped and then jerked upward, dragging up a column of water droplets, and one or more whistle calls are given. The drake then resumes the normal swimming position, and immediately adopts the head-high posture, giving a series of '<u>rab-rab</u>' calls.

Unlike the head-up-tail-up and grunt-whistle, there is no obvious directional component of the down-up display. Down-ups may also be given outside the context of the display session.

Down-ups are sometimes performed in a less exaggerated form than that described above, but the other two major displays are highly stereo-

typed, reportedly occurring with very little variation in duration or form (WEIDMANN, 1956).

Female displays

The female does not possess displays comparable to the major displays of the male, but females often perform nodswimming, similar in form to the nodswimming of the male, during social display sessions. A head-nodding movement is often given as a prelude to nodswimming in the female, and head-nodding may be performed on its own.

Synchronisation of displays

As stated above, the major displays of the males usually occur in synchronised bursts, with several drakes displaying simultaneously or in rapid succession. Sometimes two or more males might initiate a display movement within the same frame of a 16 frames per second cine film (WEIDMANN & DARLEY, 1971b).

Occasionally major displays are performed singly, and the grunt-whistle is the most common as an isolated display (WEIDMANN, 1956; JOHNS-GARD, 1960a; deLANNOY, 1967), whilst the head-up-tail-up and down-up occur more frequently in multiple-display bursts. LORENZ (1941) believed that it was a matter of chance which of the three major displays would be given by each male participating in a burst, but it has since been demonstrated that 'pure bursts', in which all the males give the same display, are much more common than would be expected by chance (WEIDMANN, 1956; FIELD, 1970; WEIDMANN & DARLEY, 1971b).

WEIDMANN (1956) suggested that the first male displaying in a burst somehow facilitated displaying by the other males, and determined the timing and also the type of displays which were to follow.

JOHNSGARD (1960a), however, believed that the males reacted independently from one another, except possibly in the case of the down-up (see later), and he proposed that males performed displays purely in res-

ponse to stimuli provided by the behaviour of the females.   JOHNSGARD
postulated that each major display was released by a specific female
action, and moreover that the same female action would elicit a different
male display depending on the season of the year.

The statistical method used by JOHNSGARD in demonstrating that
the males reacted independently, that of fitting the frequency distribution
of bursts to a Poisson distribution, has been criticised by FIELD (1970)
and WEIDMANN & DARLEY (1971b).   Furthermore, WEIDMANN & DARLEY demon-
strated that the synchronisation of displays in an all-male group was as
good if not better than with a female present.   These authors suggested
that the synchronisation of male displays might be possible if mallards
have a very quick reaction time, or alternatively the males might be able
to respond in a specific way to the head-flicks of the other males which
precede the major displays.

An analysis of behaviour sequences in films of social display
sessions (WEIDMANN & DARLEY, 1971a) did not support JOHNSGARD's hypothesis
of a simple stimulus-response relationship of female behaviour and male
displays.   Pure bursts of head-up-tail-ups were mostly preceded by a
female turning towards or nodswimming towards the male who initiated the
burst, but a variety of female actions were found to precede bursts of
grunt-whistles or down-ups.

Other behaviour in display sessions

Besides the displays described above, several other types of
social behaviour occur during the course of a display session.   These in-
clude agonistic interactions and pair displays (see following sections).

Sometimes jump flights may be performed by the males.   These
short ritualised flights, described by LEBRET (1958), are characterised by
the male rising steeply from the water, flying a short distance and then
landing, often directly in front of a female.   This activity appears to

be contagious, in that several males may perform jump flights in quick succession. Sometimes the whole displaying group may fly a short distance and resettle nearby (DZUBIN, 1957).

Extraneous factors influencing social display

The factors responsible for the initiation of a display session are not fully understood. Sometimes social display may begin when members of a flock come together, or are joined by a newcomer (LEBRET, 1961). A display session may also start after a flock 'alert' caused by the appearance of a predator on the bank or by some other disturbance (WEID-MANN, 1956; RAITASUO, 1964).

A female nodswimming through a group of males may initiate a display session (RAITASUO, 1964). Displays may also be performed spontaneously in an all-male group, although females invariably join in before long (RAITASUO, 1964; PALMER, 1976).

RAITASUO (1964) analysed the effect of the weather on social display and other social activities. It was difficult to isolate the effect of any one climatic factor, but RAITASUO demonstrated that cold air temperature had a general inhibitory effect on display activity. The apparent temperature threshold varied throughout the year, and the prevailing wind and light intensity may also have modifying effects.

Temporal distribution of display activity

The seasonal distribution of social display has been recorded in a number of populations, for instance in Germany (WEIDMANN, 1956; BEZZEL, 1959), Holland (LEBRET, 1961) and New York (JOHNSGARD, 1960a). Basically the display period of the mallard extends continuously from the time the flock convenes after moulting until the time of the dispersal of pairs in spring. Most of the authors cited above recorded peak frequencies of display in October-November and February-March (the precise dates varied from place to place), with a reduction in activity during the coldest winter

months.

BALTHAZART (1976b) studied the daily distribution of social dis-
play in a flock of 'semi-wild' mallards on a Belgian nature reserve, during
February and March.   Sporadic outbursts of displaying occurred throughout
the day, but the frequency of displays was highest in the early morning and
late afternoon.   This pattern was positively correlated with counts of the
number of males present on the water at different times of the day.   In
contrast, copulations and the associated sexual displays were recorded most
frequently around midday.

2.2.   Pair displays

The displays which are classified under the title of pair dis-
plays (WEIDMANN, 1956) or directed courtship (von de WALL, 1965) are those
which are characteristic of situations where a male and female are close
together, i.e. the members of a pair or potential pair.   These displays
may be performed when other birds are present, even during social display
sessions, but the male and female always give the displays in close proxi-
mity to each other, and the displays are clearly addressed to the partner.

Leading and inciting

The drake tries to lead the female by swimming in front of her
whilst adopting the head-high and turn-back-of-head posture.   If the fe-
male follows the male she may perform the inciting display.   This involves
her swimming closely behind the male, repeatedly jerking her head backwards
over one shoulder and uttering the loud, tremulous inciting call.   The
male often gives rab-rab calls whilst the female is inciting, and this
mutual performance is called a pair-palaver.   This may occur not only when
the male is leading and the female following, but also when the pair is
stationary.

When performing inciting the female always aligns her body so
that she is facing her mate (or 'favoured' male), and the backward head

movements are sometimes directed towards a second male. She may even swim towards the second male, in which case the inciting gesture may turn into an overt threat with the neck extended towards the latter (BROCK, 1914; JOHNSGARD, 1965).

The inciting display is believed to have evolved from a situation where the female is simultaneously following her mate and threatening a rival male. The name for the movement is derived from the idea that the female is 'inciting' her favoured male to attack his rival (e.g. LORENZ, 1941). The display is widespread in the Anatinae, and occurs in different species with varying degrees of ritualisation (LORENZ, 1941). In the mallard the backward head movements may or may not be directed towards a specific rival male, and sometimes inciting is performed when there is no third individual present at all. For example, a paired male and female usually engage in a pair palaver when they meet after a temporary separation, whether or not other birds are nearby.

Ceremonial preening and drinking

Ceremonial drinking is an exaggerated drinking movement; the bill is dipped into the water and then lifted up. Drinking is seen most frequently in the members of an established pair. Either one partner may 'drink to' the other, or both male and female may drink in succession. Paired birds perform drinking especially when they meet, though also at other times, and two members of a flock who are not paired may drink when they approach one another.

Ceremonial preening or mock-preening displays are also given by paired birds when they are close together. Mock-preening is more often performed by the male, though females sometimes show the display too.

Various kinds of mock-preening have been described by McKINNEY (1965a); these include preen-behind-wing, preen-dorsally, preen-belly and preen-breast. It is often difficult to distinguish display preening from

functional preening movements. The preen-behind-wing display is the most exaggerated and the easiest to recognise, and it is this version alone which is refered to as 'mock-preen' by many authors. In this movement the male (usually) bill dips, turns his head sharply over his shoulder on the side nearest the female, and passes his bill along the inside of his partially raised wing. This action causes a characteristic 'rrrrr' sound as the bill comes into contact with the secondary flight feathers. After this movement the drake turns his head and drinks to his partner.

Separation behaviour

It will be useful to mention here the characteristic behaviour exhibited by paired birds when they are separated, although these are not strictly pair displays.

When a female has lost visual contact with her mate she often gives intermittent decrescendo calls. Each call is a series of loud far-carrying 'quack' notes. The separation call of the drake is the slow Raeb call, a series of drawn-out nasal notes.

There is a great deal of variation in the decrescendo calls of different females, and ABRAHAM (1974) has demonstrated that each female gives decrescendos of a consistent pattern. It has been demonstrated ex-perimentally (LOCKNER & PHILLIPS, 1969; ABRAHAM, 1974) that the decres-cendo call of each female is sufficiently specific to enable a male to identify his mate by her voice alone. McKINNEY (1975b) considers that the decrescendo and Raeb calls are of major importance in individual recogni-tion of mates and prospective mates.

These calls are also given in other circumstances. The female's decrescendo is sometimes triggered by other females calling or by ducks flying overhead, and the slow Raeb call is utilised by males as an alarm call to alert other members of the flock.

2.3.   Sexual behaviour

Copulation

The mallard has an elaborate behavioural ritual associated with copulation, including pre-copulatory and post-copulatory displays.

Except for the special case of rape (see below), matings always follow the same behavioural sequence.   This begins with the pre-copulatory head-pumping display;   the head is rhythmically and repeatedly stretched vertically upward and jerked down.   This is similar to the pre-flight head-pumping, but in the latter case the emphasis is on the upward movement, and the two displays are in fact visually quite distinct.   Pre-copulatory head-pumping is performed by both the male and the female as they swim alongside each other, but it may be initiated by either partner.

Mutual head-pumping is continued for a variable duration, gradually increasing in speed and intensity, until the female adopts the prone posture, stretching her head forward and holding her body flat on the water.   At this stage the male mounts, grasping the duck's head or neck feathers in his bill, and copulation occurs.   The male then dismounts and, sometimes still holding on to the female's neck feathers, throws his head back and raises his chest in the bridling display, and gives a single whistle.   He then nodswims in a circle around the female, and lastly wing-flaps and bathes.   The female has no post-copulatory display, but she proceeds to bathe immediately after the copulation.

In nearly all copulations between paired birds the male does not attempt to mount the female until she has adopted the prone position.

When only one partner performs head-pumping the mating sequence will not proceed any further, and occasionally both partners engage in head-pumping for a while and then stop.   Copulations do not usually occur during social display, and the pair often swims a short distance away from other flock members in order to mate.   The behavioural sequence may be

terminated at any stage by interference from other birds.

The head-pumping display has been interpreted as self-stimulation (McKINNEY, 1961) or stimulation of the partner (WEIDMANN, 1956; RAITASUO, 1964), and the increasing rate of pumping leading up to copulation probably indicates that the readiness to mate becomes precisely synchronised in the two partners.

Paired mallards copulate several times a day, starting in the autumn and continuing until the onset of incubation. The autumnal matings occur several months before fertilisation is possible, since spermato-genesis and full ovarian development do not occur until the spring.

Rape

Forced copulations, or rapes, differ from 'normal' copulations in that the precopulatory displays are omitted, and the drake mounts the duck without waiting for her to adopt the prone posture.

Although a male may force a copulation on his own mate, espe-cially if the female has just been raped by a strange male (BARRETT, 1973; BARASH, 1977), attempted rapes are usually performed on females other than the mate. Rape attempts are characteristic of the breeding period; they have been recorded as early as the end of January (WEIDMANN, 1956), but in most wild populations rapes begin during March (BEZZEL, 1959; LEBRET, 1961; RAITASUO, 1964).

The activity appears to be contagious, and a rape attempt in pro-gress may be joined by several other males who are nearby. The so-called 'attempted rape flights' (LEBRET, 1961) seen during spring and early summer involve a number of males (up to 20 and sometimes even more) chasing a single female. These aerial pursuits may last quite a long time; the female may eventually escape into cover but often the males succeed in forcing her to the ground, whereupon they attempt to rape her. When a drake performs the bridling and nodswimming displays after an attempted

rape this is believed to indicate that the copulation was successful (ABRAHAM, 1974).

Breeding females which are harassed by strange males may give repulsion behaviour. The female draws her head back on her shoulders, ruffles her feathers and fans her tail. The bill is opened wide and the harsh repulsion call is given. The repulsion gesture is adopted by females which are incubating or leading young when they are approached by other conspecifics. This situation often arises when a female is harassed by a strange male or males intent on rape.

2.4. Agonistic behaviour

Four types of aggressive actions may be distinguished; threatening, chasing, pecking, and fighting, as well as the aggressive display known as the 'rab-rab palaver'.

A threat involves stretching out the neck and thrusting the bill towards the adversary, with the bill open or closed. When one bird chases another the aggressor generally assumes the neck-extended threat posture. If he catches his opponent he may peck him vigorously or grasp his feathers and hold on.

Pecking is fairly self-explanatory; one bird pecks at the plumage of another, sometimes grasping the feathers in his bill, or sometimes merely using the bill to jab or thrust. Often the pecked bird does not retaliate, but sometimes a little mutual pecking is exchanged, or a fight may take place.

A fight usually begins with two birds facing each other on the water, with their bills lowered. They spar at one another with their bills, jabbing and pecking at the opponent's chest. Then they grasp each other by the chest feathers and, with their chests thrust together, attempt to push each other back. If neither gives way the two birds then begin thrashing their wings at each other, often very vigorously, and when

fighting occurs on the water this may result in the combatants slowly rotating on the spot. Eventually one bird gives way, and the victor may chase him off.

The rab-rab palaver is when two or more males swim or stand close together, each adopting the head-high and bill raised posture, uttering rapid 'rab-rab' calls. HEINROTH (1910) first associated the rab-rab palaver with hostile situations, and WEIDMANN (1956) considered that the display was characteristic of encounters when attack and escape tendencies were both present.

Rab-rab palavers often precede rival flights between males (WEIDMANN, 1956; McKINNEY, 1969), and rab-rab displays at other times are sometimes terminated by one male pecking or chasing one of the others (CRAMP & SIMMONS, 1977). McKINNEY (1975b) reported that the posture of males giving rab-rab displays was variable, and he postulated that a 'graded threat code' was expressed in the display. Sometimes one or more males engaged in a rab-rab palaver give down-up displays.

Aggressive behaviour occurs all year round, though it is probably rare during the summer moulting period, and overt aggression is less common in autumn flocks than during the spring (BROCK, 1914; WEIDMANN, 1956; LEBRET, 1961; RAITASUO, 1964).

Agonistic behaviour arises in a variety of situations, and may occur, in fact, whenever two or more individuals meet, for instance at feeding and preening places, during social display sessions, and particularly when a pair meets another pair or a single drake.

Most aggressive interactions occur between two males, and are usually associated with rivalry over a female, but agonistic behaviour may be exhibited by a male and a female or by two females. Aggression between females is rare but occasionally occurs when two females meet, especially females with broods (RAITASUO, 1964).

I.3. PAIR FORMATION

3.1. Behavioural characteristics of a pair

The male and female of an established pair exhibit certain behavioural characteristics by which they may be distinguished from non-paired individuals in the flock (WEIDMANN, 1956; LEBRET, 1961). Many of these characteristics are shared by related species, and some have been quantitatively confirmed in the gadwall by SCHOMMER (1978).

A mallard pair may be recognised by:

(i) Persistence of pair displays, addressed only to the mate.

(ii) The male and female often follow one another, and spend much of their time in close proximity to each other. DESFORGES & WOOD-GUSH (1975) noted that even in very crowded artificial conditions the average 'individual distance' between two birds was smaller for paired birds than for non-paired members of a group.

(iii) The activities of paired birds tend to be synchronised more closely with one another than with other flock members, during the months when mallards tend to live in flocks as well as during the breeding season.

(iv) Mates rarely if ever show aggression towards each other, even when feeding, unlike other members of a flock who may chase a bird who has picked up a tasty food item.

(v) Hostility may be exhibited towards other individuals who come near, especially by the paired male towards other drakes.

(vi) Mates may call persistently (the female gives decrescendo calls and the male slow Raeb calls) when separated and give the 'pair palaver' when they are reunited.

(vii) A paired male addresses his social displays to his mate if she is present.

(viii) A criterion of perhaps doubtful usefulness is the regular performance of pre-copulatory displays and copulation (not including rape).

WEIDMANN (1956) observed copulations only occasionally between unpaired birds, and RAITASUO (1964) reported that paired females copulated only with their mates although paired males sometimes copulated with 'other' females. JOHNSGARD (1960a), on the other hand, observing unmarked birds, reported that matings between non-paired birds were fairly common.

3.2. Phenology of pair formation in the wild

Many authors have commented on the rate of pairing in wild populations of unmarked birds, by estimating the proportion of pairs within the flock throughout the year.

Sometimes a few very early pairs have been recorded, immediately the flock is re-formed after the summer moult. It is considered likely that these are birds which were paired during the previous breeding season and have remained together or have been quickly reunited (GEYR von SCHWEPPENBURG, 1953; LEBRET, 1961; RAITASUO, 1964; DWYER et al. 1973).

The new season's pair formation does, however, begin very soon, and in most residential populations the majority of the flock members are paired within two or three months. In a Bavarian population BEZZEL (1959) reported that sixty per cent of the pairs were established by the end of September, and over eighty per cent of the flock members were paired by the end of October. LEBRET (1961) observed a rapid increase in the proportion of paired birds during August and September in the Netherlands, seventy per cent of the flock being paired by early October, and a more gradual increase between October and February. A Finnish population comprised only 25-30 per cent paired birds during autumn, with the majority of the pair bonds being established during February and March (RAITASUO, 1964).

In a mallard flock in central New York some eighty per cent of the flock was paired by early January (JOHNSGARD, 1960a), and this figure is fairly typical of other North American studies quoted by BELLROSE (1976) and PALMER (1976).

It should be mentioned that these studies do not provide evidence that the early pair bonds remained intact until the breeding season, and WEIDMANN (1956) has indicated that the earliest pairings in mallard may be temporary. It is evident, though, that a great deal of pair formation does occur during the early part of the flocking period, and it is probable that most of the pairs are established several months before the breeding dispersal of the flock. The significance of these points will become clear shortly.

3.3. The process of pair formation

A feature of pair formation in many duck species, certainly in the mallard, is the active selection of a mate by each female. Some authors have expressed the opinion that the male has an insignificant role in the selection of a partner, and that the choice rests entirely with the female (BROCK, 1914; JOHNSGARD, 1960a,b; RAITASUO, 1964). But it is now apparent that the males may also be selective, by addressing courtship displays to a specific female. It has also been suggested that a male may prolong his 'courtship' of a preferred female by other behaviour, such as persistently following and remaining close to the female in question (SCHOMMER, 1978).

WEIDMANN (1956) described a gradual process in the development of a personal bond between a male and a female. A variety of behaviour is involved in this process, including (a) approaching and following, (b) directed courtship or pair displays such as ceremonial drinking, mock-preening, leading and inciting, (c) a gradual reduction in aggression and individual distance, and (d) spending an increasing amount of time in each other's company. Each bird may pursue this behaviour with several potential partners before affirming a bond with a particular individual. According to McKINNEY (1975a) these 'trial liaisons' enable a male or female to test the qualities of a potential mate.

The various pair displays and other behaviour mentioned above are considered to be effective in allowing a male or female to advertise his or her own qualities and to attract and hold the attention of a potential mate (McKINNEY, 1975a). There has been considerable controversy, however, over the role of social display in courtship.

3.4. Social display and pair formation

Since the early work of HEINROTH (1910), many authors have proposed that social display promotes pair formation, and the social display of the mallard male has thus been equated with courtship (e.g. BROCK, 1914; HOHN, 1947; WEIDMANN, 1956; JOHNSGARD, 1960a; WEIDMANN & DARLEY, 1971a). This view has been challenged, however, and other biological functions have been ascribed to social display.

(i) It has been suggested that the displays, which tend to advertise species-specific plumage characters, have evolved as a reproductive isolating mechanism to prevent hybridisation between sympatric species (JOHNSGARD, 1960c, 1963, 1965; PALMER, 1976). As support for this hypothesis JOHNSGARD (1965) states that in some island species closely related to the mallard the displays have degenerated, along with the loss of plumage dimorphism. This is because, according to JOHNSGARD, morphological and behavioural isolating mechanisms are no longer necessary where a species is geographically isolated.

In the view of von de WALL (1965) courtship in the mallard is effected by the directed courtship displays, but the social displays, which are 'easier to recognise and more species specific' than directed displays, function in bringing together birds of the same species. deLANNOY (1967) does not think that these two functions are really distinct, and SIEGFRIED (1974) and McKINNEY (1975a) have criticised the concept that the complex display repertoire and the bright nuptial plumage of male ducks have evolved as species-isolating mechanisms. SIEGFRIED and McKINNEY favour

the view that these morphological and behavioural features have evolved as
a result of enhanced sexual selection, brought about by a mating system in
which males compete for females.

(ii)   RAITASUO (1964) believed that pair formation in the mallard was
achieved solely by directed courtship, and that social display bore no
direct relationship to either pair formation or mating.   He considered
that the biological function of social display activity was "to stimulate
through the central nervous system such changes in the hormone secretion
of the hypophysis that cause activation of the gonads and thereby also the
proper stimulus for pair formation and mating".

It has long been known (LEHRMAN, 1964) that in the ring dove be-
haviour affects gonadal development and hormone secretion.   The synchro-
nisation of breeding in many colonial avian species is believed to result
from a stimulation of reproductive development by the courtship behaviour
of other individuals (see IMMELMANN, 1973).

In the mallard, however, no evidence has been forthcoming to
support RAITASUO's (1964) hypothesis.   It is unlikely that social display
is effective in accelerating reproductive development, since the activity
is common several months before breeding, and DESFORGES (1972) has con-
firmed that ovarian development is not influenced by male behaviour.

(iii) In the goldeneye duck group display activity often leads directly to
mating.   DANE & van der KLOOT (1964) observed that a male and female some-
times copulate immediately after participating in a flock display session,
and they speculated that one function of the male displays is to stimulate
the female for mating.

In the mallard, however, social display does not appear to be
associated with mating.   Mallard pairs usually copulate away from social
display groups (RAITASUO, 1964), and BALTHAZART (1976b) has shown that the
daily distributions of social displays and mating behaviour are entirely

different.

(iv) LEBRET (1961) was doubtful that the social display is involved in courtship, and he considered it more likely that display activity is an expression of hostile interactions between males.

In many residential populations most of the birds are paired during the autumn, but social display continues at a high frequency for many months after this. Thus LEBRET considered it unlikely that social display was related to pair formation, since for much of the year social display groups comprise mainly paired birds. LEBRET (1961) and WEIDMANN (1956) have even seen paired males leave their mates asleep on the bank to participate in a display session.

LEBRET postulates that, since hostility will inevitably exist between paired drakes which live in the close company of a flock, social display may be a substitute for overt aggression, which would otherwise result in the break-up of the flock. He mentions two points in favour of this hypothesis. Firstly, social display sessions are often initiated by the re-forming of the flock after a disturbance, or by the arrival of a newcomer. These situations are more likely to release hostility than courtship behaviour.

Secondly, aggressive behaviour, especially fighting, is much more prevalent in spring than in autumn, although more aggression is seen in the autumn than in the preceding months of the moult.

Thus LEBRET believed that social display may be important as a canaliser of aggression during the autumn, when hostile tensions are moderate. In the spring however, the frequency of aggressive behaviour rises. According to LEBRET this is because, with the onset of breeding, aggression between rivals becomes so great that it can no longer be contained by display.

(v)   There is evidence too, however, that social display is important in courtship and pair formation.   Many years ago BROCK (1914) remarked that the nodswimming of the female seems to stimulate males to give displays, but other authors (e.g. LEBRET, 1961; von de WALL, 1965) have since suggested that females have little or no role in social display.   WEID-MANN & DARLEY (1971a), however, performing experiments on mallards of wild stock which were kept in captivity, showed that the presence of a female has a strong facilitating effect on the displaying of males.   Social displays were rarely given by males kept in a monosexual group, when they were observed alone or after the introduction of a strange male.   The introduction of a strange female, however, often resulted in intense display activity;   this was found in experiments conducted both in autumn and during spring.   A facilitation of social display in a group of males after the introduction of a female has also been demonstrated in other species, for instance the green-winged teal (McKINNEY, 1964) and the gadwall (SCHOMMER, 1978).

WEIDMANN & DARLEY (1971a) were also able to show that the behaviour of a female has specific effects on the males' displaying.   In particular, the female nodswimming display was shown to stimulate the male social displays, whereas other female behaviour did not.   A computer sequence analysis revealed that the grunt-whistle, head-up-tail-up, down-up and head-flick were all significantly associated with (i.e. they were immediately preceded by) female nodswimming, whereas the pair display turn-back-of-head was associated with inciting/following by the female.   In one group a more broadly based analysis indicated an association of the occurrence of male displays and female inciting, such that social display and inciting were likely to occur in the same introduction.   Since inciting does not stimulate social display, WEIDMANN & DARLEY speculated that social display might facilitate inciting, which in turn suggests that the male displays are effective in courtship.

The grunt-whistle and head-up-tail-up displays contain elements which are directed towards a particular bird (see section 2.1). A paired male will generally display to his mate, if she is present (WEIDMANN, 1956), and it has been proposed that males which are not firmly paired will address their displays to the female they 'prefer' (von de WALL, 1965; SIMMONS & WEIDMANN, 1973). McKINNEY (1975a) states that a major function of courtship displays must be to attract and hold the attention of the courted female, a function which appears to be well served by the conspicuous directed components of the grunt-whistle and head-up-tail-up. A directional bias has been demonstrated in the so-called secondary social displays - head-flick, head-shake and introductory shake. The first lateral head movement of these shaking displays is usually directed towards a female. In a group containing several females the shakes are generally directed to the same female to whom the male addresses his major displays (SIMMONS & WEIDMANN, 1973).

FIELD (1970) and WEIDMANN & DARLEY (1971a) have established that in a group comprising several males and a single female the drakes perform social displays in certain prefered spatial positions relative to the position of the female.

For the grunt-whistle and head-up-tail-up displays the males generally adopt a body orientation at right angles to or occasionally parallel to the body of the female, and furthermore the head-up-tail-up appears to be given preferentially from a position directly in front of the female.

It is most often the 'dominant' male in a group who displays from the optimal position (WEIDMANN & DARLEY, 1971a), whilst the positions of the other displaying males are more variable. The constant manoeuvring of the males in a display session is believed to result from attempts by each male to attain the best position from which to display to a female.

The performance of displays from optimal positions and/or dis-

tances relative to a female has been recorded in the group display of several other ducks, for instance the goldeneye (DANE & van der KLOOT, 1964), the pintail (SMITH, 1968), the green-winged teal (McKINNEY, 1975a) and the gadwall (SCHOMMER, 1978).

In the case of the grunt-whistle and head-up-tail-up, then, the males seem preoccupied in addressing the displays to a female. Social display has been observed, in exceptional circumstances, in an all-male group (WEIDMANN & DARLEY, 1971b) but here the performing males were apparently spatially disorganised, and each male tended to display to the male who performed the preceding display in the burst.

There is, however, some circumstantial evidence that the down-up display may be due to interactions between males, possibly in aggressive situations.

(a) The down-up display contains no obvious element which is directed towards a female.

(b) In the green-winged teal, a species which possesses a display re-pertoire fairly similar to that of the mallard, a male may occasionally give a grunt-whistle or head-up-tail-up to a female with no other males present, but at least two males must be present for the down-up to occur (McKINNEY, 1975a). The down-up is the most highly synchronised of the three major displays in both the green-winged teal and the mallard (McKINNEY, 1975a), which also implies a high level of male-male inter-action.

The phenomenon whereby a display by one individual elicits the performance of the same display by a second individual has been recorded in many species, and it is often hostile displays which are characterised by this property (MOYNIHAN, 1955).

(c) The down-up display of the mallard is usually accompanied by the rab-rab vocalisation which is itself often associated with aggressive situa-tions (HEINROTH, 1910; WEIDMANN, 1956; McKINNEY, 1969). Synchronised

down-ups are occasionally given outside the context of a display group, and in this situation the males may also peck each other or even fight (LORENZ, 1941). Overt aggressive actions may also follow down-ups which occur during social display (WEIDMANN, 1956).

Some authors (e.g. ANDERSON, 1976) are confident that the context in which a particular display is performed is indicative of the motivation of the display, though WICKLER (1976) referring to McFARLAND & SIBLEY (1975) considers that one cannot always infer motivation from observed behaviour.

(d) In the case of the mallard, details from an analysis of the spatial aspects of social display supports the contention that the down-up involves male-male interaction. In a film study of mixed display bursts FIELD (1970) was able to show that a male performing a down-up tends to have his body aligned parallel to the body of the male who gave the preceding display if this also was a down-up, but not if it was a grunt-whistle or head-up-tail-up. Two males giving successive down-ups were also physically closer together than two males who performed different displays.

Precisely the same observations, relating to the orientation and individual distance of males performing down-ups compared with males giving grunt-whistles or head-up-tail-ups, have been reported in the green-winged teal (McKINNEY, 1965c, 1975a).

(e) In a behavioural comparison of mallards and Aylesbury ducks DESFORGES & WOOD-GUSH (1976) reported a reduction in the proportion of down-ups performed during social display in the domestic breed. About 38 per cent of the major displays given by mallard drakes were down-ups, corresponding with 6-8 per cent in the Aylesbury males. The authors interpreted this finding in terms of species isolating mechanisms, but the reduction in the frequency of down-ups may be related to the marked reduction in aggressivity which has accompanied domestication in the Aylesbury (DESFORGES & WOOD-GUSH, 1975).

3.5. Aggression and pair formation

In a situation where a flock of animals with an uneven sex ratio in favour of males sort themselves out into pairs, it is conceptually quite easy to postulate an adaptive mechanism whereby the more aggressive males are more likely to achieve success in pairing.

In the mallard many authors believe that aggression is of little significance in pair formation, since aggressive interactions between males are much less common during the autumn, when most of the pairing occurs, than during the spring (BROCK, 1914; WEIDMANN, 1956; LEBRET, 1961).

In captivity, however, autumnal fighting does occur (WEIDMANN & DARLEY, 1971a; DESFORGES, 1974), and WEIDMANN & DARLEY reported that the introduction of a female to a group of males in autumn often resulted in intense aggressive behaviour whereas the introduction of a male did not. deLANNOY (1967) considers that a male must be aggressive to be attractive to a female, and he cites an experimental observation where a change in the relative aggressivity of two males was followed by a change in the mating preference of a female between the two males in question.

Although the existence of dominance hierarchies has not been recorded in the wild (WEIDMANN, 1956; PULLIAINEN, 1963), a peck order will rapidly develop in a captive group (HOCHBAUM, 1944; WEIDMANN & DARLEY, 1971a; DESFORGES, 1974). Apart from a potential direct effect of male dominance on pairing success, it is conceivable that a dominant male might enhance his courtship potential via an increase in the efficacy of his displays. This would apply if the attention-catching properties of a male's displays are directly related to his spatial position relative to the female when performing the display. WEIDMANN & DARLEY (1971a) have already observed that the dominant male in a social display group usually attains what seemed to them the optimum displaying position.

So far very little experimental evidence has been published con-

cerning the role of male dominance and aggression in pair formation;
these factors have received much less attention than social display.

I.4. AIMS OF THE STUDY

The basic mating system of the mallard is one of monogamous
pair bonds. The primary purpose of the present study was to analyse the
behaviour involved in pair formation, particularly the role of social
display.

As we have seen, there is some controversy over the role of
social display in courtship. Whilst the grunt-whistle and head-up-tail-
up displays are directed specifically towards females, the same does not
apply to the down-up, and no quantitative evidence has been produced, at
the individual level, that any of the social displays are effective in
courtship. The data from studies of wild populations are of limited
value in this respect, because it is difficult to follow the behaviour and
relationships of individual birds. As RAITASUO (1964) says, "an analysis
of the process of pair formation in autumn and winter is particularly
difficult in conditions where most members of the flock cannot be indivi-
dually identified". A second limitation of field studies is touched on
by SIEGFRIED (1974): "features of social behaviour can vary considerably
within a species, with different populations showing adaptive modifica-
tions most effectively appropriate to the ecological circumstances under
which they live".

The importance of detailed studies of individuals in the inter-
pretation of social behaviour has been emphasised by HAILMAN (1973), and
in the opinion of McKINNEY (1965b), "the need for a complete knowledge of
the history of individual birds under observation is obvious".

It was believed that the facilities available at the field

station at Leicester could be utilised to yield valuable information; the behaviour of individually marked birds of known history and past relationships could be followed under 'semi-natural' conditions. It would also be possible to design experiments to examine specific questions. Although there is a risk that the behaviour of captive ducks might be abnormal in some way (BROCK, 1914; JOHNSGARD, 1965; McKINNEY, 1975a; SCHOMMER, 1978), quantitative data could be readily obtained by experimental manipulation of variables believed to be affecting some aspect of behaviour observed in the wild. The value of this approach was emphasised by McKINNEY (1967) in a study of the breeding behaviour of captive shovellers.

In this study an attempt was made to analyse the role of social display in courtship, by asking such questions as:

"Do mallard drakes give more displays when they are competing for mates than when they are stably paired?"

"Will a single male perform grunt-whistle, head-up-tail-up and down-up displays in courting a female, or is the presence of at least two males a prerequisite for these displays to be given?"

It would be informative to provide an answer to the simple question:

"Does a drake who engages in social display have a greater success in pairing than one who does not perform displays?"

A problem with this approach lies in the social nature of social display. Whenever one male in a group performs displays all the other males present are likely to display as well. It would clearly be useful to manipulate the behaviour of the birds so that displaying and non-displaying drakes could be brought together at the same time. In view of the evidence presented in Chapter IV, Section 1, it was thought that juvenile males could be induced to give social displays by injecting them with testosterone. This might be a valuable approach for a number of

reasons:

(i)   It would be possible to compare the behaviour of females towards males who performed social displays and others of a similar age and appearance who did not display.

(ii)   Juvenile birds of an appropriate age for the experiment would be available during the summer.   At this time of year adult males do not normally engage in display activity, and females are either moulting or leading young.   Would the precocious displaying of the juveniles be sufficient to stimulate the females to show an unseasonal interest in pairing?

(iii) The young males would not have attained the nuptial plumage, so it would also be possible to see if females can be attracted by the displays themselves, without the accompanying plumage features which are exhibited by adult drakes as they display.

Several experiments involving the administration of testosterone to juvenile males were conducted (Chapter IV);   this work also provided some new information on the hormonal basis of social display and other social behaviour in the male mallard.

Previous behavioural studies on pairing in the mallard have concentrated on the effects of epigamic displays.   The possible significance of other behaviour, such as male aggressiveness, has been neglected. SCHOMMER (1978) has pointed out the danger of over-emphasising the importance of social display, since it is the most conspicuous behaviour to the human observer.   In Chapter V the importance of male aggression and dominance in pairing success is investigated.

CHAPTER II

GENERAL METHODS

II.1.   OBSERVATION SITE

All observations were made at the field station of the
Psychology Department, University of Leicester.   This contained a
1,000 m^2 man-made pond, which was fed and drained by a small brook, and
was surrounded by trees and meadows.   Part of the pond, with about
2,000 m^2 of land on either side, was surrounded by a high fence to keep
out predators, and part of this area was further subdivided into covered
pens.   A plan of the field station is provided in Figure II.1.

The Main Pond was used for keeping birds which were not in current use in
experiments.   The pond was well supplied with trees at its borders,
mainly willows, which provided shade and shelter for the ducks.   In
spring and summer there was an abundance of undergrowth;   grasses, nettles
and bushes.

The Large Pens were used for experiments, and also for keeping small
groups of ducks separate from other groups.   All of the large pens in-
cluded an area of land, with some undergrowth, and also a water area.
Those pens which did not include part of the main pond itself were fitted
with concrete ponds which were refilled periodically with pumped water
from the main pond.

The roofs and sides of the pens were constructed of wire or
nylon netting.   A sheet of hardboard some two or three feet high was
tacked onto the sides at ground/water level.   This maintained visual
separation of the birds in adjacent pens, provided they had been wing-
clipped to prevent flight.   The field station contained no facility for
keeping birds in auditory isolation.

The pens were provided with doors for human use, and also trap
doors at ground level which opened into small covered areas, to facilitate
catching of the ducks.
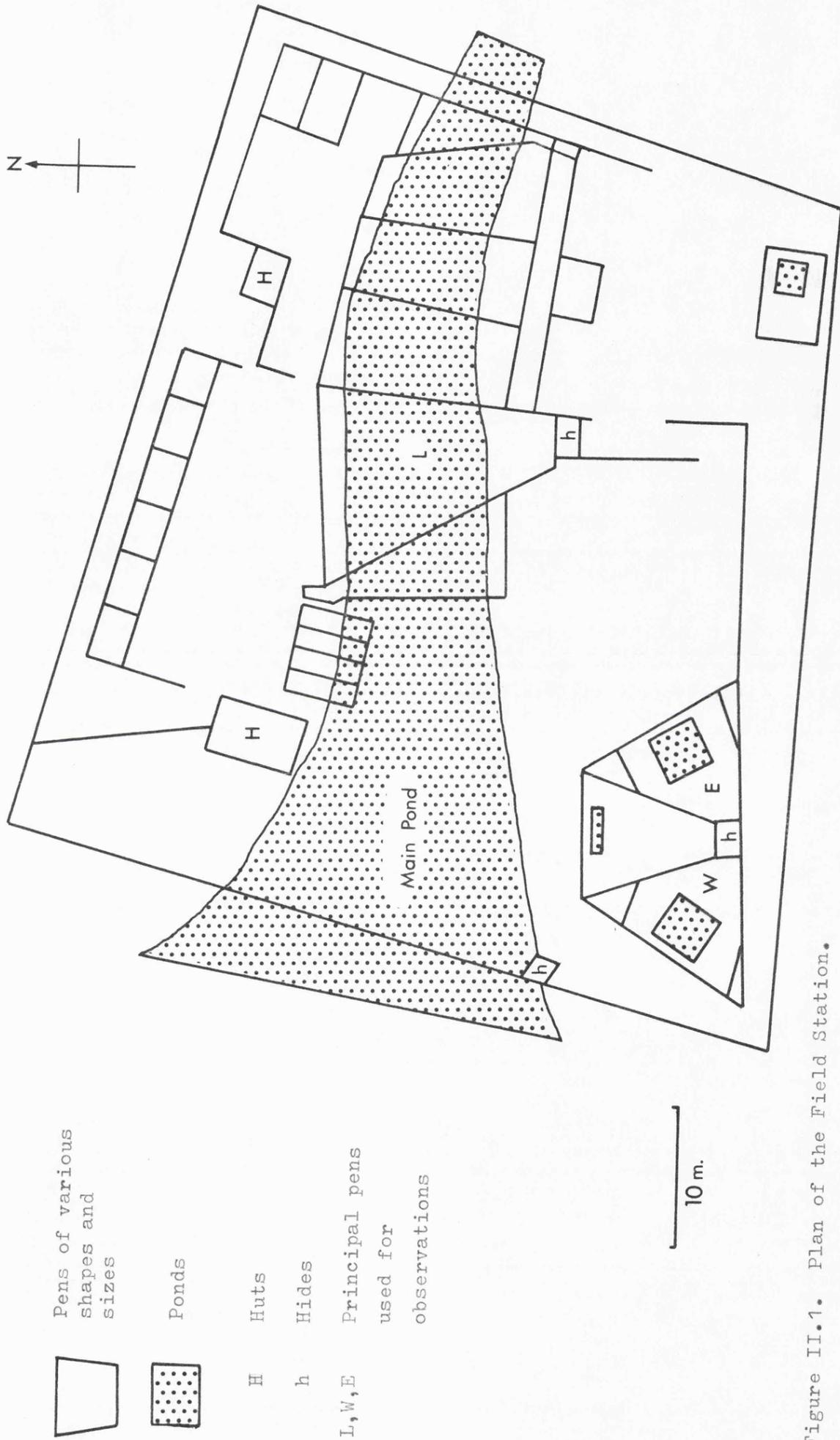
Figure II.1. Plan of the Field Station.

The principal pens used for the experiments were E., W. and L. pens. These pens were each provided with a covered hide with a rear entrance, to allow 'unseen' observations of the birds.

The Small Pens were used for the isolation of individual birds during experiments, and also for the rearing of small groups of ducklings. The water area was either part of the main pond or a refillable polythene-lined trench. When very young ducklings were kept in the pens, covered wooden structures were provided for additional protection.

The huts were used for storage of equipment and grain, and one hut contained a special area where the hormone injections were made.

II.2. BIRDS

2.1. Breeding stock

The mallard colony was founded in 1968, from eggs supplied by the Wildfowl Trust, Slimbridge, Gloucestershire. The ducks always bred readily at the field station, but the flock was occasionally supplemented with wild birds which flew in, and with further acquisitions from Slimbridge.

The ducks nested successfully on the main pond and also in many of the large pens. Some birds utilised the nest boxes which were provided, but there was always an ample supply of undergrowth and dead vegetation in the breeding season in which many of the ducks built their nests. Some even made their nests in areas where there was little or no cover.

2.2. Hatching and early rearing

Each female was allowed to incubate her clutch until a couple of days before the expected hatching date. The eggs were then removed and

hatched in an incubator maintained at 102°C, which was situated in the Psychology Department.

After hatching the ducklings were left in the incubator for 12 to 24 hours to dry out, after which they were transferred to indoor cages under heat lamps. The ducklings were kept in groups of ten to thirty individuals, called 'rearing-groups'. Each rearing-group comprised birds of the same age (within a few days) of which some, though not all, would be siblings.

The indoor cages were made of wire mesh, with a floor of newspaper or sacking. Sacking was provided for ducklings in their first week of life, when their feet were liable to slip on newspaper, which might have resulted in injury. The ducklings were given a constant supply of fresh water for drinking, but were only allowed occasional supervised bathing, as hand-reared ducklings do not have a fully waterproof down. The young were given a basic diet of turkey starter crumbs, supplemented with boiled egg, duckweed, hay and grass. After a couple of weeks wheat and grit were gradually added to the diet.

2.3. Later rearing and keeping conditions

At three to four weeks of age the ducklings were transferred to the field station. Each rearing-group was kept at first in one of the small pens. In due course the birds were transferred to larger pens, but each rearing-group was kept separate from the others until the birds were first used in an experiment. Most of the birds had the primary flight feathers clipped on one side (they were never pinioned) when they were full grown. This prevented the birds from seeing over the hardboard sides into neighbouring pens. When separation from other groups was no longer necessary many of the birds were transferred to the main pond, where older mallards and some ducks of other species were living.

The juvenile and adult birds were fed on a mixture of wheat and

poultry-rearing pellets, with oyster shell grit added during the breeding season for the benefit of the laying females. The ducks also took some natural food items; small aquatic and terrestrial animals and some seeds and other plant material. During all experiments the birds were fed ad libitum; a food container was provided in each pen and was regularly topped up.

II.3. EXPERIMENTAL METHODS

3.1. Individual marking

When they were fully grown, all birds were banded with numbered metal rings and/or colour coded plastic rings (the latter could be distinguished at a distance of several metres).

For the experimental observations it was essential that the birds could be identified from the hide whilst they were in the water. A second method of marking was used for this purpose; a small patch of coloured plastic tape was stuck on the bill. The billmarks came off occasionally, but the birds could be rounded up and the billmarks replaced when necessary.

3.2. Observation methods

Two methods of observation were utilised; 'undisturbed watching' and 'introductions'.

Undisturbed watching

The hide was entered, from the rear, and the birds were observed for a pre-determined period. Efforts were made to ensure a minimum of disturbance to the ducks from other human-controlled sources. The field station was partially skirted by a fenced walkway, so that an observer could move around the site unseen by the ducks in the pens.

Whilst the ducks were relatively 'quiet' socially, behavioural interactions could be recorded on paper, but intense social activity sessions were recorded as a spoken commentary on a casette tape, which was later transcribed onto paper.

Introductions

Following the work of McKINNEY (1964) on green-winged teal, WEIDMANN & DARLEY (1971a) noted that the introduction of a female mallard to a resident group of males often resulted in immediate social activity. This technique was used in some of the experiments in the present study, so that the social behaviour of the birds could be sampled in a relatively short time, and several observations could be made of a number of groups during the course of a day.

The bird to be introduced (not always a female) was placed in a box within the pen, and released by opening the lid of the box via a string leading from the hide. The taped commentary was begun immediately and lasted for either 15 or 30 minutes. After this the introduced bird was caught and removed.

II.4. BEHAVIOUR RECORDS

The displays and other social behaviour patterns which were recorded are listed in Table II.1. Following LORENZ (1941), WEIDMANN (1956) and JOHNSGARD (1965) the behaviour patterns have been divided into four categories, social displays, pair displays, sexual behaviour and aggressive behaviour. These categories are not necessarily mutually exclusive; the classification has been used for convenience, and should not be taken to imply causal or functional differences. The behaviour patterns themselves were all described in section I.2.

During the experimental observations the identity of the bird

Table II.1

Displays and other behaviour patterns recorded during the experimental
observations

		MALE BEHAVIOUR		FEMALE BEHAVIOUR

A. SOCIAL DISPLAYS

	HF	Head-flick	NS	Nodswimming
	IS	Introductory shake		
1	GW	Grunt-whistle		
1,2	HU	Head-up-tail-up		
2	NS	Nodswimming		
2	TBH	Turn-back-of-head		
1	DU	Down-up		

B. PAIR DISPLAYS or DIRECTED COURTSHIP

3	TBH	Turn-back-of-head	INC	Inciting
4	MPR	Mock-preen		

C. SEXUAL BEHAVIOUR

PU	Head-pumping	PU	Head-pumping
GNF	Grasping-neck-feathers	PR	Prone posture
MA	Mounting attempt	COP	Copulation
M	Mounting		
COP	Copulation		
BR	Bridling		
NS	Nodswimming		
RA	Rape attempt		

D. AGGRESSIVE BEHAVIOUR

TH	Threat	TH	Threat
PK	Peck	PK	Peck
CH	Chase	CH	Chase
FT	Fight	FT	Fight

Notes

1. The three major displays.

2. The three components of the head-up-tail-up sequence.

3. Occurrence of turn-back-of-head when not preceded by head-up-tail-up
   and nodswimming.

4. The preen-behind-wing display only.

performing the display or behaviour was recorded.   Many of the behaviour

patterns are clearly addressed or directed towards a second individual:

in these cases the 'addressee' was also identified wherever this was

possible.

Most of the behaviour patterns were quantified simply by re-

cording their frequency of occurrence in a given observation period.   For

some of the displays, however, for instance nodswimming and inciting, the

duration (in seconds) of each incidence was also recorded.

II.5.   ADMINISTRATION OF TESTOSTERONE

The experiments in Chapter IV describe the behaviour of juvenile

males injected with testosterone propionate.   The hormone was obtained as

a powder (from Schering Chemicals Ltd.), and was dissolved in sesame oil

at a concentration of 50 mg/ml.

Injections were made in the wing muscle, alternating between the

right and left sides to reduce the risk of soreness at the injection site.

This in fact was not a problem in these experiments.

The males were given injections every day or every second day,

usually between 10.00 a.m. and 12.00 noon.   The males were caught from

their pen and carried in boxes to a hut for the injections.

The dosage varied in different experiments, but the control

birds in a given experiment were always given injections of sesame oil

alone at a volume equivalent to that administered to the experimental

birds.

CHAPTER III

SOCIAL DISPLAY AND PAIR FORMATION IN ADULTS

III.1.   EXPERIMENT 1

1.1.   Introduction

In this experiment it was proposed to test the hypothesis that social display is involved in courtship.

A group of adult mallards comprising only firmly paired individuals was observed regularly.   In this situation one would expect very little sexual competition between the drakes, since each male was already paired and there were no excess males (or females) present.   Would any social display be exhibited by these birds?

After several days of observation the females of the group were removed, and replaced with females which were previously unknown to the males.   The males now had the opportunity to compete for new mates.   If social display is an important aspect of courtship, one would expect to see an increase in the frequency of social displays performed by the males in comparison with their behaviour during the first experimental period. Would any other male behaviour occur more frequently in the competitive situation, and would the new females give more nodswimming (a display which stimulates males to give social displays) than the paired females had done?

It was also possible to examine the relationship between social display and pair formation in more detail, by looking closely at the orientation of the males' displays.   In the situation in which all the birds were paired, would the males display (if at all) each only to his own mate, or would they address some displays to other females?   In the competitive situation, would the females pair with the males who displayed to them?

It was proposed to use the orientation of the inciting display as the main criterion in assessing the sexual preferences of the females. WICKLER (1976) has emphasised that the most reliable indication of a per-

sonal attachment between two individuals is the addressing of a particular behaviour exclusively from one to the other, rather than, say, spatial proximity or general synchronisation of behaviour.

By performing inciting a female is presumably advertising her sexual preference for a particular drake. Certainly a paired female in the wild will generally address inciting only to her mate (WEIDMANN, 1956), and preliminary observations showed that this was also true of paired mallards at the field station. Other workers (e.g. KLINT, 1973, 1975; DESFORGES & WOOD-GUSH, 1976) have determined the pairing preferences of females in experimental conditions by the orientation of their inciting.

1.2. Methods

The experiment was conducted between mid-October and early December, a period when much of the pair formation in a wild flock occurs. The birds were kept in L. pen, one of the larger observation pens (see Figure II.1).

The initial group comprised four males and four females, which had hatched in the spring of the previous year and had been raised together in the same rearing-group. These birds had formed into four pairs during their first autumn, and had remained paired until the breeding season, when they were allowed to breed at the field station.

Early in the following October these birds were observed to ascertain that they had paired again with their old mates, which was indeed the case. They were placed together in L. pen and were allowed a couple of weeks to become familiarised with their surroundings before the experiment was begun.

The observations were begun on 21st October; the group was observed on 7 occasions in the next 16 days. Each one was a three-hour 'undisturbed observation' (see Section II.3), made between 9.00 a.m. and 12.00 noon.

The social behaviour patterns recorded are those listed in Table II.1, with the omission of the male displays head-flick, introductory shake and turn-back-of-head. The head-up-tail-up complex was recorded as a single display (HU). In addition general notes were made during each observation session on the social behaviour and interactions of the subjects.

On the 7th November the four resident females were removed and placed in one of the pens on the other side of the field station, where they were out of visual, but not auditory contact with their mates.

On the following day four new females were billmarked and placed in L. pen. These birds were the same age as the males, but were 'strangers' to them, i.e. they had never before been kept in the same pen as the males. The females were also themselves selected from four different rearing-groups, to reduce the likelihood of homosexual behaviour which was seen in some other experiments when females which were familiar with each other were transferred to a new group of males with whom they were unfamiliar.

The observations were resumed; the new group was observed on 14 mornings (always 9.00 a.m. - 12.00 noon) between 8th November and 6th December.

The two observation series are referred to as the 'old female' observations (the males with their original mates present) and the 'new female' observations (after the strange females were introduced).

For the presentation of the results the birds are identified not by their original ring numbers, but by new code numbers chosen for ease in reading the data. Thus the four pairs in the 'old female' observations are: Male 01 and Female 11; Male 02 and Female 12; Male 03 and Female 13; Male 04 and Female 14.

The four 'new' females were numbered 21, 22, 23 and 24.

1.3. Results and discussion

The results are examined in three sections:

(a) A description of the social behaviour of the birds in the 'old female' observations.

(b) A quantitative comparison of behaviour frequencies in the 'old female' and 'new female' observations.

(c) A detailed analysis of the orientation of displays in the 'new female' observations.

(a) Social behaviour in the group of paired birds

The general impression obtained during the first observation series was that of a fairly stable social organisation.   The four pairs co-existed with very few aggressive interactions, their pair bonds all appeared to be very stable and many of the behavioural characteristics which other workers have found to be typical of paired birds in the wild (see Section I.3.1) could be recognised here.

All pair displays were addressed exclusively to the mate.   In each observation period several pair palavers were recorded, with the female giving the inciting display and her mate performing turn-back-of-head with rab-rab vocalisations.   On three occasions a male was seen to give the mock-preen or preen-behind-wing display to his mate.

Sexual behaviour was not of frequent occurrence, but all sexual behaviour which was recorded was addressed only to the mate.   Several bouts of pre-copulatory head-pumping and at least one copulation were seen within each pair during the course of the observations.

As mentioned above, overt agonistic behaviour was not common. A few male-male aggressive actions were recorded;   these were chiefly threats, with a few pecks and chases but no fighting.   On the basis of these aggressive encounters the males could be classified into a linear dominance hierarchy.   The hierarchy was of the 'peck-right' type, as first

described by SCHJELDERUP-EBBE (1922) in domestic fowl. That is to say

each male was seen to behave aggressively towards some (though not

necessarily all) of those lower in the hierarchy, but a male never

threatened, pecked or chased one of higher rank. DESFORGES (1974) also

observed peck-right hierarchies in captive mallards. In the present group

Male 01 was at the top of the hierarchy, Male 02 was second, Male 03 was

third and Male 04 bottom. Consequently Male 04 performed no aggressive

behaviour at all. Aggressive behaviour performed by females or directed

by males towards females was extremely rare in the 'old female' observa-

tions.

Some social displays were given by the males in six of the seven

observation periods. Most of the grunt-whistle and head-up-tail-up dis-

plays were addressed by each male, as expected, to his own mate (see

Appendix 3 for details). Most of the display sessions involved all four

males, but these occurred without active participation of the females, in

that the female nodswimming display was seldom recorded. Nodswimming has

been shown to facilitate the performance of social displays by drakes

(WEIDMANN & DARLEY, 1971a), and McKINNEY (1975a) considered that nod-

swimming stimulates the interest of the males in courtship. These authors

emphasised, however, that a nodswimming female is not an essential require-

ment for males to display, and this is confirmed in the present study.

The social displays performed by the males were presumably not

functional in courtship in the strict sense of the word, since the males

in the group were already firmly paired. Paired males would not be ex-

pected to be active in competition for females, especially when no unpaired

drakes were present who might initiate courtship behaviour. It is possible

that social display (in males, but not female nodswimming) is involved in

some way in the maintenance of the bond. This and other suggestions for

the function of social display in paired birds are considered fully in the

light of other evidence in Chapter VI.

For the first few days after their mates were removed (the 'new female' observations) the males showed typical 'separation behaviour'. The males at first spent much of their time swimming singly along the side of the pen, uttering the monosyllabic 'slow Raeb' call. This behaviour was almost certainly promoted by vocal contact between mates; the 'old' females were heard to give frequent decrescendo calls and persistent quacking from their new pen. These calls are believed to function in helping visually separated mates find each other (McKINNEY, 1975b).

Although auditory contact was not prevented, the separation behaviour did not continue indefinitely. Male O1 stopped giving Raeb calls after one day, Male O4 after two days, but the other two males took a little longer. Male O2 was still giving Raeb calls, at a gradually decreasing frequency, until the 17th November.

(b) Comparison of behaviour frequencies in the 'old female' and 'new female' observations

The tables accompanying this section show the mean frequency of each display or behaviour pattern performed by each bird in the 'old female' and the 'new female' observations. The behaviour frequencies recorded in each separate observation period are listed in Appendix 2. For some of the behaviour patterns these daily scores are presented graphically, in Figures III.1. - III.5.

Social displays

The males gave more social displays in the 'new female' observations than in the 'old female' observations (Table III.1). The difference in the mean scores was significant for the total of the major displays and also for grunt-whistles, head-up-tail-ups and down-ups when these were analysed separately.

The highest daily frequencies of displays were recorded in the 'new female' observations, but there was also a greater variation in daily

Table III.1

Experiment 1. Social displays and sexual behaviour performed by the males. The table shows the mean frequency per 3-hour observation period of each behaviour pattern, given by each male in the 'old female' and the 'new female' observations, and the mean of the four scores in each set of observations are compared by t-test; the t-values are given in brackets and the significance levels of the associated probabilities (2-tailed) are expressed as; N.S. not significant (p >0.05)

* p <0.05

** p <0.01

Behaviour		Grunt-whistle	Head-up-tail-up	Down-up	Total major social displays	Pre-copulatory head-pumping	Copulation
'Old female' observations	Male 01	4.29	1.43	2.29	8.00	2.43	1.00
	02	2.29	1.43	2.29	6.00	0.57	0.14
	03	2.57	0.29	1.71	4.57	0.71	0.29
	04	1.71	1.43	2.57	5.71	1.57	0.14
	Mean	2.72	1.15	2.22	6.07	1.32	0.39
'New female' observations	01	7.43	4.43	3.79	15.64	4.43	0.93
	02	3.21	3.64	3.00	9.86	1.07	0.29
	03	4.43	3.57	4.00	12.00	1.57	0.21
	04	3.21	2.93	4.71	10.86	2.93	0.71
	Mean	4.57	3.64	3.88	12.09	2.50	0.54
t value		* (3.95)	** (6.21)	* (4.61)	** (6.58)	* (3.63)	N.S. (0.94)
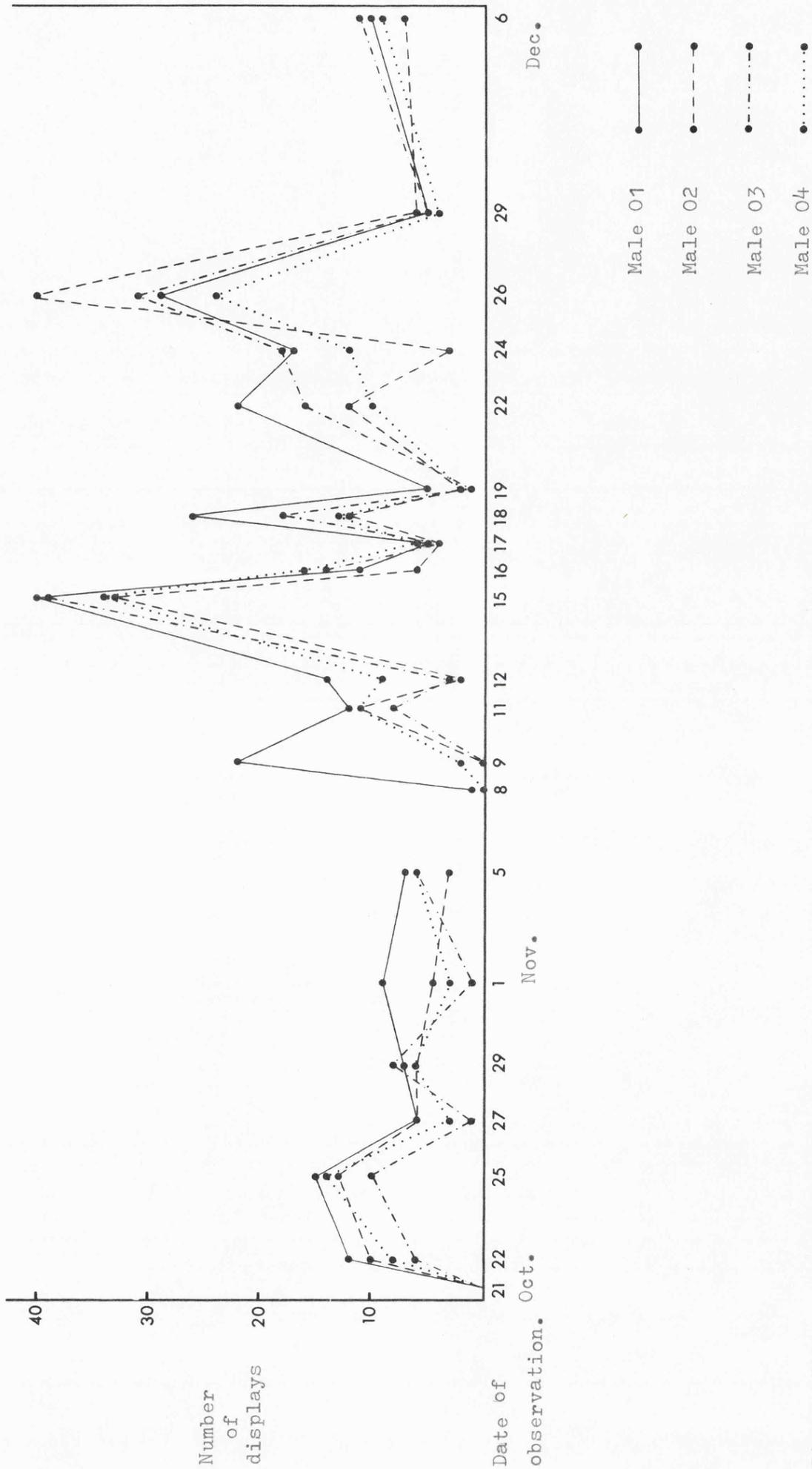
Figure III.1 Experiment 1. Social displays (total major displays) of the males.

frequencies in the 'new female' than in the 'old female' series

(Figure III.1).   Despite these daily fluctuations, however, it was

apparent that the display behaviour of the four males was fairly consistent.

On some days all four males gave a relatively large number of displays, and

on other days very few displays were recorded from any individual.   This

is to be expected in view of the fact that social displays tend to occur

in synchronised bursts and in discrete display sessions.   Figure III.1

records the daily frequencies of 'total displays', but the pattern for each

of the display movements was very similar.

The first two observation periods of the 'new female' series,

when the males were showing a great deal of separation behaviour, were

characterised by fairly low levels of displaying, but this also applied to

some of the days later in the experiment.

The relative proportions of the three major displays given by

each male in the two observation series are shown in Table III.2.   All

four males gave relatively more head-up-tail-ups in the 'new female' ob-

servations, with a corresponding reduction in the proportions of both

grunt-whistles and down-ups.

The female social display, nodswimming, was given significantly

more often by the 'new females' than by the 'old females' (Table III.3).

The females did not show the same individual consistency in daily nod-

swimming frequencies as was found for male displays (Figure III.2).   Three

of the females exhibited nodswimming on most observation days, but Female

22 gave the display during only two observation periods.   She was the only

one of the 'new' females to show separation behaviour.   She gave decres-

cendo calls, persistently during the first few days and intermittently un-

til 24th November.   She also exhibited some homosexual behaviour during

this period, by following and addressing inciting to one of the other fe-

males (see Table III.3).

The increase in female nodswimming and male social display fre-

Table III.2

Experiment 1. Comparison of the relative proportions of the three major
social displays, grunt-whistle (GW), head-up-tail-up (HU), and down-up
(DU) given by the males in the 'old female' and the 'new female' observa-
tions. The table shows the number of displays performed in each set of
observations, and each display is also expressed as a percentage of the
total given by each male.

Display		Male 01			Male 02			Male 03			Male 04			All Males		
		GW	HU	DU	GW	HU	DU	GW	HU	DU	GW	HU	DU	GW	HU	DU
'Old female' observations	No.	30	10	16	16	10	16	18	2	12	12	10	18	76	32	62
	%	54	18	29	38	24	38	56	6	38	30	25	45	45	19	37
'New female' observations	No.	104	62	53	45	51	42	62	50	56	45	41	66	256	204	217
	%	48	28	24	33	37	30	37	30	33	30	27	43	38	30	32

Table III.3

Experiment 1.   Female behaviour

The table shows the mean duration in seconds of nodswimming and inciting and the mean frequency of pre-copulatory head-pumping and copulation per 3-hour observation period given by each of the 'old' females and by each of the 'new' females.   The scores of the two groups of females are compared by t-test (the significance levels are expressed as in Table III.1)

Behaviour		Nodswimming	Inciting /	Pre-copulatory head-pumping	Copulation
	Female				
'Old' females	11	1.00	20.71	2.14	1.00
	12	0.00	5.29	0.57	0.14
	13	0.00	9.57	0.57	0.29
	14	1.43	28.00	1.43	0.14
	Mean	0.61	15.89	1.18	0.39
'New' females	21	11.71	51.29	1.50	0.29
	22	1.93	57.14	1.14	0.29
	23	11.14	38.21	3.07	0.86
	24	11.71	81.43	2.86	0.71
	Mean	9.12	57.02	2.14	0.54
t value		* (3.51)	* (3.94)	N.S. (1.57)	N.S. (0.58)

/ Only male-directed inciting is included.   Female 22 also addressed a little inciting to a female during the 5 observation periods from 15th - 19th November (see Appendix 2).
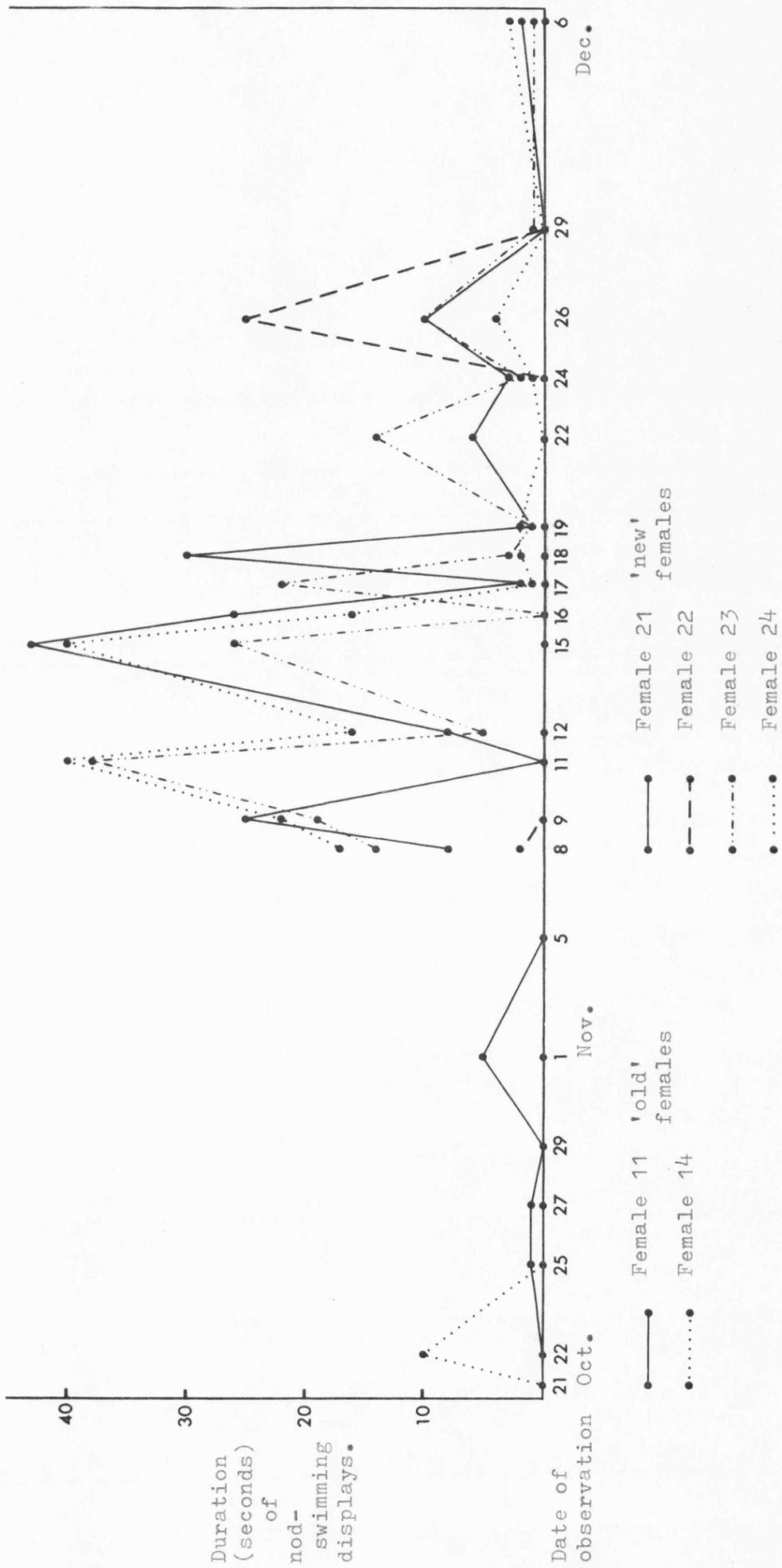
Figure III.2 Experiment 1. Nodswimming displays of the females.

quencies in the 'new female' observations might be interpreted in the following way. Firstly, the 'new females' performed nodswimming to attract the courtship interest of the drakes. The males consequently gave more social displays than when they were firmly paired and displaying to their mates, perhaps as a result of a direct facilitation by the females' behaviour and also due to competition between the males themselves.

It might also be speculated that the head-up-tail-up display is more important than the grunt-whistle and down-up in the early stages of pair formation, compared with a situation where pair bonds are well established. In the ring dove ERICKSON & MORRIS (1972) and ERICKSON (1973) have described quantitative differences in the courtship patterns of males displaying to their mates or to 'strange' females.

In the gadwall SCHOMMER (1978) reported that paired males could sometimes be distinguished from unpaired males by differences in the relative proportions of directed courtship and social displays performed in communal sessions. There have been no comparable observations reported, however, on the social display of mallards.

Pair displays

The male pair display turn-back-of-head was not analysed in detail in this experiment. The mock-preen display ('preen-behind-wing') was of rare occurrence in both series of observations, although other forms of mock preening (McKINNEY, 1965a) may have occurred.

Inciting was performed significantly more often by the 'new' females than by the 'old' females (Table III.3, Figure III.3). This might be a reflection on the competitive situation in the 'new female' observations. The inciting display has presumably evolved as a method for the female to demonstrate her sexual preference to the favoured drake and also to other birds (LORENZ, 1941; McKINNEY, 1975a). It may be expected, then, that a female will give more inciting if unpaired males and females (poten-
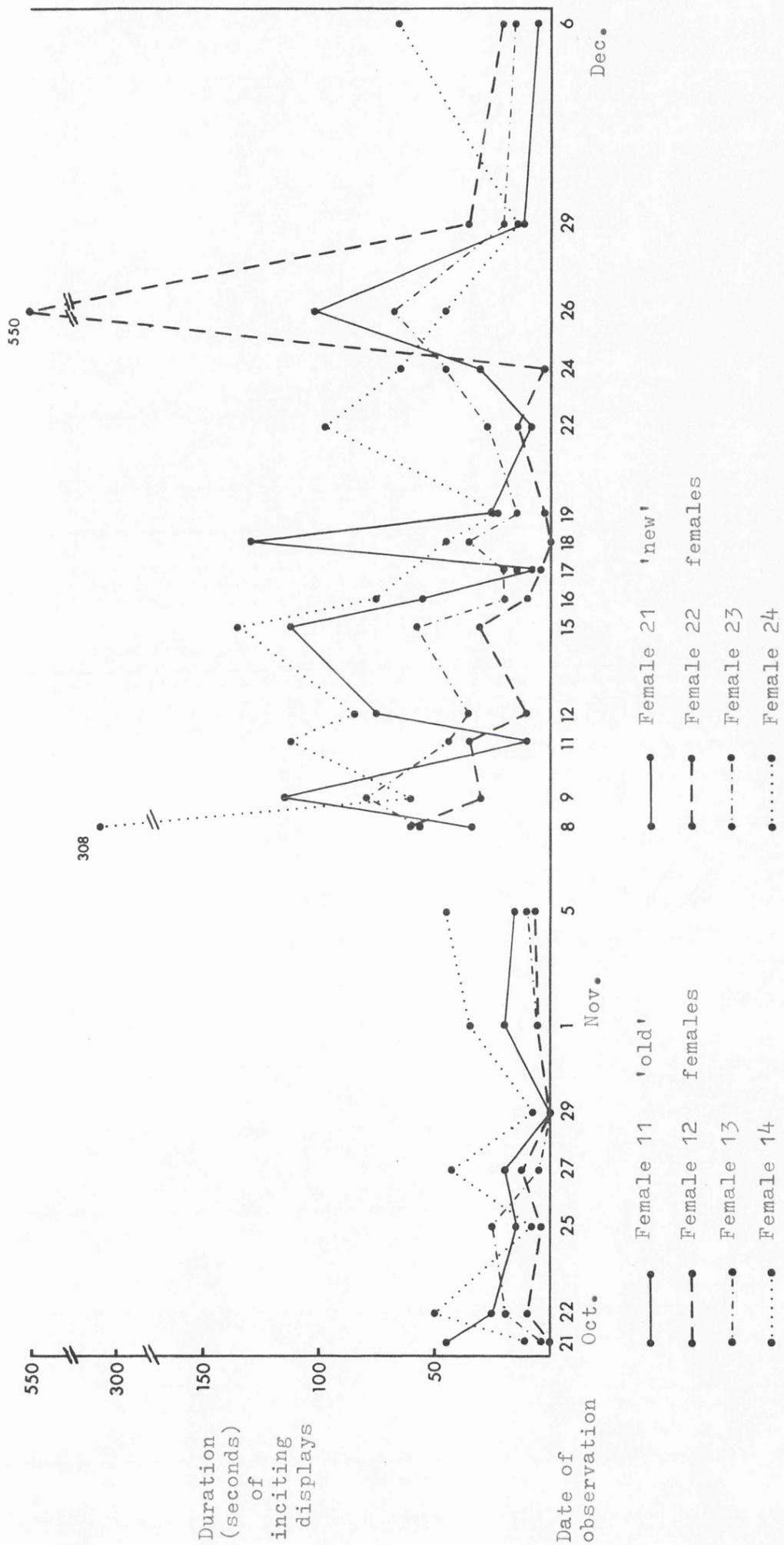
Figure III.3 Experiment 1. Inciting displays of the females.

tial rivals) are present than if the only other birds in the vicinity are already firmly paired.

Sexual behaviour

Copulations did not occur at a significantly different frequency in the two observation series in either the males (Table III.1) or the females (Table III.3). The males did, however, perform the pre-copulatory head-pumping display significantly more often in the 'new female' observations, but the difference in the frequency of this display given by the two sets of females was not significant.

The possibility should perhaps be considered that the head-pumping display of the mallard drake might have a role in attracting a potential mate. The usual function attributed to autumnal copulations, with the accompanying pre- and post-copulatory displays, is that the behaviour operates to strengthen an existing bond (McKINNEY, 1975a). In the gadwall, however, SCHOMMER (1978) observed that head-pumping often occurs between a male and a female who are not paired but are apparently 'interested' in one another, as deduced from their directed courtship displays.

Aggressive behaviour

The frequencies of male-directed aggressive actions performed by the males were not significantly different in the two observation series (Table III.4). During the last few observation periods of the experiment, however, Males 01, 02 and 03 were very aggressive towards other males (Figure III.4). This included threatening, pecking and chasing; there was still no fighting. In view of the clear discontinuity in daily frequencies a comparison based on mean scores is hardly meaningful. The implications of the individual peaks in aggressiveness are considered in section (c) below.

It will be noted that Male 04 was never aggressive towards the

Table III.4

Experiment 1.   Male-directed aggressive behaviour of the males.

Explanation of table as in Table III.1.

Behaviour		Threat	Peck	Chase	Total
'Old female' observations	Male 01	2.43	0.14	1.00	3.57
	02	0.43	0.00	0.14	0.57
	03	3.14	0.43	0.71	4.29
	04	0.00	0.00	0.00	0.00
	Mean	1.50	0.14	0.46	2.11
'New female' observations	01	1.36	1.36	0.64	3.36
	02	1.50	0.71	0.79	3.00
	03	5.00	0.36	2.07	7.43
	04	0.00	0.00	0.00	0.00
	Mean	1.97	0.61	0.88	3.45
t value		N.S. (0.73)	N.S. (1.51)	N.S. (1.09)	N.S. (1.58)
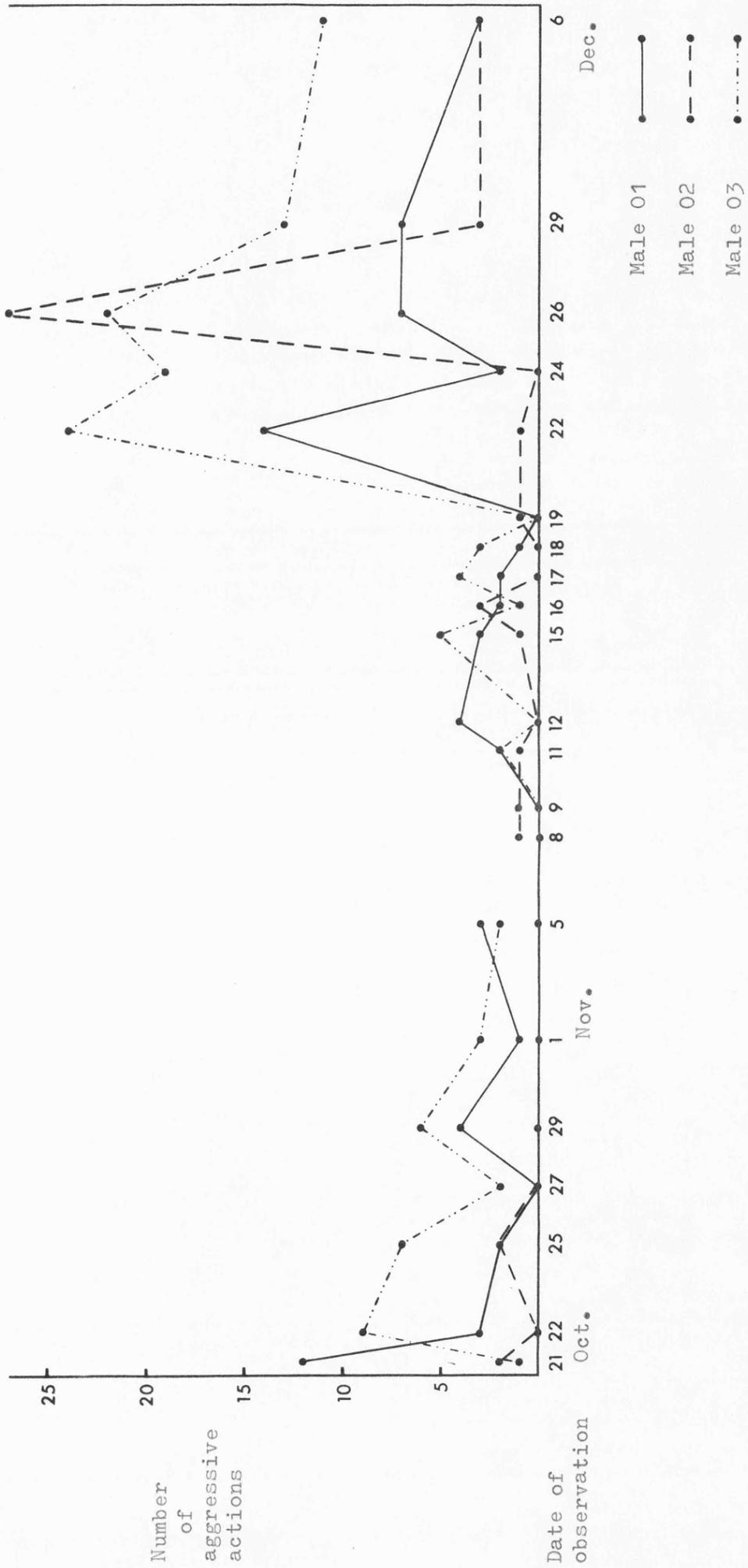
Figure III.4   Experiment 1.   Male-directed aggressive behaviour (threats, pecks and chases) of the males.

Table III.5

Experiment 1. Female-directed aggressive behaviour of the males.

Explanation of table as in Table III.1.

Behaviour		Threat	Peck	Chase	Total
	Male				
'Old female' observations	01	0.00	0.00	1.57	1.57
	02	0.00	0.00	0.00	0.00
	03	0.29	0.00	0.00	0.29
	04	0.00	0.00	0.00	0.00
	Mean	0.07	0.00	0.39	0.47
'New female' observations	01	0.79	1.43	0.21	2.43
	02	0.36	2.14	0.14	2.64
	03	0.29	0.64	0.00	0.93
	04	0.36	0.71	0.00	1.07
	Mean	0.45	1.23	0.09	1.77
t value		N.S. (2.34)	* (3.50)	N.S. (0.86)	N.S. (2.87)
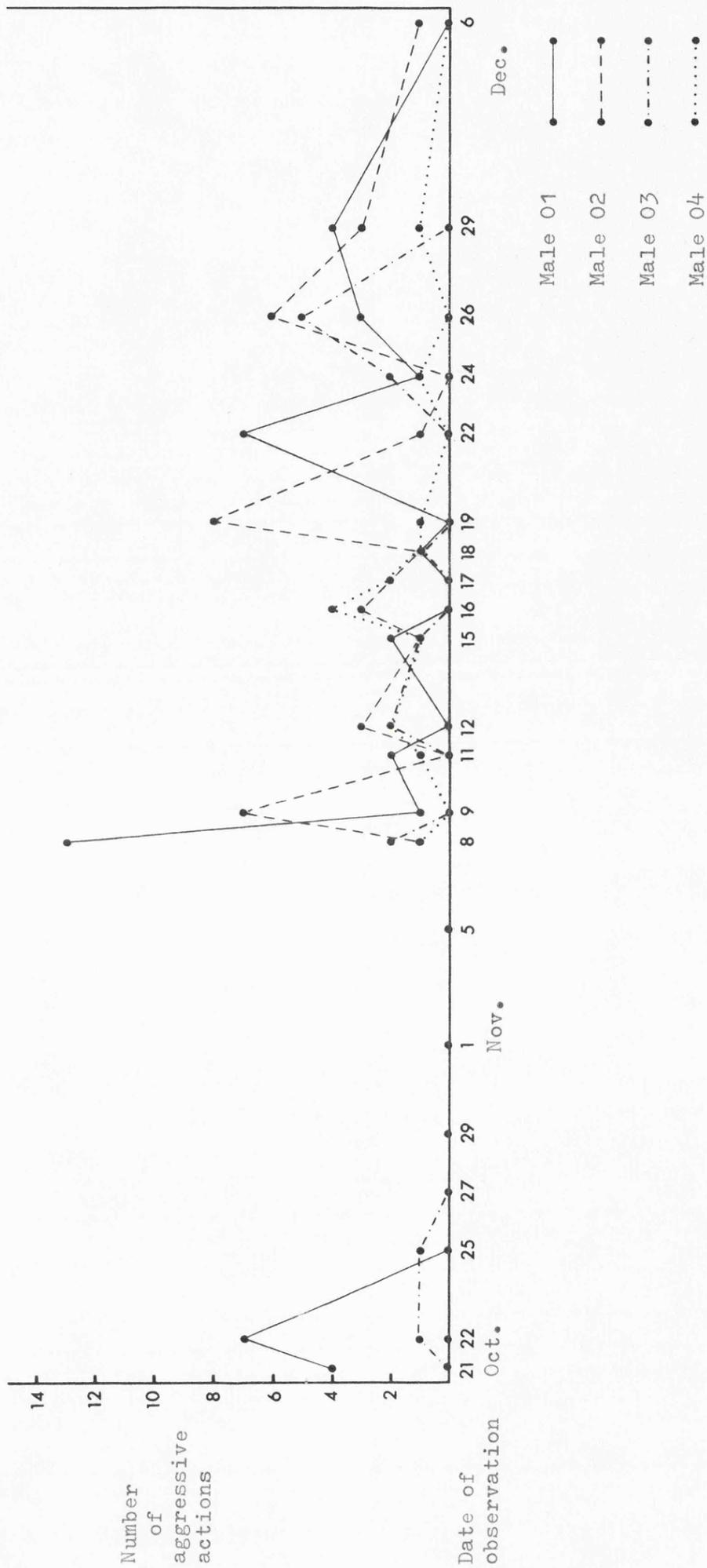
Figure III.5 Experiment 1. Female-directed aggressive behaviour (threats, pecks and chases) of the males.

other males. The linear dominance hierarchy which was apparent in the 'old female' observations remained the same throughout the experiment, and no male was ever seen to behave aggressively towards one of higher rank.

The males appeared to be more aggressive towards the 'new' females than they had been towards the 'old' females (Figure III.5), although the difference in mean frequencies was significant only for pecks (Table III.5). It is not clear if this result has any particular significance in relation to pair formation in the competitive situation. The increase in female-directed pecking might simply have been a function of strangeness and familiarity. It has often been noted that mallards may behave aggressively towards unfamiliar conspecifics (e.g. HOCHBAUM, 1944; DESFORGES, 1974).

Aggressive actions were seldom exhibited by either the 'old' or the 'new' females.

(c) The orientation of displays and the development of pair bonds in the 'new female' observations

In the 'new female' observations, as in the earlier series, each female copulated only with a male to whom she also addressed inciting, and the sexual behaviour performed by each male was addressed only towards a female who had already demonstrated her preference for him. As stated earlier, the assumption of the sexual preference of a female was based on her inciting displays. It was of interest to see if each female preferred only a male who had addressed social displays to her. The orientation of the males' social displays and the females' inciting displays in each observation period are presented in Appendix 3.

During the first few observation periods Male 01 addressed social displays to three females, and Males 02 and 03 each displayed to two females. Male 04 displayed only to Female 24, who in turn addressed inciting only towards him. The other three females incited almost exclusively to

Male 01, thus some of the males' attentions were not reciprocated at this time.

The orientation of the males' displaying and the females' preferences changed somewhat during the course of the experiment. The situation in the latter part of the experiment is summarised in Figure III.6.

Two firm pair bonds had apparently been established, between Male 04 and Female 24, and Male 02 and Female 22. In both cases the male concerned displayed only to his new mate and the female incited exclusively to this male. Male 01 and Female 21 displayed mainly to each other, but they also addressed other individuals as well. In these three cases it was not possible to say that the male displayed to the female before her preference was demonstrated, which would have indicated a possible effect of the displays in attracting her.

Female 23 had initially preferred Male 01, but she later switched her preference and during the last four observations she addressed inciting only to Male 03. This male copulated with her several times during the last few days, but he continued to address his social displays to a different female. The evidence relating male social displays and female preferences, then, is equivocal.

Two of the females, Females 22 and 24, each performed a great deal of inciting on one particular day (see Figure III.3). In both cases this was the day when the female's preference for a male was first established. Following on from the argument given earlier concerning the signal value of this display, these data would suggest that a female's need to express her choice of mate to the favoured and/or rival males is strongest when she first makes her decision. The same was not found for Females 21 and 23, but the development of their sexual preferences was more gradual. Female 23, for instance, addressed inciting to Male 01 and Male 03 during four observation periods before she restricted her display to Male 03.

Figure III.6

Experiment 1.   Sexual preferences of the females, and females
addressed by the males during social display, in the latter part
of the 'new female' observations.

An arrow 01————————→21 indicates that Male 01 addressed most or
all of his social displays to Female 21.
An arrow 01←——————21 indicates that Female 21 addressed most or
all of her inciting to Male 01.

MALES   FEMALES

01 ⇄— — — — — — — 21

02 ⇄— — — — — — — 22

03 ← — — — — — — — 23

04 ⇄— — — — — — — 24
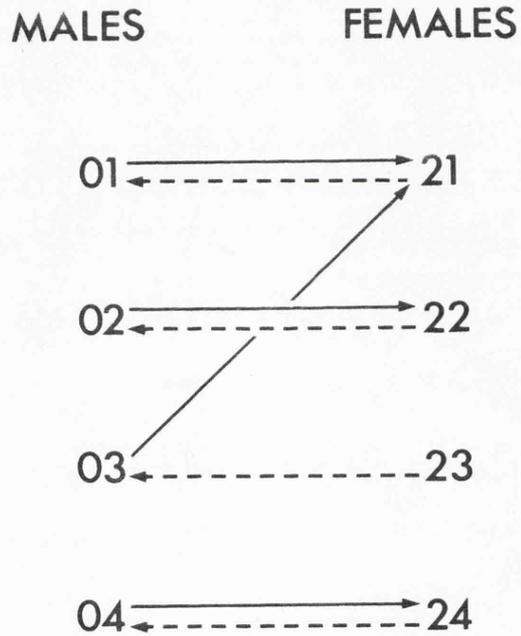
Some of the data from this experiment suggest that male aggressiveness might be related in some way to pair formation. Male 03, on the 22nd November, and Male 02 on the 26th, each behaved very aggressively towards other males on the day that a female first demonstrated a preference for them (see Figure III.4). However, if a positive relationship between female preference and male aggressiveness does exist, there is no evidence here to indicate which is the primary factor from which the other follows.

The other two males did not show an increase in aggression coincident with pair formation. Male 01 was selected by two females very early in the experiment, but he performed few male-directed aggressive actions until much later. He was at his most aggressive, in fact, on the day when Female 23 changed her preference _from_ him to another drake. Male 04 occupied the position at the bottom of the hierarchy and performed no male-directed aggressive actions throughout the experiment. The relationship between inter-male aggression and female pairing preferences is studied more fully in Chapter V.

III.2.   EXPERIMENT 2

2.1.   Introduction

In the spring, with the advent of the breeding season, a wild mallard flock begins to disperse, each pair moving off to seek a nest site. The type of social behaviour seen in autumn and winter, particularly social display activity, becomes less frequent and other behaviour, such as pursuit flights and rape, begins to appear.

If a male loses his mate at this stage, through mortality or some other means, there would appear to be three possible strategies open to him:

(i)   Abandon any further attempt at breeding for the season,

(ii)   Seek to form a pair bond with a second female,

(iii) Rely on promiscuous rape to father progeny.

The literature does not include an extensive study of marked individuals in the wild to provide evidence for these alternatives. These questions were examined in the present experiment using the field station population.

A number of paired mallards was first observed in an undisturbed group at the beginning of the nesting season. The females were then removed and the males were provided with 'strange' females. Would there be an increase in the frequency of promiscuous sexual activity performed by the males, or would the males attempt to form new pair bonds? If the latter alternative held, this might provide a valuable insight into the behaviour involved in courtship. It would be interesting to see if there was a resumption in social display activity, or if the males utilised other behaviour in courting the new females.

2.2. Methods

The experiment was conducted at the end of April and the beginning of May, using as the first group the same birds as those of the 'old female' observations of experiment 1. After the completion of experiment 1 in December, the males were reunited with their former mates, and the four pairs were kept in L. pen without further disturbance.

The design of the experiment was broadly similar to that of experiment 1. The males were observed (3-hour daily 'undisturbed' observations) for a few days in the presence of their mates, and then for a period after the 'old' females had been exchanged for an equal number of initially unfamiliar females. There were two modifications to the previous design. (i) The 'old' females were removed from the pen a few days prior to the start of the experiment and were replaced with four unfamiliar females.

The 'old' female observations were then initiated by the removal of the strange females and the replacement of the old mates. This was to ensure that both observation series were started in the same way, that is by the removal of the females currently present in the pen. This procedure would meet a criticism which could be levelled at the first experiment, that any difference in the behaviour of the males in the 'old' and 'new' female observations was simply due to the disturbance of the social structure of the group caused by changing the females.

(ii) The temporal sequence of observations in the 'old female' and 'new female' series was equalised; in each series the group was observed on five consecutive days. This allowed a more powerful statistical analysis of the data, a 2-way analysis of variance with ''old female' observations vs. 'new female' observations' as one factor and 'days after introduction of the females' as the other (WINER, 1973).

The experimental procedure was as follows:

April 21st: The resident ('old') females were removed and re-placed with four females with whom the males were unfamiliar.

April 26th: 9.00 a.m. The strange females were removed.

9.30 a.m. The 'old females' were reintroduced, and the group was observed until 12.30 p.m. (i.e. the first of the 'old female' observations, day 1).

April 27th-30th: Daily observations, each 9.30 a.m. to 12.30 p.m. (days 2-5).

May 3rd: 8.20 a.m. The resident females were removed. The four males were watched for an hour.

9.30 a.m. Four 'strange' females were introduced, and the group was observed until 12.30 p.m. (i.e. the first of the 'new female' observations, day 1). These females were unfamiliar with the males; they

were not the ones which were used from April 21st-
April 26th, nor those used in experiment 1. Pre-
vious to their introduction to L. pen they had been
kept on the main pond of the field station.

May 4th-8th: Daily observations, from 9.30 a.m. to 12.30 p.m.
(i.e. 'new female' observations, days 2-5).

The behaviour patterns recorded were the same as those in
experiment 1. Additional notes on the social behaviour and interactions
of the birds were made during each observation session.

2.3. Results

(a) The 'old female' observations

In contrast to the behaviour of these same four pairs in the pre-
vious autumn, the birds were never seen swimming or preening together in a
group. Each pair remained for most of the time in a particular area of
the pen; four fairly discrete 'home areas' could be defined, and social
interactions between members of different pairs were rare.

Social display was virtually non-existent. On day 2, Males 01
and 02 each gave a single grunt-whistle, but no further male displays were
recorded and the females never engaged in nodswimming.

Pair displays were also uncommon. One of the females performed
no inciting, the other three gave respectively 1, 3 and 11 brief bouts of
inciting (always addressed to their own mate) during the fifteen hours of
observation. The male mock-preen display was not recorded, and turn-back-
of-head occurred only in response to inciting. There was no doubt, however,
over the existence of four very firm pair bonds. The members of each pair
remained almost entirely within their home area, often swimming or standing
very close together and often engaged in the same activity.

Mates engaged in very little sexual behaviour. Male 02 and

Female 12 copulated twice, Male 01 and Female 11 once, Male 03 and Female
13 once, and the last pair not at all, during the five observations. One
of the females (Female 11) was laying during the experiment, and for the
early part of some of the observations she remained on her nest, which was
situated in her home area.

The only 'social' interactions between non-paired birds were
aggressive ones (including rape attempts). The males threatened, pecked
and chased each other (Tables III.8 and III.9), but there was no fighting.
There was no dominance hierarchy; Table III.15 shows that each male
directed at least one aggressive action towards each of the other males
during the five observations. In many cases two males would peck or chase
each other on the same day. The aggressive interactions of the males were
in fact indicative of some degree of territoriality. Each male was seen
to react aggressively towards any other male who entered his home area.
An aggressive encounter between two males was sometimes reversed a short
while later, when the former aggressor entered the home area of the other.

Several rape attempts were recorded in each observation period
(Table III.12). One, two or sometimes three males chased and attempted to
mount the mate of the other male. The mated male usually tried to prevent
the rape, by trying to keep his body between his mate and the would-be
rapist(s) and, occasionally, by pecking the pursuing male(s). On some
occasions one of the males succeeded in copulating with the female (and
performed post-copulatory displays), and sometimes the female managed to
evade the pursuing drakes until they gave up the chase. The rape attempts
invariably involved the males encroaching upon another pair's home area,
and it was on these occasions, during or more often after the actual rape
struggle, that many of the 'territorial' male-male aggressive encounters
occurred.

The data in Table III.11 indicate that the males often chased the
females; most of the chases occurred during the course of an apparent rape

pursuit. Threats and pecks directed against females (Table III.10) were seldom observed.

It should be mentioned that none of the males ever directed aggressive actions or rape attempts at his own mate, but each male chased and attempted to rape each of the other three females on at least one occasion during the five days. None of the females was ever seen to perform a single aggressive action throughout the experiment.

(b) Removal of the 'old females'

The behaviour of the males was observed for an hour between the removal of their original mates and the introduction of the 'new' females.

The males immediately left their home areas, and began to swim and walk over the whole area of the pen. Although the drakes often passed close to each other and sometimes even swam together for a while, no agonistic behaviour was seen. The males uttered intermittent slow Raeb calls.

(c) The 'new female' observations

There was virtually no sign of 'separation behaviour' by the males after the 'new' females were introduced. Only two or three Raeb calls were recorded on the first day, and none subsequently.

The social behaviour in the group differed markedly in several respects from that of the previous week. There was no indication of a persistence of the home areas. The males, and also the females, passed through all parts of the pen, and they did not appear to remain preferentially in any particular area. The males often swam fairly closely together, and also sometimes close to the females, and social activity of various kinds was recorded.

Social display

There were several sessions of social display. The analysis of variance (Tables III.6 and III.7) revealed a highly significant rise in the

<u>Experiment 2.</u>   Tables III.6 - III.12

Comparison of the social displays (Tables 6 and 7), aggressive actions (Tables 8 to 11) and rape attempts (Table 12) performed by the males in the 'old female' and 'new female' observations.

Each table shows:

1)   The frequency of the display or behaviour pattern given by each male on each observation day.

2)   The results of a comparison of group means by 2-way analysis of variance, the two factors being 'females' (old female observations vs. new female observations) and 'days' (observation days 1 to 5). For each factor and for the interaction the table shows the sum of squares (SS), the degrees of freedom (DF), the mean square (MS) and the F value (F).

The significance of the F value is represented by

$$* \quad p < 0.05$$

$$** \quad p < 0.01$$

$$*** \quad p < 0.001$$

Table III.6

Social displays: grunt-whistle and head-up-tail-up

DAILY FREQUENCIES		Grunt-whistle				Head-up-tail-up			
Males		01	02	03	04	01	02	03	04
	Days								
'Old female' observations	1	0	0	0	0	0	0	0	0
	2	1	1	0	0	0	0	0	0
	3	0	0	0	0	0	0	0	0
	4	0	0	0	0	0	0	0	0
	5	0	0	0	0	0	0	0	0
	Total	1	1	0	0	0	0	0	0
'New female' observations	1	18	2	1	0	10	7	0	1
	2	4	0	0	0	2	3	1	3
	3	12	0	2	2	1	9	2	1
	4	10	1	0	2	0	1	1	2
	5	6	3	2	6	2	8	2	8
	Total	50	6	5	10	15	28	6	15

ANALYSIS OF VARIANCE

Source of variation	SS	DF	MS	F	SS	DF	MS	F
Females	119.0	1	119.0	9.03**	102.4	1	102.4	19.88***
Days	15.7	4	3.9	0.30	21.4	4	5.34	1.04
Interaction	25.9	4	6.5	0.49	21.4	4	5.34	1.04
Error	395.3	30	13.2		154.5	30	5.15	
Total	555.8	39	14.3		299.6	39		

Table III.7

Down-up and total social displays

DAILY FREQUENCIES   Down-up   Total social displays

Males		01	02	03	04	01	02	03	04
	Days								
'Old female'	1	0	0	0	0	0	0	0	0
observa-	2	0	0	0	0	1	1	0	0
tions	3	0	0	0	0	0	0	0	0
	4	0	0	0	0	0	0	0	0
	5	0	0	0	0	0	0	0	0
	Total	0	0	0	0	1	1	0	0
'New female'	1	9	2	0	0	37	11	1	1
observa-	2	3	2	1	0	9	5	2	3
tions	3	4	1	3	1	17	10	7	4
	4	1	0	0	1	11	2	1	5
	5	4	1	3	7	12	12	7	21
	Total	21	6	7	9	86	40	18	34

ANALYSIS OF VARIANCE

Source of variation	SS	DF	MS	F	SS	DF	MS	F
Females	46.2	1	46.2	16.08[***]	777.4	1	774.4	20.16[***]
Days	12.2	4	3.04	1.06	121.3	4	30.3	0.79
Interaction	12.2	4	3.04	1.06	137.9	4	34.5	0.90
Error	86.3	30	2.88		1152	30	38.4	
Total	156.8	39			2186	39	56.1	

Table III.8

Male-directed aggression;   threats and pecks

<u>DAILY FREQUENCIES</u>   Threats   Pecks

Males		Threats				Pecks			
		01	02	03	04	01	02	03	04
	Days								
'Old female' observations	1	1	3	4	7	0	0	1	1
	2	2	0	1	0	1	0	0	0
	3	0	0	1	0	1	1	1	1
	4	1	2	2	0	1	3	1	0
	5	1	0	0	0	1	3	0	0
	Total	5	5	8	7	4	7	3	2
'New female' observations	1	12	2	1	1	6	0	1	0
	2	7	0	1	1	2	0	0	1
	3	14	0	1	0	9	0	0	0
	4	10	0	1	0	4	0	0	0
	5	16	0	2	4	5	0	1	2
	Total	59	2	6	6	26	0	2	3

<u>ANALYSIS OF VARIANCE</u>

Source of variation	SS	DF	MS	F	SS	DF	MS	F
Females	57.6	1	57.6	3.39	5.63	1	5.63	1.33
Days	28.2	4	7.04	0.42	6.15	4	1.54	0.36
Interaction	31.2	4	7.79	0.46	3.25	4	0.81	0.19
Error	509.0	30	16.97		126.75	30	4.23	
Total	625.9	39			141.78	39		

Table III.9

Male-directed aggression;   chases and total male-direoted aggressive actions

DAILY FREQUENCIES   Chases   Total

Males		01	02	03	04	01	02	03	04
	Days								
'Old female' observations	1	0	0	0	1	1	3	5	9
	2	1	0	0	0	4	0	1	0
	3	1	1	2	1	2	2	4	2
	4	1	4	2	0	3	9	5	0
	5	2	2	0	0	4	5	0	0
	Total	5	7	4	2	14	19	15	11
'New female' observations	1	9	1	0	2	27	3	2	3
	2	2	0	0	0	11	0	1	2
	3	8	0	0	0	31	0	1	0
	4	3	0	0	0	17	0	1	0
	5	12	0	0	0	33	0	3	6
	Total	34	1	0	2	119	3	8	11

ANALYSIS OF VARIANCE

Source of variation	SS	DF	MS	F	SS	DF	MS	F
Females	9.03	1	9.03	1.17	168.1	1	168.1	2.25
Days	12.25	4	3.06	0.40	95.0	4	23.8	0.32
Interaction	17.35	4	4.34	0.56	74.9	4	18.7	0.25
Error	230.8	30	7.69		2242	30	74.7	
Total	269.4	39			2580	39		

Table III.10

Female-directed aggression; threats and pecks

DAILY FREQUENCIES   .Threats   Pecks

Males		01	02	03	04	01	02	03	04
	Days								
'Old female'	1	0	1	0	0	0	0	0	0
observa-tion	2	0	0	0	1	0	0	0	1
	3	0	0	0	0	0	2	0	0
	4	0	0	0	0	0	0	0	0
	5	0	0	0	0	0	0	0	0
	Total	0	1	0	1	0	2	0	1
'New female'	1	0	0	0	0	0	0	0	0
observa-tion	2	3	0	0	0	0	0	0	0
	3	3	0	1	0	1	0	0	0
	4	1	0	0	1	2	0	0	1
	5	5	0	0	0	0	0	1	0
	Total	12	0	1	1	3	0	1	1

ANALYSIS OF VARIANCE

Source of variation	SS	DF	MS	F	SS	DF	MS	F
Females	3.60	1	3.60	3.17	0.10	1	0.10	0.37
Days	1.35	4	0.33	0.29	0.90	4	0.23	0.84
Interaction	2.65	4	0.66	0.58	1.40	4	0.35	1.31
Error	34.0	30	1.13		8.00	30	0.27	
Total	41.6	39			10.40	39		

Table III.11

Female-directed aggression; chases and total female-directed aggressive
actions

DAILY FREQUENCIES		Chases				Total			
Males		01	02	03	04	01	02	03	04
Days									
'Old female' observations	1	2	7	13	11	2	8	13	11
	2	2	2	1	2	2	2	1	4
	3	3	4	10	2	3	6	10	2
	4	0	7	13	3	0	7	13	3
	5	1	2	5	0	1	2	5	0
Total		8	22	42	18	8	25	42	20
'New female' observations	1	16	53	19	58	16	53	19	58
	2	3	1	1	11	6	1	1	11
	3	7	3	3	8	11	3	4	8
	4	8	0	0	3	11	0	0	5
	5	4	0	6	1	9	0	7	1
Total		38	57	29	81	53	57	31	83

ANALYSIS OF VARIANCE

Source of variation	SS	DF	MS	F	SS	DF	MS	F
Females	275.6	1	275.6	4.67*	416.0	1	416.0	6.46*
Days	2385	4	596.3	10.11***	2148	4	537.1	8.34***
Interaction	1340	4	335.1	5.68**	1183	4	296.0	4.59**
Error	1769	30	58.98		1932	30	64.4	
Total	5770	39			5681	39		

Table III.12

Rape attempts

DAILY FREQUENCIES

Males		01	02	03	04
	Days				
'Old female' observa- tions	1	1	3	6	5
	2	1	1	0	1
	3	2	1	3	1
	4	0	4	4	1
	5	1	0	2	0
	Total	5	9	15	8
'New female' observa- tions	1	8	26	7	26
	2	1	0	1	3
	3	2	1	3	3
	4	2	0	0	1
	5	1	0	2	1
	Total	14	27	13	34

ANALYSIS OF VARIANCE

Source of variation	SS	DF	MS	F
Females	65.03	1	65.03	5.02[*]
Days	514.0	4	28.5	9.92[***]
Interaction	278.6	4	69.65	5.37[**]
Error	388.8	30	12.96	
Total	1246	39		

frequencies of the three major displays over the 'old female' observations, with no main effect of nor interaction with the factor 'days after introduction of the females'.

The males displayed in the face of very little active participation of the females. No nodswimming was recorded, and only one of the 'new' females showed any sign of interest in the males:

Female 32 was the only female to address inciting or sexual behaviour to a male (see below).

Female 31 had recently lost her clutch of eggs, which she had been incubating (they had been taken to the incubator two days previously). She exhibited repulsion behaviour towards any bird who approached her, and spent much of the time swimming along one side of the pen, apparently trying to get out.

Females 33 and 34 mostly swam around together, exhibiting some homosexual behaviour (see below).

The relative proportions of the three major displays performed by the males are shown in Table III.13. There was a large variation between individuals in this measure, but the percentages were based on fairly low frequencies. These data are compared with those obtained in experiment 1, and also with those of JOHNSGARD (1960a) who published overall monthly figures for the display frequencies in a 'semi-tame' flock of mallards in New York.

The overall display proportions obtained in experiment 1 (October 21st-December 6th) are not strikingly different from those of JOHNSGARD for the month of November. Both studies find the grunt-whistle to be the most frequent and the head-up-tail-up the least common display. JOHNSGARD records a seasonal variation in the relative proportions of the three dis﹣ plays, but by April (the last month for which he presents data) the proportions are approximately similar to the November levels. In experiment 2

Table III.13

Experiment 2.   Relative proportions of the social displays grunt-whistle
(GW), head-up-tail-up (HU) and down-up(DU) given by the males.   The table
shows the numbers of displays given by each male, and each display is
expressed as a percentage of the total.   For comparison the corresponding
data from Experiment 1 ('old female' and 'new female' observations com-
bined) are shown, and also the data presented by JOHNSGARD (1960a) for
seasonal variation in the proportions of displays in a mallard population
in New York.

Male		01			02			03			04			All Males		
Display		GW	HU	DU	GW	HU	DU	GW	HU	DU	GW	HU	DU	GW	HU	DU
Expt.1 (Nov.)	No.	134	72	69	61	61	58	80	52	68	57	51	84	332	236	279
	%	49	26	25	34	34	32	40	26	34	30	27	44	39	28	33
Expt.2 (May)	No.	50	15	21	6	28	6	5	6	7	10	15	9	71	64	43
	%	58	17	24	15	70	15	28	33	39	29	44	27	40	36	24

JOHNSGARD (1960a)

		GW	HU	DU
September	No.	40	35	20
	%	42	37	21
October	No.	279	185	163
	%	45	29	26
November	No.	379	202	239
	%	46	25	29
December	No.	170	95	187
	%	38	21	41
January	No.	59	19	90
	%	35	11	54
February	No.	150	71	212
	%	35	16	49
March	No.	102	41	101
	%	42	17	41
April	No.	74	46	49
	%	41	26	33

Table III.14

Experiment 2. Addressees of the social displays (grunt-whistle and head-up-tail-up combined) of the males in the 'new female' observations. The table shows the number of displays addressed to each female and the number for which the addressee was not determined ('X').

Male	01					02					03					04				
Addressee	Females 31 32 33 34				X	Females 31 32 33 34				X	Females 31 32 33 34				X	Females 31 32 33 34				X
Observation Day																				
1	0	13	9	4	2	0	3	4	0	2	0	0	0	0	1	0	0	0	0	1
2	0	2	1	0	3	0	0	0	0	3	0	1	0	0	0	0	0	0	2	1
3	0	11	0	0	2	0	5	0	0	4	0	2	0	0	2	0	1	0	0	2
4	0	10	0	0	0	0	0	0	0	2	0	0	0	0	1	0	1	0	3	0
5	0	6	0	0	2	0	2	0	0	9	0	1	0	1	2	0	0	0	10	4
Total	0	42	10	4	9	0	10	4	0	20	0	4	0	1	6	0	2	0	15	8

(May 3rd-7th) the grunt-whistle was still the most frequently occurring display, but in contrast to JOHNSGARD head-up-tail-ups are more common than down-ups.

The addressees of the grunt-whistle and head-up-tail-up displays performed by the males in the 'new female' observations are shown in Table III.14. Male 01 addressed displays to three females on the first day, but by the third day he displayed only to Female 32. Males 02 and 03 also displayed chiefly to Female 32, whilst Male 04 addressed most of his displays to Female 34. No displays were addressed to Female 31.

Pair displays and sexual behaviour (excluding rape)

The pair displays and sexual behaviour are not tabulated but may be summarised briefly. The pair displays mock-preen (male), turn-back-of-head (male) and inciting (female), and the sexual behaviour head-pumping and copulation (both sexes) all occurred at a fairly low rate, not significantly different from the 'old female' observations.

On day 1 Male 01 addressed six bouts of turn-back-of-head to Female 33 and sixteen bouts of head-pumping to Female 32. No other pair displays or sexual behaviour occurred on the first day.

Subsequently pair displays and sexual behaviour were exhibited by four individuals. Female 32 addressed 4 to 8 bouts of inciting per day to Male 01, some but not all of which were accompanied by the male turn-back-of-head to Female 32. These two birds gave occasional head-pumping displays, and on two such occasions a copulation resulted.

Females 33 and 34 gave occasional bursts of inciting and head-pumping, addressed to each other.

Aggression directed against males

It soon became apparent that a stable, linear dominance hierarchy had arisen amongst the males (see Table III.15). The descending rank order was Male 01, Male 03, Male 04, Male 02; the table shows that almost

Table III.15

Experiment 2.   Aggressive exchanges between the males.
The table shows the number of aggressive actions (threats, pecks and chases combined) directed by each male (the 'aggressor') to each of the other males (the 'recipient').   The figures are total frequencies for each observation series.

'Old female'
observations

		Recipient Male			
		01	03	04	02
	01		3	1	10
Aggressor Male	03	1		6	8
	04	7	1		3
	02	6	7	6	

'New female'
observations

		Recipient Male			
		01	03	04	02
	01		41	30	48
Aggressor Male	03	0		7	1
	04	0	0		11
	02	3	0	0	

Figure III.7

Experiment 2.   Analysis of variance, interaction profiles.

a. Female-directed chases
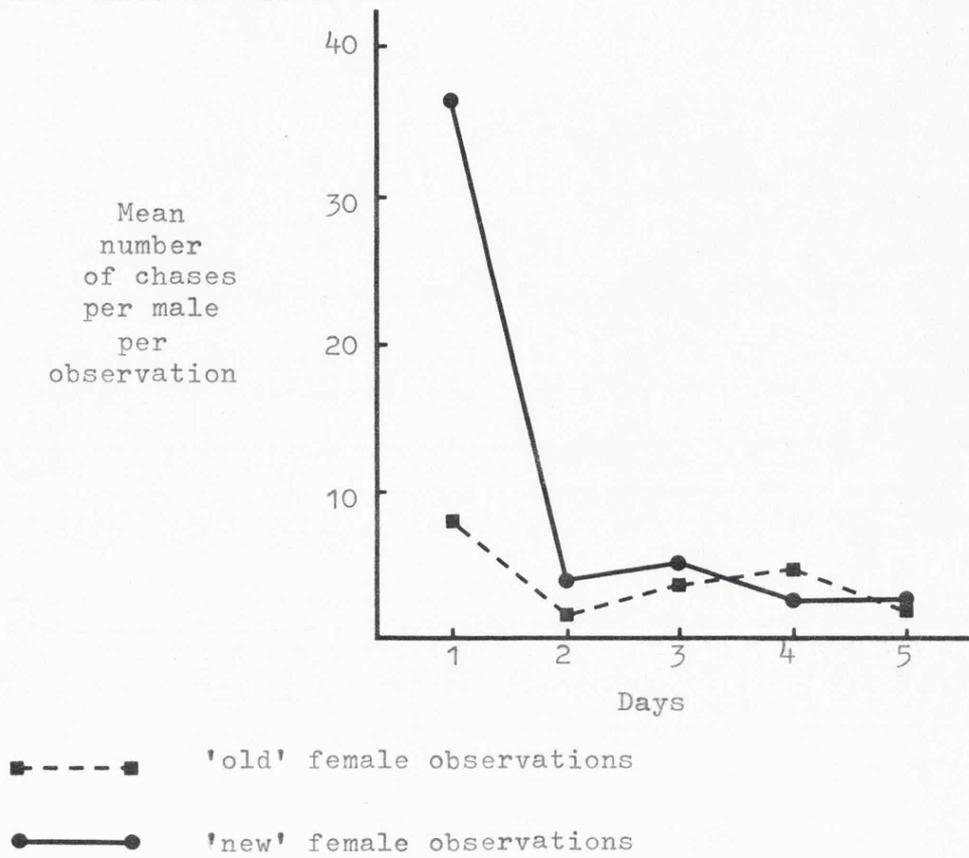
b. Rape attempts
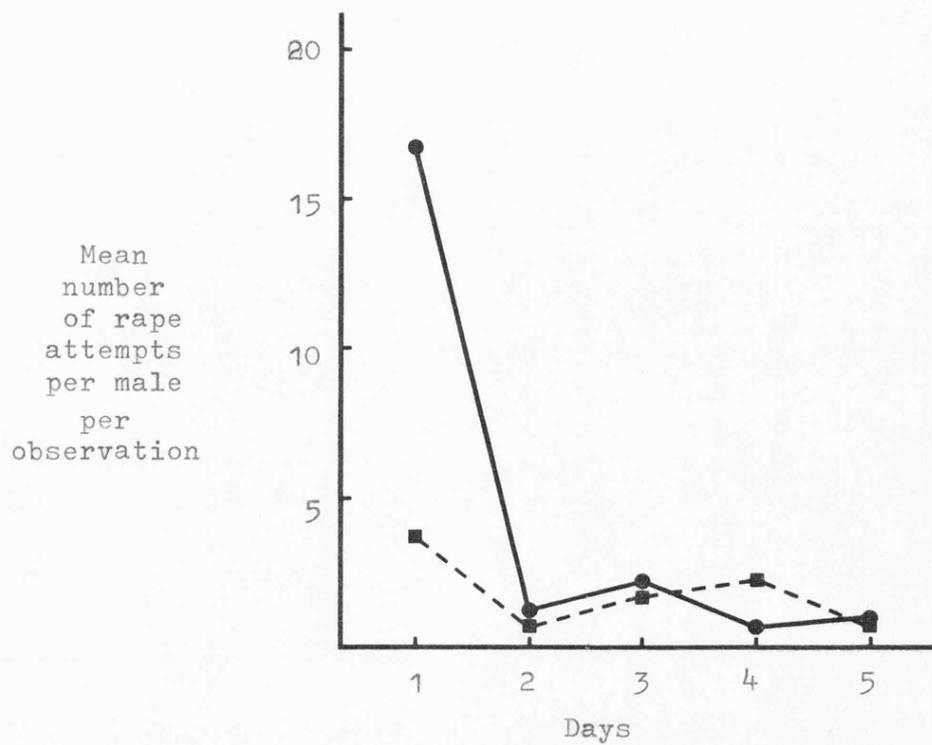
without exception the males were not aggressive towards those of higher

rank. The only exception occurred early on day 1, when Male 02 threatened

Male 01 three times.

The analysis of variance revealed no significant differences in

the frequencies of any of the male-directed aggressive actions in the 'old

female' and 'new female' observations (Tables III.8 and III.9). It is

obvious from the individual scores, however, that Male 01 (the male who

became dominant) exhibited a substantial increase in aggressiveness in the

second series of observations, whereas the other three males showed, if

anything, a slight decrease.

There was no fighting between the males, and none of the 'new

females' performed any aggressive actions.

Aggression and rape attempts on females

Few female-directed threats and pecks were performed by the males

(Table III.10) and the frequencies of these actions were not significantly

different from those in the 'old female' observations. Chasing of females

was comparatively more frequent than threatening or pecking, as in the

first observation series.

The analysis of variance revealed a significant interaction for

both female-directed chasing (Table III.11) and rape attempts (Table III.12).

The profiles of these interactions are shown in Figure III.7, and the source

of the interactions is immediately clear.

On day 1 of the 'new female' observations the frequencies of both

chasing and attempted rape were extremely high, but both subsequently fell

to similar levels to those of the 'old female' observations. There was no

such massive peak on the first day of the 'old female' observations, al-

though the mean frequencies of chasing and rape attempts were very slightly

higher on day 1 than on subsequent days.

On day 1 of the 'new female' observations Male 01 chased and

attempted to rape all four of the females, but on days 2-5 he did not

chase or rape Female 32. The other three males chased and tried to rape

all four females throughout. For the five observations combined, 20 rape

attempts were directed at Female 31, 31 at Female 32, 14 at Female 33 and

23 at Female 34.

2.4. Discussion

(a) Social behaviour in a group of paired birds in the spring

The social behaviour during the 'old female' observations pro-

vided in many respects a striking contrast to the behaviour of the same

birds in the autumn (experiment 1).

There was virtually no social display in the spring observations,

even immediately after the re-introduction of the resident females on day 1.

These findings are in agreement with studies of wild or semi-wild popula-

tions, in which only sporadic social display occurs at this time of year

(WEIDMANN, 1956; BEZZEL, 1959; JOHNSGARD, 1960a; RAITASUO, 1964). It

has already been remarked, however, that a wild flock will have begun to

disperse to breed at this time; it is noteworthy that the highly crowded

conditions in which the birds were here observed do not facilitate the

occurrence of social display in paired birds in April.

Secondly, the female inciting display was of rare occurrence in

the spring group, compared with the regular performance of this display by

the paired females in October. It is true that close social encounters

between pairs, which may release the display, were largely avoided by the

confinement of the birds to their home areas, but even after rape attempts

inciting was rarely observed. Perhaps by this advanced stage in the

season the affirmation of a paired female's preference is unnecessary, or

is provided by other behaviour.

The stable dominance hierarchy which characterised the October-

November observations had clearly broken down by the end of April. The

dominance hierarchies in the captive groups of mallard observed by DES-
FORGES (1974) persisted throughout the year, but these birds were kept at
a much greater density than the L. pen group, which may have prevented the
establishment of home areas by each pair.

It is important to emphasise that the occupation of the home
area, and the aggressive behaviour of the male towards other birds within
this area, ceased abruptly (within minutes) after the removal of the fe-
males. Thus the territoriality of the males did not extend to a site
attachment as demonstrated by SEYMOUR (1974c) in breeding shovellers, but
the males seemed rather to be occupying and defending an area around their
mates. The subject of 'territorial' behaviour in mallards is duscussed
further in Chapter VI.

A final comparison with experiment 1 also concerns the behaviour
of the males after the removal of their original mates. In the current
experiment the drakes did not exhibit 'separation behaviour' after the 'new'
females were introduced, whereas in November persistent Raeb vocalisations
had been recorded for at least a day, much longer in some of the males.
It appears that late in the season the drakes are not willing to spend time
in searching for their lost mates when there are other unaccompanied fe-
males present to whom their attentions could be directed.

(b) Social behaviour after the introduction of the 'new females'

The behaviour of the males in the 'new female' observations
differed substantially from their behaviour in the presence of their mates,
and resembled in some respects the social behaviour seen in the autumn ex-
periment. Most importantly there was an immediate disappearance of home
areas, a reformation of the dominance hierarchy and a resumption of social
display.

These behavioural changes clearly resulted from the loss of the
paired status of the drakes. It might logically be deduced that the

social display of the drakes represented courtship of the unfamiliar fe-
males for the purpose of establishing new pair bonds.   This conclusion
cannot be stated with certainty, however.   The observed behaviour may
simply reflect the resumption of the flock structure of the group.   The
hypothesis of LEBRET (1961), that male social displays serve as a substi-
tute for overt aggression, might be invoked here.   Close encounters be-
tween males were undoubtedly more frequent in the second series of observa-
tions, although there was no general increase in male-directed aggressive
behaviour.

The artificial situation created for this experiment reveals the
great flexibility of mallard social behaviour.   It is clearly quite within
the capacity of the ducks to exhibit, part way through the breeding season,
a social pattern characteristic of a much earlier period.

Although all four males performed social displays, the females
did not give nodswimming, and only one of them showed any indication of a
sexual interest in the drakes.   The majority of the males' displays were
addressed to this female.   A few displays were addressed to the two homo-
sexual females, but none to the female who exhibited repulsion behaviour.
It could be argued that the drakes considered this female an inappropriate
object for courtship, perhaps as a direct result of her repulsion displays.

There was ample evidence that Male 01 and Female 32 soon formed
a pair bond, exhibiting behaviour more similar to that of the autumn pairs
than to that of the pairs in the April 'old female' observations.   The fe-
male incited to the male, sexual behaviour was performed by both birds ex-
clusively with each other, and after the female had demonstrated her pre-
ference on day 2 the male addressed all his social displays and turn-back-
of-head to her as well.   Male 01 did not attempt to rape Female 32 after
the first day (a feature which characterised the paired birds in the 'old
female' observations).   The other three males did not develop personal
relationships with the new females, though this result may well have been

different if more than one of the introduced females had been 'receptive'.

That the drakes probably did seek to establish new pair bonds after their original mates were taken away, is compatible with the finding that they apparently did not invest a greater amount of time in pursuing the alternative breeding strategy, that of promiscuous rape. Apart from the first day that the 'new' females were introduced, the daily frequencies of rape attempts remained at the same level as that of the 'old female' observations.

On the first day of the 'new female' observations, most of the attempted rapes occurred in fact during the first half hour after the introduction of the females. This appears to be a common response of males towards unfamiliar females at this time of year. FIELD (1970) also described intense chasing and raping behaviour when strange females were introduced to all-male groups of mallard in April and May.

In the 'new female' observations the drakes attempted to rape all the females, including Female 31 whose repulsion behaviour persisted through-out the week. Some authors (e.g. McKINNEY, 1975a; CRAMP & SIMMONS, 1977) have assumed that repulsion behaviour functions in discouraging males from pursuit or rape, as implied by the name given to the display and the fact that it is usually restricted to females who are or have recently been in-cubating (WEIDMANN, 1956; LEBRET, 1961; RAITASUO, 1964). Other workers, however, have suggested the reverse, that repulsion behaviour might actually attract males to chase (PHILLIPS & van TIENHOVEN, 1962; ABRAHAM, 1974; see further discussion in Chapter VI). In the present experiment the be-haviour of Female 31 appeared to have neither effect - this female was not immune from rape pursuits, nor was she chased more often than the other females. Of course the relatively crowded conditions in the pen might have reduced any tendency of the males to select rape victims (apart from not raping their own mates), but the males probably recognised the con-dition of Female 31 because they did not address her during social display.

III.3.   EXPERIMENT 3

3.1.   Introduction

Mallard social display is, of course, basically a social activity.
A displaying group will often be joined by other males who are nearby, and
in the wild a male performing displays with no other drakes present is an
extremely rare occurrence (e.g. RAITASUO, 1964).

McKINNEY (1975a), in support of an argument for a classical
'courtship' role of social display, is of the opinion that the existence of
group sessions can be explained in terms of the non-social interests of the
individuals concerned.   He theorised that drakes will join an ongoing dis-
play session because it is likely that the males already displaying have
discovered a female who may be a potential mate.

This interpretation, if correct, implies that there is no in-
trinsic reason why a single male should not address social displays to a
female even if no other males are present.   This situation is, of course,
unlikely to occur in the field, where mallards live in flocks throughout
the display season, and any drake displaying alone would soon attract others.
The hypothesis can, however, be tested at the field station, where a male
and a female can be separated from other conspecifics.

The behaviour of an isolated male and female could be sampled if
they were watched for long enough in an 'undisturbed' state, but if social
display was to occur this event could probably be advanced by the technique
of introducing a female to an isolated drake.

If social display does occur in such an experiment, would the
three major displays be given with similar relative frequencies to their
occurrence in group sessions?   It might be postulated that the down-up would
not be performed by a single male;   this display is often associated with
aggressive interactions between males (Section I.3.4).

deLANNOY (1967) has described displays performed by captive

mallard drakes in the absence of other males. One such individual never gave down-ups, and another was recorded as giving 91 grunt-whistles, 59 head-up-tail-ups and a single down-up. These birds, however, had been reared and were observed in unnatural conditions of partial isolation from conspecifics. The first drake was reared in a pen with two mallard females and the second with only a pair of pochard (Netta rufina). These abnormal rearing conditions might have restricted the development of a complete behavioural repertoire. Social display has not yet been described in socially-reared mallards which were tested later in the absence of conspecific males.

In this experiment mallard drakes were housed singly and, for comparison, in groups of two and four, and their behaviour was observed on the introduction of females.

3.2. Methods

Social display was studied in six adult male mallards. Each male was observed in four experimental situations.

(a) Four-male situation; four drakes were kept together in a pen, and were observed on the introduction of a single female.

(b) Two-male situation; two males were kept together, and observed on the introduction of a female.

(c) One-male one-female situation; a male was kept in isolation, and observed on the introduction of a single female.

(d) One-male two-females situation; two females were introduced simultaneously to an isolated male.

Four tests were made of each male in each situation. The observations were made by introducing a female (or two females) to the male(s); all social displays given by the male(s) were recorded for 15 minutes, after which the female(s) were removed.

For the four-male and two-male tests the six drakes were first divided into two groups, one of four and one of two. After a number of observations the males were re-arranged so that two of the males in the original group of four now comprised the group of two. Finally the groups were re-arranged so that the remaining two drakes were observed as the two-male group. For the single-male observations each drake was isolated and subjected to four separate introductions of one female (a different female was used each time) and four introductions of two females.

The experiment took several days to complete. The males were kept overnight in groups with females present, and during the day they were kept in the observation pens (E. and W. pens were used) in their appropriate all-male groups. About 1½ hours was allowed between each observation of the same group.

The six males were familiar with each other before the start of the experiment, and were also familiar with all the females used, but personal relationships e.g. pair bonds were not examined. The experiment was conducted in December, and the birds were in their first year.

3.3. Results

Tables III.16 and III.17 list the displays given by the six drakes in each experimental situation. Analysis of variance (single factor analysis of variance with repeated measures; WINER, 1973) revealed that the frequency of each display was significantly different in the different situations.

The results are illustrated in Figure III.8, which shows the mean number of displays per male under each condition. The profiles of the three displays were drawn on the same graph to show their relative frequencies in the different situations. Tests were made for the significance of the differences between pairs of means (for grunt-whistles, head-up-tail-ups and down-ups in turn) by the Newman-Keuls method (WINER, 1973).

Social displays: analysis of variance

1.   Summary of data

The table shows the number of displays given by each male in the four observations in each experimental situation;

4M: four-male situation

2M: two-male situation

1M1F: one-male one-female situation

1M2F: one-male two-females situation

2.   Analysis of variance

The data for each display in turn were analysed by single-factor analysis of variance with repeated measures.   For the partition of the variation the table shows the sum of squares (SS), degrees of freedom (DF), mean square (MS) and F ratio (F).   In all three cases the F ratio was significant ($p < 0.01$, **).

Table III.16

Summary of data

Experi-mental situation	Grunt-whistles				Head-up-tail-ups			
	4M	2M	1M1F	1M2F	4M	2M	1M1F	1M2F
Male 225	20	9	5	10	24	25	3	6
247	22	19	0	8	27	22	0	0
228	22	25	0	5	23	30	0	3
242	12	8	2	5	15	18	1	2
213	18	2	3	7	44	8	4	5
234	11	0	0	6	13	0	0	8
Total	105	63	10	41	146	103	8	24

Analysis of variance

Source of variation	SS	DF	MS	F	SS	DF	MS	F
Between subjects	241.4	5			299.7	5		
Within subjects	1189.3	18			3135.3	18		
Exper. sit'ns	797.5	3	265.8	10.18	2137.5	3	712.5	10.71
Residual	391.8	15	26.1	**	997.8	15	66.5	**
Total	1430.6	23			3434.9	23		

Table III.17

Summary of data

Down-ups.

Experimental situation		4M	2M	1M1F	1M2F
Male	225	17	14	0	0
	247	11	10	0	0
	228	21	12	0	0
	242	16	11	0	0
	213	18	0	0	0
	234	9	0	0	1
Total		92	47	0	1

Analysis of variance

Source of variation	SS	DF	MS	F
Between subjects	94.3	5		
Within subjects	1163.0	18		
Exper.situations	962.3	3	320.8	23.9
Residual	200.7	15	13.4	**
Total	1257.3	23		

Figure III.8

Experiment 3. Social displays of the males.

a. Frequency of displays in the different experimental situations
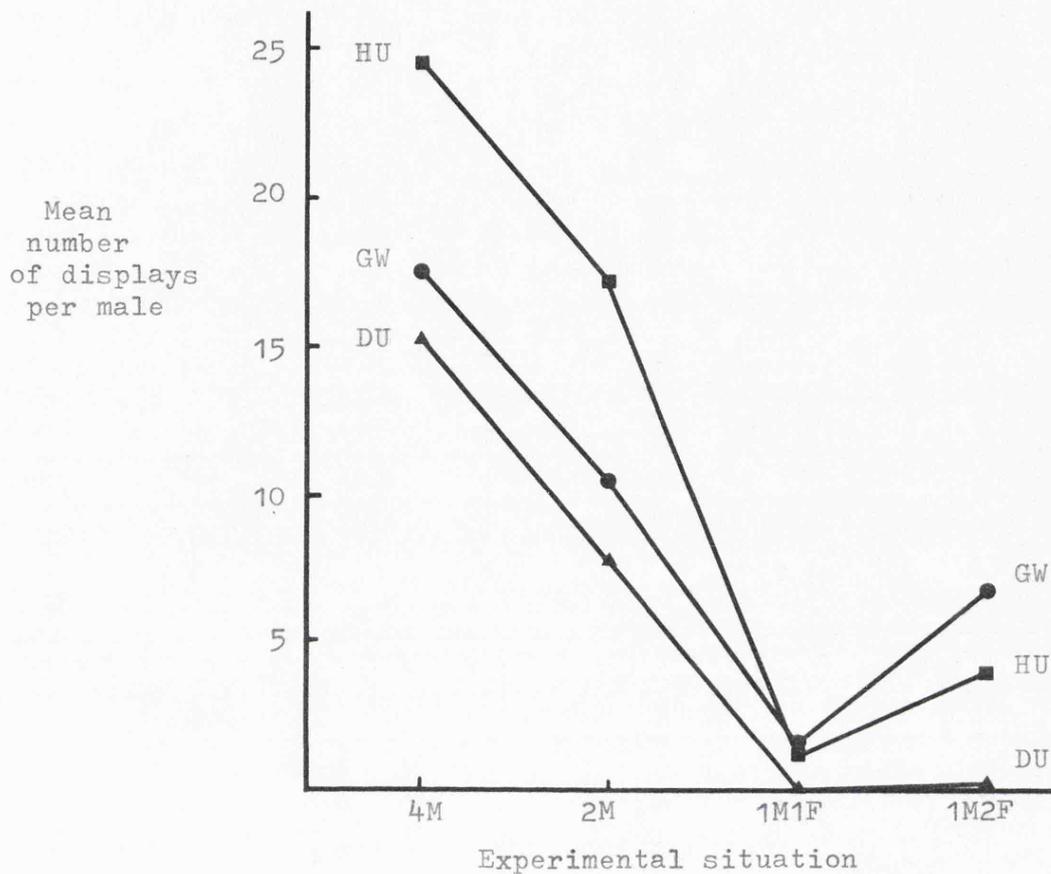
b. Pairs of means significantly different at the 1% level

Grunt-whistle (GW):   4M ** 1M1F;   4M ** 1M2F.

Head-up-tail-up
             (HU):   4M ** 1M1F;   4M ** 1M2F.

Down-up (DU):   4M ** 1M1F;   4M ** 1M2F; 2M ** 1M1F;   2M ** 1M2F.

Clearly the display rate was higher when a larger number of drakes was present. The difference between the four-male and two-male situations was not significant, but the males gave significantly more grunt-whistles, head-up-tail-ups and down-ups in four-male groups than in either of the single-male situations, and significantly more down-ups in the two-male groups than when they were displaying alone.

Some displays were recorded in the single-male observations. These were almost entirely grunt-whistles and head-up-tail-ups; of a total of 84 displays given by males displaying on their own only one down-up was recorded. There was a tendency for more grunt-whistle and head-up-tail-up displays to be given when two females were introduced to a single male than when one female only was introduced, but the Newman-Keuls procedure did not find the means to be significantly different.

The data revealed a difference in the relative frequency of grunt-whistles and head-up-tail-ups in the different situations. When the drakes were displaying in groups of two and four head-up-tail-ups were more common than grunt-whistles, but the grunt-whistle was the most abundant display given when the males were displaying alone.

3.4. **Discussion**

This experiment has demonstrated that a mallard drake observed under controlled conditions will perform social displays in the absence of other males. It is clear that social facilitation is provided by other drakes, since higher display frequencies were recorded in groups of more than one male. This may be due to competition between the drakes for the attentions of the female, as proposed by McKINNEY (1975a). Nevertheless, this social aspect is not a pre-requisite for a male to address grunt-whistle and head-up-tail-up displays to a female.

This finding is consistent with the hypothesis that the displays are used in courtship. For the grunt-whistle and head-up-tail-up at

least, the data do not support the suggestion of LEBRET (1961) that social
displays result only from interactions between males. The situation with
the down-up, however, is somewhat different. As in the green-winged teal
(McKINNEY, 1975a), it appears that a mallard drake will not perform down-
ups unless other males are present. The functional significance of the
down-up is discussed further in Chapter VI.

The higher relative frequency of the grunt-whistle in the display
repertoire of a single male, compared with the group situations, is in
agreement with other analyses of mallard social display. Several authors
(WEIDMANN, 1956; JOHNSGARD, 1960a; deLANNOY, 1967; FIELD, 1970) have
produced evidence that the grunt-whistle is more common than the other two
as an isolated display given by a single male during a group session.
Head-up-tail-ups and down-ups, on the other hand, are more characteristic
of bursts in which several drakes display simultaneously.

CHAPTER IV

ADMINISTRATION OF TESTOSTERONE TO JUVENILE MALES

IV.1. INTRODUCTION

Androgens have long been implicated in the control of male
reproductive behaviour in birds. The early work in this field has been
reviewed by BULLOUGH (1945), BEACH (1948), COLLIAS (1950) and YOUNG (1961).
Courtship and mating behaviour in the adult male are abolished by castra-
tion, but may be reinstated by the administration of exogenous androgen,
and injections of androgens will also induce precocious sexual behaviour
in immature birds.

The peripheral application of testosterone, usually by intra-
muscular injection or subcutaneous implantation, has been found to elicit
sexual responses in the males of a number of species. These include the
wood pigeon (ERPINO, 1969; MURTON et al.,1969), the ring dove (ERICKSON
et al., 1967; MARTINEZ-VARGAS, 1974), the turkey (SCHEIN & HALE, 1959),
the domestic fowl (ANDREW, 1975a,b), the budgerigar (BROCKWAY, 1974), the
Japanese quail (ADKINS & ADLER, 1972) and the zebra finch (ARNOLD, 1975).

Experiments involving intracranial implantation of testosterone
(e.g. BARFIELD, 1969, 1971; HUTCHINSON, 1970) indicate that the site of
action of the hormone is the preoptic and anterior hypothalamus. It has
been suggested that androgen binding to receptors on steroid-specific tar-
get cells in these regions is the initial stage in the activation of male
reproductive behaviour (HUTCHINSON, 1976), although there is as yet no
direct evidence linking steroid binding with behavioural mechanisms.

For a recent comprehensive survey of the neural and endocrine
control of avian courtship and sexual behaviour the reader is referred to
CREWES & SILVER (1979).

Evidence concerning the endocrine basis of social display in
ducks is available from two different lines of investigation:
a) comparison of seasonal variations in hormone levels and behaviour fre-
    quencies.

b) effects of the administration of exogenous hormones.

a) <u>Seasonal variations in hormone levels and behaviour frequencies</u>

From intensive studies of social behaviour in wild mallard populations (see Chapter I) it has been established that social display occurs from early autumn through to the beginning of the breeding season in spring. There are usually two peaks in display frequency separated by a reduction in activity at the height of winter, although the timing of the peaks varies between different populations.

Early work relating seasonal variations in behaviour and hormone levels relied on an indirect estimation of hormone secretion obtained from histological examination of the testis. Spermatogenesis in the testis tubules is confined to the spring period (HÖHN, 1947; JOHNSON, 1966) but the interstitium is active during the autumn. HÖHN (1947) reported that the number of interstitial (Leydig) cells was minimal only during July and August, and they began to increase in the early autumn. This finding led HÖHN to suggest that the autumnal social display of the mallard was controlled by the secretion of the Leydig cells, presumably androgen.

It is now known that the Leydig cells produce androgen, as a result of stimulation by the pituitary gonadotrophic hormone Luteinizing Hormone (L.H.) (e.g. BROWN et al., 1975). It has also recently become possible to measure seasonal fluctuations in the secretion of these hormones directly; gas chromatography and radioimmunoassay techniques have allowed the estimation of hormone concentrations circulating in the plasma. The annual cycles of gonadotrophin and steroid hormone secretion in wild and domestic ducks have been studied by a number of workers (see review by FARNER & FOLLETT, 1979).

In wild mallards the major peak in plasma L.H. in males occurs in the spring, but there is also a resurgence of L.H. secretion in the autumn (HASSE, SHARP & PAULKE, 1975a; DONHAM, DANE & FARNER, 1979). These

studies demonstrated some individual variation in the precise timing of the autumnal rise, but in females there is no increase in L.H. concentration above basal levels until the onset of the laying period (DONHAM et al., 1979).

Similarly, plasma testosterone in wild mallard drakes also reaches its highest concentration in spring, with a secondary peak in the autumn (PAULKE & HASSE, 1978). In the opinion of these authors the linear correlation of the seasonal cycles of L.H. and testosterone provides confirmation of the stimulatory effect of L.H. on androgen secretion by the Leydig cells. The deferral of spermatogenesis until the spring has led HASSE et al. (1975a) and DONHAM et al. (1979) to agree with HÖHN (1947) that the function of the autumnal androgen secretion in the male is the facilitation of social display.

GORMAN (1974, 1977) believes that the courtship display of the male eider is controlled by androgen. He was able to demonstrate a significant correlation between the annual cycle of display frequency and the abundance and enzymic activity of the Leydig cells (GORMAN, 1974), although there was no quantitative correlation of display frequency and circulating androgen levels (GORMAN, 1977).

The only other wild duck species to have been investigated in this way is the teal, in which autumnal increases in L.H. and testosterone secretion have been confirmed (JALLAGEAS, TAMISIER & ASSENMACHER, 1979), but extensive endocrine data have been produced for various domestic breeds of the mallard.

ASSENMACHER (1974) considers that domestication of the mallard has not changed the general course of the annual reproductive cycle, and the seasonal changes in hormone levels appear to be basically similar to those occurring in wild birds. Vernal and autumnal peaks in L.H. secretion have been reported in Pekin ducks (JALLAGEAS et al., 1979) and in Khaki-Campbells (HASSE et al., 1975b). Similarly, plasma testosterone reaches high

concentrations both in the spring and in the late summer-early autumn in Pekins (GARNIER & ATTAL, 1970; GARNIER, 1971; JALLAGEAS et al., 1979), Khaki-Campbells (PAULKE & HASSE, 1978) and Rouen drakes (BALTHAZART & HENDRICK, 1976).

Again there is some individual variation in the timing of the maxima, and the autumnal secretion of testosterone is sometimes characterised by multiple peaks (GARNIER, 1971; PAULKE & HASSE, 1978).

Slight differences in hormonal patterns may exist between wild and domestic forms. In a comparative study of wild mallard and Khaki-Campbell drakes, PAULKE & HASSE (1978) recorded higher absolute concentrations of testosterone, and seasonal fluctuations of smaller amplitude, in the domestic breed. Game-farm mallards also appear to have higher circulating levels of testosterone than those of truly wild stock (DONHAM et al., 1979).

A study of the daily variations in behaviour frequencies and plasma testosterone levels in the Rouen duck (BALTHAZART, 1976a) has revealed a reasonably close fit of testosterone fluctuations with those of both sexual behaviour and social display. This correlation does not necessarily demonstrate a causal link, but one possible explanation of the result is that there is a direct, short-term effect of testosterone on the behaviour patterns mentioned.

Most authors are of the opinion that social display in male ducks is controlled by testosterone, but this conclusion has been questioned. BALTHAZART & HENDRICK (1976) made regular behavioural observations and assays of plasma testosterone and follicle-stimulating hormone (F.S.H.) in five male Rouen ducks, over a ten-month period. They found that the seasonal cycles of both hormones correlated with frequencies of sexual behaviour, but the seasonal variation in social display frequency correlated more closely with F.S.H. than with the steroid. These data, together with other results (see next section) have led these authors to

suggest that social display may depend on high circulating levels of F.S.H. rather than of testosterone. Furthermore the highest testosterone concentration was reached in March, coincident with the decline in social display activity in the experimental birds, from which BALTHAZART & DEVICHE (1977) postulate that testosterone could in fact play a part in the termination of social display in the spring.

b) **Effects of exogenous hormones**

Several authors have demonstrated that exogenous testosterone has a strong stimulatory effect on male sexual behaviour, that is the behaviour patterns directly associated with copulation.

Wild mallard ducklings injected with testosterone propionate (PHILLIPS & McKINNEY, 1962; ETIENNE, 1964) gave pre-copulatory head-pumping and mounting attempts. Copulatory behaviour in adult male mallards was abolished by castration (ETIENNE & FISCHER, 1964) but some sexual responses were seen in the castrates after testosterone injections.

In the domestic Aylesbury breed, injections of testosterone propionate facilitated the performance of head-pumping by castrated males, and of head-pumping, grasping-neck-feathers and mounting attempts by newly hatched ducklings (DESFORGES, 1974).

Numerous studies have reported the occurrence of head-pumping, grasping-neck-feathers and mounting attempts in male Rouen ducklings injected with testosterone (BALTHAZART, 1974; BALTHAZART & STEVENS, 1975, 1976), and the treatment has occasionally facilitated copulation (BALTHAZART & STEVENS, 1976) and the post-copulatory bridling and nodswimming displays (BALTHAZART & STEVENS, 1975) in this breed.

The effect of testosterone on social display, however, is less clear. In wild mallards castration of adult males reduced the frequency of social displays, and the behaviour was more common after testosterone injections (PHILLIPS & McKINNEY, 1962; ETIENNE & FISCHER, 1964). Treat-

ment with testosterone did not have such a strong facilitating effect on social display in mallard ducklings; in the studies of PHILLIPS & Mc-KINNEY (1962) and ETIENNE (1964) social displays were performed by only one of the injected birds in each case, whereas sexual behaviour was seen much more extensively in these experiments. In the experiments conducted by SHERROD (1974), 80-day old mallard males were injected with testosterone propionate, but no social displays were observed.

Sporadic social display was seen in castrated Aylesbury drakes after testosterone injections, but the hormone did not facilitate the occurrence of displays in ducklings of this breed (DESFORGES, 1974). In the Pekin duck too, juvenile males did not give social displays after testosterone treatment (SHERROD, 1974).

Some courtship displays have been facilitated by exogenous testosterone in male ducklings of other duck species; redhead and pintail (PHILLIPS & McKINNEY, 1962) and gadwall (SCHOMMER, 1978). GORMAN (1974) implanted a single male eider with testosterone propionate in August, a time when courtship displays were absent in untreated birds, and found that this male gave most of the pair-formation displays which are normally seen in spring.

More extensive data have been published for the domestic Rouen duck, by BALTHAZART and co-workers. Testosterone injections induced social display in six-month old male Rouens observed in the presence of females (BALTHAZART, 1974). All but one of the major and secondary display movements were recorded, the exception was the down-up display.

The same result, however, was not obtained from younger ducklings. Exogenous testosterone did not facilitate displays in one-month old male ducklings observed in monosexual groups (BALTHAZART & STEVENS, 1975) or in the presence of females (BALTHAZART & STEVENS, 1976). In the latter experiment some of the females were injected with oestradiol monobenzoate and were 'sexually receptive' in that they addressed head-pumping displays and

prone posture to the males.

In an experiment conducted with three-month old Rouen ducklings (BALTHAZART, personal communication) head-flicks were given by the testosterone-injected males, but none of the major social displays was seen. Male Rouen ducklings subjected to testosterone treatment by DEVICHE & BALTHAZART (1976) did not show social display at one month of age, but after a second course of injections at two months old the experimental birds did give more displays than the controls, although only some of the differences were significant.

Thus in many experiments exogenous testosterone has failed to promote social display in Rouen ducklings. BALTHAZART and co-workers have cited further evidence that testosterone alone does not control social display:

i)   BALTHAZART, DEVICHE & HENDRICK (1977a) studied individual differences in social display frequencies and plasma testosterone levels in adult male Rouens, and found that these two measures were negatively rather than positively correlated, although not significantly so.

ii)   Injections of testosterone propionate in adult males resulted in a suppression of social displays (BALTHAZART & DEVICHE, 1977), whilst concurrent hormone assays confirmed that the treatment had raised the circulating levels of testosterone in these birds compared with uninjected controls. These authors suggested that high testosterone levels may have an inhibitory rather than a stimulatory effect on social display. They postulated further that social display may instead be controlled by another hormone, possibly the gonadotrophin F.S.H. Testosterone treatment in adult males caused a suppression of the secretion of endogenous gonadotrophins, both F.S.H. and L.H. (BALTHAZART et al., 1977a).

iii) A direct effect of gonadotrophin on behaviour has been implicated in other species, for instance starlings (MATHEWSON, 1961; DAVIS, 1963), weaver birds (CROOK & BUTTERFIELD, 1968, 1970) and pigeons (MURTON et al.,

1969). In the latter study purified mammalian F.S.H. injected into intact male pigeons facilitated the sexual-aggressive components of the courtship sequence, whereas exogenous androgen facilitated a more natural sequence of reproductive behaviour. MURTON et al. postulated that the initial courtship patterns in this species are dependent on a synergistic action of F.S.H. and testosterone, although it was not established whether the gonadotrophin acted directly to produce the behavioural effects, or via a stimulation of the release of endogenous androgen.

In the Rouen duck, BALTHAZART (1978) observed a significant increase in the frequency of sexual behaviour in ducklings after repeated injections of purified ovine L.H. Assays of plasma testosterone in these birds confirmed that the behavioural effects were not mediated by a stimulation of testosterone secretion, which implied a direct effect of the exogenous gonadotrophin.

Direct evidence for an effect of gonadotrophin on social display, however, is sparse. Injections of mammalian gonadotrophins (Pregnant Mare's Serum, P.M.S. and Human Chorionic Gonadotrophin, H.C.G.) did not facilitate social display in male Rouen ducklings (DEVICHE & BALTHAZART, 1976; BALTHAZART, 1978) or in adults (BALTHAZART & DEVICHE, 1977), and in the latter case the treatment did not prevent the seasonal decline in display frequency seen in control males.

These studies did, however, reveal some minor changes in display patterns following the gonadotrophin injections. The treatment with P.M.S. altered the ratio of head-up-tail-ups and down-ups performed by adult males (BALTHAZART & DEVICHE, 1977). The young males observed by DEVICHE & BALTHAZART (1976) were injected with testosterone following an earlier pre-treatment with either testosterone or mammalian gonadotrophin. Small differences were found in the displaying of the two groups of males; firstly in the relative proportions of head-up-tail-up and down-up displays, and secondly in the specificity of the males' responses to females.

These differences may simply have been due to the difference in the total duration of the testosterone treatment, but the possibility of a real effect of the gonadotrophin cannot be excluded.

On the basis of these data, and also the apparent correlation between the annual cycles of social display and circulating F.S.H. mentioned earlier, BALTHAZART et al. (1977a) speculated that F.S.H. is important in promoting social display activity in autumn and winter, whereas rising testosterone levels in the spring inhibit F.S.H. secretion and the occurrence of social display.

In view of the controversy over the role of testosterone in the control of social display, the aims of the four experiments described in this chapter were two-fold:

i) To establish the effect of testosterone injections on the behaviour of the young mallards kept at the field station, and to provide further information on the hormonal basis of social display and other social and sexual behaviour in this species.

ii) If the treatment was effective in facilitating social display, to examine the response of females to the behaviour of the juvenile males, with a view to determine the importance of social display in pair formation.

IV.2.   EXPERIMENT FOUR

2.1.   Introduction

In this experiment young male mallards were injected with testosterone propionate, and their behaviour was compared with that of untreated controls.   The birds were kept in two groups, and the behavioural observations were made by introducing an unfamiliar female to a group.   It was decided to use strange rather than familiar females so that the stimuli provided by the females would be the same for all the males in the group.

If familiar females had been used there might have been different be-
havioural responses from the males depending on their personal relation-
ships with the female in question.

The behaviour of the experimental males was examined before and
during a course of injections, and again some days afterwards to see if
the effects of the treatment would persist.

2.2. Methods

The two experimental groups were formed by taking ducklings from
three different rearing-groups when they were two months old. Each ex-
perimental group comprised six males and six females; two males and two
females from each of the rearing-groups.

One experimental group was placed in W. pen, the other in E. pen.
The observations were made of the males only; the females were removed
prior to the first observations, and remained separated from the males for
most of the experiment. A schematic account of the experimental procedure
is presented in Table IV.1.

The males of one group (the T.P. group) each received a daily in-
jection of 10 mg testosterone propionate dissolved in sesame oil over a
twelve-day period; a total of 110 mg per bird (on one day the injections
were omitted, see Table IV.1). The males in the other group (the C. group,
the controls) were given daily injections of the carrier oil only. The
injection procedure was described in Section II.5.

Three series of observations were made:

> PRE-INJECTION OBSERVATIONS: Four observations of each group of males,
> before the injections were begun.
>
> INJECTION OBSERVATIONS: Ten observations of each group, made during
> the last few days of, and the day following the injection period.
>
> POST INJECTION OBSERVATIONS: Four observations of each group, made on
> the third and fourth days after the final injections.

Table IV.1

Experiment 4. Timetable of events

The table indicates the major events after July 28th, the day on which the experimental groups were formed and placed in their respective observation pens.

The six familiar females were present in the observation pens on the days indicated (P). The males were injected with testosterone propionate or with carrier oil on the days indicated (I).

Date	July				August																		
	28	29	30	31	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Females present	P	P	P					P	P	P	P	P											
Injections made								I	I	I	I	I		I	I	I	I	I	I				
Number of observations				1		2	1										2	3	3	2		2	2
Observation series	PRE-INJECTION OBSERVATIONS																INJECTION OBSERVA-TIONS				POST-INJEC-TION OBSER-VATIONS		

To make an observation a strange female was introduced to the group of males, and the behaviour of the birds was recorded for fifteen minutes, after which the female was removed. The behaviour patterns recorded were those listed in Table II.1. The females used for the introductions were of the same approximate age as the experimental males, but they had not previously been in visual contact with the males. The females had, however, been kept in the observation pens (apart from the males) for a few days before the experiment was begun, so that they would not be entirely unfamiliar with their surroundings.

The observations were made in pairs; a particular female was introduced first to one group then immediately afterwards to the other group. A different female was used for each pair of observations. Half of the females were introduced to the T.P. group first, the other half were introduced to the C. group first. About two hours was allowed between each pair of observations which were conducted on the same day.

2.3. Results

PRE-INJECTION OBSERVATIONS

The results of the PRE-INJECTION observations are not presented in detail, but may be summarised briefly. None of the males in either group, nor any of the females used, performed any major social displays, pair displays or sexual behaviour. No aggressive encounters occurred between males, but the males occasionally threatened and pecked the introduced females.

INJECTION OBSERVATIONS

a. Behaviour of the males

Social displays

The social displays given by the males are shown in Table IV.2. The total frequency of each display in the ten observations is shown, and also the median of the ten measurements. The scores of the T.P. and C.

Table IV.2

Experiment 4.   Social displays given by the testosterone-treated (T.P.) and control (C.) males in the INJECTION observations.
The total (T) and median (M) frequency of each display given by each male is shown.   The abbreviations of the displays are explained in Table II.1. At the foot of the table are the results of a comparison of the median scores of the T.P. and C. males by Mann-Whitney U-test.   The significance levels of the probabilities (2-tailed) associated with the U-value are expressed, in this and subsequent tables, as N.S.   Not significant ($p > 0.05$)
* $p \leqslant 0.05$
** $p \leqslant 0.01$

Display		HF T	HF M	IS T	IS M	GW T	GW M	HU T	HU M	NS T	NS M	DU T	DU M	Total major displays T	Total major displays M
T.P. Males	Male 01	108	10.5	22	2.5	1	0	20	1.5	10	1.0	15	1.0	36	2.5
	02	66	6.0	34	3.0	17	1.5	22	2.0	6	0	10	1.0	49	4.5
	03	94	8.0	22	2.0	31	1.5	20	2.0	5	0	6	0	57	4.0
	04	71	7.0	7	0.5	4	0	50	3.5	6	0.5	3	0	57	5.0
	05	26	2.5	2	0.0	0	0	0	0.0	0	0	0	0	0	0.0
	06	13	1.0	18	1.0	4	0	18	1.5	4	0	0	0	22	2.0
Total		378		105		57		130		31		34		221	
C. Males	11	3	0	0	0	0	0	0	0	0	0	0	0	0	0
	12	2	0	0	0	0	0	0	0	0	0	0	0	0	0
	13	5	0	5	0	0	0	0	0	0	0	0	0	0	0
	14	2	0	2	0	0	0	0	0	0	0	0	0	0	0
	15	7	0.5	1	0	0	0	2	0	1	0	0	0	2	0
	16	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Total		20		8		0		2		1		0		2	
U =		0		3		12		3		12		12		3	
P:		**		*		N.S.		*		N.S.		N.S.		*	

males were compared using the Mann-Whitney U-test. There was substantial variation in the scores across the ten observations, so it was thought appropriate to use medians in the analysis rather than the total frequencies (or means).

The T.P. males clearly gave more social displays than did the C. males. Significant differences were found for head-flicks, introductory shakes, for the total of the major displays (grunt-whistles, head-up-tail-ups and down-ups combined) and for the head-up-tail-up display analysed separately. The other two major displays, grunt-whistle and down-up, were performed by five and four of the T.P. males respectively, but not consistently in all observations, and the difference in the median scores of the T.P. and C. males was not significant for these displays.

The nodswimming display, the second component of the head-up-tail-up sequence, was performed irregularly by five of the T.P. males, but the final movement of the complex, turn-back-of-head, was not seen at all. One of the T.P. males, Male 05, did not give any major displays, although he did give head-flicks and introductory shakes.

The C. males exhibited a few head-flicks and introductory shakes, but only one C. male gave major displays, and then only two head-up-tail-ups in a single observation.

The observations were not recorded on film, but it was nevertheless noted that whilst many of the displays appeared comparable in form to adult displays, some of the grunt-whistles and head-up-tail-ups were not of the characteristic 'typical intensity'.

Grunt-whistle: some of these displays were performed without the accompanying whistle and grunt vocalisations, or with a hoarse 'croak' in place of the clear fluted whistle which is so characteristic of the adult display. On some occasions, too, a noticeably poor arch was made by the body in this movement.

Head-up-tail-up sequence: the head-up-tail-up movement itself

appeared to be quite regular, but the latter components of the sequence were often omitted. The nodswimming display was variable, sometimes given in full, sometimes represented by a brief downward nod of the head, and sometimes omitted completely. As stated above, none of the males was seen to perform turn-back-of-head, the final movement of the sequence.

Most of the grunt-whistle and head-up-tail-up displays given by the T.P. males were addressed to a particular individual. This information is presented in Table IV.3; it can be seen that nearly every one of these displays was addressed to a male rather than to the introduced female. Moreover, four of the T.P. males displayed almost exclusively to a single partner. Male 01 and Male 02 addressed most of their displays to each other, as did Males 03 and 04. Males 01 and 02 had in fact been members of the same rearing-group and Males 03 and 04 had been partners in another rearing-group.

Pair displays

None of the males performed either of the pair displays, mock-preen and turn-back-of-head.

Sexual behaviour

The sexual behaviour of the males is summarised in Table IV.4. Male-directed and female-directed behaviour were analysed separately, and the table includes a comparison of the median scores of the T.P. and C. males.

The T.P. males performed significantly more grasping-neck-feathers than did the C. males, and almost all occurrences of grasping-neck-feathers were addressed to a female. A few bouts of head-pumping, always addressed to a male, were seen in five of the T.P. males, and on three occasions a T.P. male attempted to mount another bird. The other behaviour in the copulatory sequence, mounting, copulation, and post-copulatory bridling and nodswimming, was not observed.

Table IV.3

Experiment 4. Addressees of the displays grunt-whistle (GW) and head-up-tail-up (HU), and pre-copulatory head-pumping (PU) given by the T.P. males in the INJECTION observations.

The three left-hand columns show the number of displays which each male addressed to the female, to other males, and the number for which the identity of the addressee was not determined (X). The six right-hand columns show the numbers of displays addressed to each individual male.

On some occasions a display was directed towards two males who were close together at the time, for instance Male 03 directed one HU towards Males 05 and 06.

Male	Display	Addressee			Identity of addressee male					
		Female	Male	X	01	02	03	04	05	06
01	GW	0	1	0		1				
	HU	0	18	2		18				
	PU	0	8	0		8				
02	GW	0	11	6	11					
	HU	0	18	4	18					
	PU	0	11	0	11					
03	GW	0	24	7				24		
	HU	1	16	3				15	1 (05–06)	
	PU	0	7	0				7		
04	GW	0	3	1			3			
	HU	0	44	6			41		1	2
	PU	0	9	0			6		1	1
05	GW	0	0	0						
	HU	0	0	0						
	PU	0	0	0						
06	GW	0	2	2			2			
	HU	2	6	10	1 (01–02)		5 (03–04)			
	PU	0	2	0			1	1		
All Males	GW	0	41	16						
	HU	3	102	25						
	PU	0	37	0						

Table IV.4

Experiment 4. Sexual behaviour of the males in the INJECTION observations.
The table shows the total (T) and median (M) frequency of each behaviour
pattern addressed to the females and addressed to other males

Behaviour		Head-pumping				Grasping-neck-feathers				Mounting attempts			
Addressed to		Females		Males		Females		Males		Females		Males	
		T	M	T	M	T	M	T	M	T	M	T	M
T.P. Males	Male 01	0	0	8	0	13	0.5	1	0	0	0	0	0
	02	0	0	11	0	13	0.5	1	0	0	0	0	0
	03	0	0	7	0	31	2.5	2	0	0	0	1	0
	04	0	0	9	0	54	5.0	4	0	1	0	1	0
	05	0	0	0	0	38	3.0	0	0	0	0	0	0
	06	0	0	2	0	2	0.0	0	0	0	0	0	0
	Total	0		37		151		8		1		2	
C. Males	11	0	0	0	0	1	0	0	0	0	0	0	0
	12	0	0	0	0	4	0	0	0	0	0	0	0
	13	0	0	0	0	0	0	0	0	0	0	0	0
	14	0	0	0	0	0	0	0	0	0	0	0	0
	15	0	0	0	0	1	0	0	0	0	0	0	0
	16	0	0	0	0	0	0	0	0	0	0	0	0
	Total	0		0		6		0		0		0	
	U =	18		18		3		18		18		18	
	P:	N.S.		N.S.		*		N.S.		N.S.		N.S.	

The identity of the male to whom each of the head-pumping bouts was addressed is shown in Table IV.3. It may be noted that the four males who addressed their social displays to a particular companion also addressed head-pumping to the same individual.

When the males performed grasping-neck-feathers, this behaviour was nearly always accompanied by chasing; the males would pursue the female and grasp at her neck feathers when they caught up with her.

Aggressive behaviour

Aggressive behaviour directed against males and against females is shown in Tables IV.5 and IV.6 respectively. Very little male-directed aggression was seen in either group, but the median frequencies of 'total' female-directed aggression (threats, pecks, chases and fights combined) were significantly higher in the T.P. males than in the C. males. This total, however, consisted almost entirely of chases, the only single behaviour for which there was a difference between the groups.

The T.P. males performed higher frequencies of female-directed chasing than male-directed chasing ($p < 0.05$, Wilcoxon matched-pairs signed-ranks test executed on the median scores), but there was no such difference in the chasing performed by the C. males.

Chasing of the introduced female was a very conspicuous feature of the observations of the T.P. group. The chases were vigorous and were often joined by several males at once, and sometimes the chases would culminate in grasping-neck-feathers as mentioned above.

b.   Behaviour of the females

None of the ten females used for the introductions gave any nodswimming, inciting or sexual behaviour, and only three of them showed overt aggression. These three were involved in brief fights with the males, and one of them also delivered a couple of pecks to the C. males.

In general the females spent their fifteen-minute sessions with

Table IV.5

Experiment 4. Male-directed aggressive behaviour of the males in the

INJECTION observations. Total (T) and median (M) frequencies are shown

Behaviour		Threat		Peck		Chase		Fight		Total	
		T	M	T	M	T	M	T	M	T	M
	Male										
	01	1	0	1	0	3	0	0	0	5	0
	02	0	0	4	0	1	0	0	0	5	0
T.P.	03	0	0	0	0	0	0	0	0	0	0
Males	04	0	0	0	0	0	0	0	0	0	0
	05	0	0	0	0	0	0	0	0	0	0
	06	0	0	0	0	0	0	0	0	0	0
	Total	1		5		4		0		10	
	11	0	0	1	0	0	0	0	0	1	0
	12	0	0	0	0	0	0	1	0	1	0
C.	13	0	0	0	0	0	0	0	0	0	0
Males	14	0	0	0	0	0	0	0	0	0	0
	15	0	0	0	0	0	0	1	0	1	0
	16	0	0	0	0	0	0	0	0	0	0
	Total	0		1		0		2		3	
U =		18		18		18		18		18	
P:		N.S.		N.S.		N.S.		N.S.		N.S.	

Table IV.6

Experiment 4.   Female-directed aggressive behaviour of the males in
the INJECTION observations.   Total (T) and median (M) frequencies are
shown.

Behaviour		Threat		Peck		Chase		Fight		Total	
		T	M	T	M	T	M	T	M	T	M
	Male										
	01	0	0	3	0	52	5.0	0	0	55	5.0
	02	0	0	2	0	13	1.0	0	0	15	1.0
T.P.	03	1	0	2	0	94	8.5	2	0	99	8.5
Males	04	0	0	1	0	122	13.0	1	0	124	13.5
	05	0	0	14	1.0	85	9.0	0	0	99	11.0
	06	0	0	0	0	6	1.0	0	0	6	1.0
Total		1		22		372		3		398	
	11	2	0	4	0	8	0	0	0	14	0.5
	12	2	0	6	0	0	0	0	0	8	0.0
C.	13	1	0	4	0	6	0	0	0	11	0.5
Males	14	1	0	3	0	5	0	1	0	10	1.0
	15	3	0	4	0	4	0	1	0	12	1.0
	16	0	0	2	0	0	0	0	0	2	0.0
Total		9		23		23		2		57	
U =		18		15		0		18		2	
P:		N.S.		N.S.		**		N.S.		**	

the C. group swimming or preening apart from the males.   When introduced
to the T.P. group the females behaved in a similar manner except when they
were forced to flee from the males' pursuits.

POST-INJECTION OBSERVATIONS

The behaviour of the males in the POST-INJECTION observations is
summarised in Appendix 4.   There were no longer any significant differences
between the T.P. and C. males in the frequencies of any of the behaviour
patterns recorded.

The behaviour patterns which had been enhanced by the treatment
in the INJECTION observations were performed less frequently in the POST-
INJECTION observations.   The Wilcoxon test was used to compare the median
scores of the T.P. males in the two observation series (Table IV.7).

The T.P. males gave significantly fewer head-flicks in the POST-
INJECTION observations compared with the INJECTION observations ($p < 0.05$,
Table IV.7).   The reduction in the frequency of introductory shakes was
not significant, although five of the T.P. males did give fewer shakes in
the POST-INJECTION observations.

The median frequency of total major displays was also reduced in
five of the males;   the sixth male gave no major displays in either ob-
servation series.   In the POST-INJECTION observations four of the T.P.
males performed the head-up-tail-up display and three gave grunt-whistles,
but the down-up display was not seen at all (see Appendix 4).

The major displays of the T.P. males in the POST-INJECTION ob-
servations were still addressed more often to another male than to the
introduced female.   Of the seventeen grunt-whistles and head-up-tail-ups
which were seen, the addressees of nine were determined;   eight of these
were males.

The pair displays mock-preen and turn-back-of-head, and the
sexual behaviour head-pumping and mounting, did not occur in the POST-

Table IV.7

Experiment 4. Comparison of the behaviour of the T.P. males in the INJECTION and POST-INJECTION observations.

The table shows, for each behaviour pattern, the median frequency given by each of the T.P. males in the INJECTION observations (I) and the POST-INJECTION observations (P-I). At the foot of the table is shown the significance of the difference between the two sets of medians as compared by the Wilcoxon matched-pairs signed-ranks test.

N.S. = not significant, p >0.05

* = p <0.05 (2-tailed)

Behaviour	Head-flick		Introductory shake		Total major displays		Grasping-neck-feathers		Chasing females	
	I	P-I	I	P-I	I	P-I	I	P-I	I	P-I
Male										
01	10.5	3.5	2.5	0.0	2.5	0.0	0.5	0.5	5.0	1.0
02	6.0	2.5	3.0	0.5	4.5	0.0	0.5	0.0	1.0	0.5
03	8.0	1.0	2.0	0.5	4.0	0.0	2.5	0.0	8.5	0.0
04	7.0	4.5	0.5	0.0	5.0	1.5	5.5	1.0	13.0	3.5
05	2.5	0.5	0.0	0.5	0.0	0.0	3.0	0.0	9.0	1.5
06	1.0	0.5	1.0	0.5	2.0	0.0	0.0	0.0	1.0	0.0
Significance	*		N.S.		N.S.		N.S.		*	

INJECTION series. There were a few incidences of grasping-neck-feathers, all of which were addressed to a female. The median frequency of grasping-neck-feathers was reduced in four of the testosterone-injected males, whilst the other two showed no change.

Male-directed aggression was rare in the POST-INJECTION observations. The most common aggressive response of the males was, again, chasing females, though this occurred significantly less often than in the earlier observation series.

The females used for the introductions in the POST-INJECTION observations gave no nodswimming, inciting or sexual behaviour, and only a few aggressive actions.

2.4. Discussion

The results of the INJECTION observations clearly demonstrated that injections of testosterone propionate induce in two month old male mallards the occurrence of many of the social display movements which are performed by adult males. These displays were rare in control birds of the same age, and were not given by the experimental males in the PRE-INJECTION observations.

The control males performed virtually no major displays, but they did give a few head-flicks and introductory shakes. These two movements, which are usually described as 'preliminary' or 'introductory' displays to the major social displays, are identical in form to comfort movements frequently used by mallards outside the context of the social display session (McKINNEY, 1965a). It is therefore not certain that the head-flicks and introductory shakes given at a low frequency (compared with the testosterone-injected males) by the control males during the experiment were truly social displays.

An important feature of the precocious social display of the testosterone-injected birds which differed from the normal adult behaviour

was that the grunt-whistle and head-up-tail-up displays were mostly
addressed to males. The same was true of the pre-copulatory head-pumping;
it appears that the young males were exhibiting homosexual tendencies.
Furthermore, four of the males had developed homosexual preferences for
the group-member with whom they were most familiar, i.e. the one-time
companion in the original rearing-groups. The two homosexual 'pairs' were
also recognisable in that the members of each pair spent much of their time
swimming closely together, as would members of a true pair of adult birds.
The homosexual partners were often seen swimming alongside each other in
the head-high posture, giving rapid rab-rab vocalisations; this is another
behaviour pattern which is characteristically used by a paired adult male
when he is accompanied by his mate.

Persistent homosexual behaviour would certainly be maladaptive
in the wild, although there have been occasional reports of two males per-
forming head-pumping together (WEIDMANN, 1956; LEBRET, 1961; RAITASUO,
1964).

The homosexual bonds of the testosterone-injected males might
have arisen during the period that they were separated from females. After
the fifth day of injections the males were visually isolated from females
for four days, and thereafter were allowed contact with a female only
during the brief observation sessions. McKINNEY (1964) stated that ducks
will readily take a 'mate' of the same sex if they are isolated from
opposite-sex conspecifics, and McKINNEY (1975b) refers to SCHUTZ (1965) who
reported that male mallards raised without females form strong homosexual
bonds and address displays only to other males. Homosexual behaviour may
also develop in adult mallards kept in monosexual groups (WEIDMANN &
DARLEY, 1971a,b; GOLDSMITH, unpublished observations).

In the present experiment homosexual bonds did not arise in the
control group, but they may have been facilitated in the testosterone-
injected birds if the hormone treatment had increased the pairing or sexual

motivation of the young males. BALTHAZART (1974) has described homosexual head-pumping in testosterone-injected male Rouen ducklings observed in the presence of a female after a period of monosexual isolation. SCHOMMER (1978) reported male-directed courtship and sexual displays in testosterone-injected gadwall ducklings which had been isolated from females for short periods.

The pair displays, turn-back-of-head and mock-preen, did not occur in the present experiment. This might suggest that the testosterone treatment was unable to activate the neural mechanisms underlying these behaviour patterns. Alternatively, however, it is possible that certain external stimuli, perhaps provided by specific female behaviour, are required to release pair displays in the male, and these stimuli were absent in the experimental observations. This suggestion is elaborated in Section IV.6, with reference to pair displays and also sexual behaviour. Grasping-neck-feathers was the only sexual pattern to occur at a significantly higher frequency in the testosterone-treated birds than in the controls, although other authors,for instance BALTHAZART & STEVENS (1976), have reported more extensive sexual responses in testosterone-treated ducklings.

It may be pointed out here, however, that the sexual behaviour of the injected males did not occur in the same behavioural context as it does in adult mallards.

It has already been noted that the head-pumping displays were homosexually oriented. Grasping-neck-feathers was addressed to females, but it did not occur as part of an orderly copulation sequence as seen in adults. The T.P. males performed grasping-neck-feathers without preceding head-pumping displays and without waiting for the female to adopt the prone posture, and they rarely attempted and never succeeded in mounting the female. In fact the males did not seem to be responding to any specific behaviour on the part of the female, but the grasping-neck-feathers was instead usually seen in conjunction with pursuit of the female.

It may be that this behaviour was a manifestation of a purely aggressive response of the males towards the strange females. One of the actions which sometimes occurs in aggressive encounters between adult mallards is rather similar to grasping-neck-feathers; a thrusting of the bill over the neck of the opponent, sometimes together with pecking of the feathers (WEIDMANN, 1956; CRAMP & SIMMONS, 1977).

Alternatively the testosterone-injected males might in fact have been attempting to force copulations with the females. Apart from the failure of the males to mount, the observed behaviour was quite similar to the rape attempts seen during the latter part of the breeding season in wild birds and in the captive mallards of experiment 2. If the exogenous testosterone had stimulated the males sexually, then possibly the preceding period of isolation from females, which would have prevented the expression of 'normal' mating behaviour, had increased their sexual motivation to such an extent that the customary pre-copulatory formalities could be superceded.

BALTHAZART (1974) reported that male Rouen ducklings injected with testosterone raped females but did not attempt 'conventional' copulations, and they addressed head-pumping only to other males. The design of BALTHAZART's experiment was similar to the present one in that the birds were kept in an all-male group during the injection period and were subjected to brief introductions of females.

McKINNEY (1965b), reviewing the literature concerning the chasing and raping behaviour of ducks, has emphasised the difficulty in attributing a sexual and/or aggressive motivation to the observed behaviour. These points are discussed again after data have been presented from the next experiments.

Finally, a note on the persistence of the behavioural effects of the testosterone treatment after the injections were discontinued. The behaviour patterns which were facilitated by the treatment were either absent or reduced in frequency in the observations made three and four days after

the final injections. There are no published accounts of a similar study of the mallard or of domestic ducks, but SCHOMMER (1978) observed the behaviour of young gadwall males for some time after a course of testosterone injections. She reported a gradual decline, over several weeks, in the expression of courtship displays and sexual behaviour which had been facilitated by the treatment.

The present experiment has provided little information concerning the response of females to the precocious social behaviour of the testosterone-injected juvenile males. Clearly the persistent chasing by the males precluded all behaviour on the part of the females other than escape. The study has however, provided a baseline from which to plan further experiments.

IV.3. EXPERIMENT FIVE

3.1. Introduction

Although the hormone treatment in the last experiment resulted in a facilitation of social display, the experimental males behaved abnormally in that they exhibited homosexual behaviour and engaged in a great deal of chasing of the females. It was hoped that these two features could be reduced or eliminated by certain alterations in experimental design, namely:

(i)   a reduction in the daily dose of hormone administered to the males,

(ii)   ensuring that the males were not separated from females for a long period, and

(iii) observing the males in the presence of females with whom they were not entirely unfamiliar.

This experiment also provided an opportunity to investigate another aspect of the social display of the mallard. The synchronised performance of social displays has already been described, and several authors (e.g. HOCHBAUM, 1944; LEBRET, 1961; McKINNEY, 1975a) have postulated a 'contagious' effect of the activity, such that an ongoing display session may stimulate nearby drakes to swim over and join in. One may ask if such a contagious effect would be demonstrable in the juvenile males, if testosterone-injected and control males were kept in the same group. Would the control birds be stimulated to give displays by the presence of males who were displaying under the influence of testosterone injections?

3.2. Methods

The experiment was conducted immediately after experiment 4, using the same males as subjects. They were now about two and a half months of age. It was decided to use the same males to see if the homosexual behaviour would persist, or whether the males would display to females now that their monosexual isolation was discontinued.

On 20th August, the males were re-arranged into two new groups, Group A. and Group B. Each group comprised three of the T.P. males and three of the C. males. One group was kept in E. pen, the other in W. pen. The homosexual partners of experiment 4 were separated by allocating them to different groups.

The hormone injections were resumed. Each T.P. male received a daily injection of 5 mg testosterone propionate for nine days, whilst the C. males were injected at the same times with the carrier oil alone.

Also on the 20th August, three females were placed with each group. These females were of the same approximate age as the males, but they were previously strangers to them, that is they came from a different rearing-group. These females were kept with the males for the duration of the experiment.

To make an observation the females were removed from the pen and two hours later they were re-introduced, and the behaviour of the birds was recorded for fifteen minutes. The behaviour patterns recorded were those listed in Table II.1, with the omission of the male 'preliminary' displays head-flick and introductory shake. Four observations were made of each group, on the last two days of the injection period (27th and 28th August).

For statistical analysis there were too few subjects to allow a separate comparison of the T.P. and C. males within each group, so the scores of all six T.P. males were combined and compared with the scores of the six C. males.

3.3.   Results

a)   Behaviour of the males

Social display

The social displays of the males are shown in Table IV.8.

The T.P. males clearly gave more social displays than did the C. males. Significant differences were found for the total of the major displays, for the head-up-tail-ups alone and also for nodswimming. The grunt-whistle display was also seen more frequently in the T.P. males (see total frequencies), although the median scores were not significantly different. The third major display, the down-up, was performed by only three birds; these were the three T.P. males in Group A.

The final component of the head-up-tail-up sequence, turn-back-of-head, was given by the T.P. males on some occasions, but this display is not included in the table because its occurrence was not recorded with a consistent degree of accuracy. This was because the social displays were often given in synchronised bursts, and there was not always sufficient time to record every occurrence of turn-back-of-head.

The social displays of the juvenile males resembled in form the

Table IV.8

Experiment 5.   Social displays given by the males.

The table shows the total(T) and median (M) frequency of each display given by each male.   The median scores of the T.P. and C. males are compared by Mann-Whitney U-test (significance levels expressed as in Table IV.2).

Display			Grunt-whistle		Head-up-tail-up		Nod-swimming		Down-up		Total major displays	
			T	M	T	M	T	M	T	M	T	M
	Male Group											
T.P. Males	01	A	1	0.0	9	2.5	8	2.0	5	1.0	15	3.5
	03	A	26	5.0	9	2.5	8	2.5	7	1.5	42	11.0
	05	A	10	2.0	14	3.0	3	0.5	5	1.0	29	7.0
	02	B	6	1.5	4	0.5	2	0.5	0	0.0	10	2.0
	04	B	4	1.0	12	3.5	12	3.5	0	0.0	16	5.0
	06	B	1	0.0	5	1.5	2	0.5	0	0.0	6	1.5
C. Males	12	A	1	0	1	0	0	0	0	0	2	0
	14	A	0	0	0	0	0	0	0	0	0	0
	16	A	0	0	0	0	0	0	0	0	0	0
	11	B	0	0	0	0	0	0	0	0	0	0
	13	B	0	0	0	0	1	0	0	0	0	0
	15	B	0	0	2	0	2	0	0	0	2	0
U =			6		0		0		9		0	
P:			N.S.		**		**		N.S.		**	

displays of adult mallards, with the same qualifications reported in experiment 4 concerning some of the grunt-whistles and head-up-tail-ups. It should, however, be noted that the latter components of the head-up-tail-up complex were more common in experiment 5 than in experiment 4. The turn-back-of-head movement, absent in the earlier experiment, did occur in experiment 5, and an examination of Tables IV.2 and IV.8 will show that the five T.P. males who performed the head-up-tail-up display in both experiments followed it with nodswimming more frequently in experiment 5 than in experiment 4.

T.P. Males 04 and 06 (Group B) addressed most of their displays to each other, whilst Male 02 and the three T.P. males in Group A displayed predominantly to females. Of the four displays given by the C. males, two were addressed to females and the other two came into the 'addressee not determined' category.

Pair displays

Two of the males, T.P. Male 01 and C. Male 13, gave some turn-back-of-head, usually whilst they were followed by an inciting female (see below). None of the males gave the mock-preen display.

Sexual behaviour

Little sexual behaviour was performed by the males in this experiment, and there were no significant differences between the T.P. and C. males.

T.P. Male 01 gave five bouts of pre-copulatory head-pumping, and three of the other T.P. males each gave a single bout.

Two of the C. males also exhibited this display, Male 12 three times and Male 14 once. In addition T.P. Male 02 once tried to mount a female, but there was not a single incidence of grasping-neck-feathers.

The head-pumping performed by the C. males and by T.P. Males 01 and 02 was addressed to females, but T.P. Males 04 and 06 addressed their

Table IV.9

Experiment 5. Aggressive behaviour of the males. Male-directed
and female-directed actions are listed separately. Only the total
frequencies are shown. Most of the median scores were zero, and the
median scores of the T.P. and C. males were not significantly different
(Mann-Whitney U-test, p >0.05, 2-tailed) for any of the individual
actions or for the totals.

The abbreviations are explained in Table II.1.

Behaviour		Male-directed aggressive behaviour					Female-directed aggressive behaviour				
		TH	PK	CH	FT	Total	TH	PK	CH	FT	Total
Male Group											
T.P. Males	01 A	0	1	0	0	1	1	1	8	0	10
	03 A	0	0	0	0	0	0	1	0	0	1
	05 A	0	0	0	0	0	0	3	2	0	5
	02 B	0	0	0	0	0	0	0	0	0	0
	04 B	0	0	0	0	0	0	0	0	0	0
	06 B	0	0	0	0	0	1	0	0	0	1
C. Males	12 A	0	4	0	0	4	0	0	0	0	0
	14 A	2	0	0	0	2	0	0	0	0	0
	16 A	0	0	0	0	0	1	1	0	0	2
	11 B	0	1	0	0	1	1	1	0	0	2
	13 B	1	2	0	0	3	0	0	0	0	0
	15 B	0	1	0	0	1	1	0	0	0	1

Table IV.10

Experiment 5.   Inciting performed by the females

The table shows the number of bursts of the inciting display addressed by each female to a male (M) and to a female (F) in each of the four observations.   Where the displays were addressed to a male, the identity of the male is also shown.

	Group A females						Group B females					
Female	21		22		23		24		25		26	
Inciting addressed to:	M	F	M	F	M	F	M	F	M	F	M	F
Observation number												
1	9	0	0	0	0	0	0	0	1	0	3	0
2	9	0	0	0	0	0	0	1	0	1	3	0
3	10	0	0	0	2	0	0	2	1	1	2	0
4	8	0	0	0	2	0	0	2	0	3	2	1
Total	36	0	0	0	4	0	0	5	2	5	10	1
Identity of male addressed	01				12				13		13	

head-pumping to each other, as they had their social displays.

Aggressive behaviour

Aggressive behaviour occurred at a very low frequency (Table IV.9), and there were no differences between the T.P. and C. males for any single action or for the totals.

b) Behaviour of the females

None of the females gave any nodswimming, sexual or aggressive behaviour in any of the observations, but five of them performed a little of the inciting display (Table IV.10).

Some of the inciting was addressed to other females, but the four females who addressed inciting to a male each addressed one male exclusively.

In Group A, Female 21 addressed a great deal of inciting to T.P. Male 01. The social displays (grunt-whistles and head-up-tail-ups) and sexual behaviour (head-pumping) of this male were addressed to Female 21. Also in Group A, Female 23 addressed a little inciting to Male 12, who was one of the control males.

In Group B, Female 26 exhibited a clear preference for Male 13. He was a control male who was not seen to give any social displays or sexual behaviour. Female 25 also addressed a little inciting to this male.

3.4. Discussion

The behaviour of the testosterone-injected males differed in several respects from their behaviour in experiment 4. The major difference was that the frequency of female-directed chasing was much lower in experiment 5, and the grasping-neck-feathers behaviour which often accompanied the chases did not occur in the latter experiment.

The reduction in the frequencies of these behaviour patterns may simply have been due to the lower dosage of testosterone administered to the males in experiment 5. The results so far do, however, support the hypo-

thesis (see Section 2.4.) that chasing females and/or rape attempts are more likely to occur if the males are deprived of female company; in experiment 5 the males were kept with females throughout the injection period. It is not yet clear, however, whether the behaviour of the males was also affected by their familiarity with the females which were used for the observations. Would the female-directed chasing have recurred if strange females were introduced to the males in experiment 5? This question is examined in the next experiment.

The homosexual tendencies of the testosterone-injected males were reduced now that they were no longer separated from females, but some displays were still addressed to males and two of the males remained entirely homosexual. Thus the effects of the earlier monosexual isolation period (during experiment 4) were still in evidence; the next experiments will show whether homosexual behaviour can be eliminated by ensuring that the males are never allowed a prolonged period of separation from females.

Although the females in the present study were not persistently chased by the males, no conclusions could be reached concerning their responses to the behaviour of the males. There were only two cases where a female showed a reliable preference for a particular drake. One female preferred a testosterone-injected male who had addressed social displays to her, whilst a second female consistently addressed inciting to a non-displaying control male.

Some of the females addressed inciting to a female partner, thus demonstrating homosexual preferences. This phenomenon has been reported in other experiments (e.g. DESFORGES, 1974; experiment 2 of this thesis) where ducks have been transferred to a new group; the females may show a temporary homosexual preference for one of their familiar companions rather than for a 'strange' bird of the opposite sex. In addition, the homosexual behaviour of some of the males is not likely to have been conducive to attracting the attentions of a female! It should now be possible to

improve on the experimental design to obtain more useful information on female responses to precocious male behaviour.

It should finally be mentioned that since very few displays were given by the control males there was no evidence of the contagious effect of social display which occurs in adults. It appears that in ten-week old males the hormonal priming is necessary to enable social displays to be released, at least under the external conditions utilised in the present experiment.

IV.4. EXPERIMENT SIX

4.1. Introduction

This experiment was designed to compare the behaviour of testosterone-injected males in the presence of either strange or familiar females.

Many workers have described the behaviour of adult male mallards on the introduction of a female. This procedure has been variously reported to result in intense social display activity and aggression between the males (FIELD, 1970; WEIDMANN & DARLEY, 1971a), rape attempts (FIELD, 1970) and persistent chasing of the female (DESFORGES, 1974). No comparative study has yet been reported on the behaviour of mallard males towards familiar and previously unknown females, either in adults or in testosterone-injected ducklings.

Since the experiments described here were completed, DEVICHE (personal communication) has found that juvenile male Rouens primed with testosterone gave more social displays in the presence of familiar females than when they were observed with unfamiliar females. The behaviour of testosterone-injected gadwall ducklings, however, does not differ in this respect (SCHOMMER, 1978).

A second variable was incorporated into the present experiment.
A group of testosterone-injected males was observed on the introduction of
either a single female or four females introduced simultaneously. It has
sometimes been suggested that social displays in adult males are performed
in response to specific behaviour on the part of the female (e.g. JOHNS-
GARD, 1960a; WEIDMANN & DARLEY, 1971a), although LEBRET (1961) considered
that the displays were solely the result of interactions between males.

If the social displays of the testosterone-injected juveniles
were dependent on behavioural stimuli provided by the females, one might
expect an increase in the frequency of displays when a larger number of
females was present. On the other hand McKINNEY (1975a) and others con-
sider that social display is promoted by competition between males for the.
attentions of a female. If such a competition was taking place between the
testosterone-primed juveniles, then this might argue for a lower frequency
of displays when four females were introduced, when the competition for
females would conceivably be relaxed.

4.2. Methods

There were two experimental groups, each comprising four males
and four females selected at random from a rearing group when they were
about three months old. The experimental groups were placed in E. pen and
W. pen. The males remained in their respective pens throughout the experi-
ment. The females were kept with the males continuously except for several
periods of a few hours when the observations of the males were conducted.

The injections were begun one week after the birds had been in-
stalled in the observation pens. The males of one group (the T.P. males)
each received a 5 mg injection of testosterone propionate every other day
for twelve days. The males of the other group (the C. males) received in-
jections of the carrier oil alone.

Sixteen observations were made of each group of males, between the

third and the twelfth days of the injection period. On each observation day the resident females were first removed from the pens. The first observation was made one hour after the removal of the females, and one hour was allowed between the subsequent observations. The resident females were replaced after the final observation of the day was completed.

To make an observation either one or four females were introduced to a group of males, and the behaviour was recorded for fifteen minutes.

There were four types of observation:

(a) Introduction of a single familiar female,

(b) Introduction of four familiar females,

(c) Introduction of a single strange female,

(d) Introduction of four strange females.

Four separate observations were made of each group in each of the above conditions.

The 'familiar' females were the resident females which were kept with the males during the experiment. Each group of males was observed once with each of the resident females and four times with all four resident females introduced simultaneously.

The 'strange' females had not been in visual contact with any of the males before the experiment (they were taken from a different rearing group, but they were of the same approximate age as the males). These females were kept in a different pen between observations, but they had been allowed a few days in E. and W. pens for familiarisation before the males were installed. Each group of males was observed four times with a single strange female (a different one each time), and four times with the four strange females introduced simultaneously.

The behaviour patterns recorded were those listed in Table II.1, with the omission of the male displays head-flick and introductory shake, and the latter components of the head-up-til-up complex, i.e. nodswimming

and turn-back-of-head.

The data from the preceding experiments have been analysed using non-parametric tests, but a concise non-parametric multifactorial test was not known. It was decided to use here the parametric 3-way analysis of variance with repeated measures (WINER, 1973), rather than a large number of single-factor non-parametric tests.

4.3. Results

Behaviour of the males

The social displays, pair displays and aggressive behaviour of the T.P. and C. males is summarised in Tables IV.11 to IV.18. The page preceding Table IV.11 explains the computation of the analysis of variance (ANOVA).

Social displays

The results of the ANOVA on the total major displays (Table IV.12) indicated a highly significant interaction of treatment with familiarity of females. The nature of this interaction is quite clear from an examination of the data; the T.P. males gave many more social displays in the familiar-female observations than in the strange-female observations, whereas the C. males displayed hardly at all in either situation. Tests were made of the simple main effects in the interaction (WINER, 1973, p. 551), and the only significant difference thus found was between the T.P. males and the C. males for the familiar-female observations (p <0.01).

Similar results were obtained from analysis of the frequencies of grunt-whistles and head-up-tail-ups separately (Table IV.11); a significant interaction of treatment with familiarity of females and a difference (p <0.01 for both displays) in favour of the T.P. males for the familiar-female observations only.

The ANOVA revealed no significant main effects nor interactions

Experiment 6.   Tables IV.11 - IV. 18

Social displays (Tables IV.11 and IV.12), pair displays (Table IV.13)

and aggressive behaviour (Tables IV.14 - IV.18) of the males in the

different situations.

1)   Summary of data

        Each cell shows the mean frequency of the display or behaviour

pattern in the four observations in the stated situation, except for the

'four strange females' situation in the C. group.   In this case the means

were calculated from three observations;   the fourth was lost due to mal-

function of equipment.

2)   Analysis of variance

        The data were analysed by 3-way analysis of variance.   The three

factors were:

i)   Treatment (Trt):   T.P. males vs. C. males.

ii)   Familiarity of females (Fam):   familiar-female observations vs.

        strange-female observations.

iii) Number of females (Num):   four-female observations vs. one-female

        observations.

        The repeated measures design required different error terms for

the between-subjects factor (Treatment) and for the different within-subjects

factors.

        For each factor and interaction the table shows the sum of

squares (SS), degrees of freedom (DF), mean square (MS) and F ratio (F).

The significance of the F values are expressed as * = $p < 0.05$

                                                      ** = $p < 0.01$

Table IV.11   Social displays grunt-whistle and head-up-tail-up

| | Grunt-whistle | | | | Head-up-tail-up | | | |

Summary of data

Females present	Familiar		Strange		Familiar		Strange	
	One	Four	One	Four	One	Four	One	Four
T.P. Males Male 601	3.75	0.75	0	0.50	2.75	1.75	0	0
602	1.50	0.75	0	0.00	4.00	4.00	0	0
603	3.75	1.25	0	0.00	2.75	2.50	0	0
604	2.75	1.75	0	0.25	1.75	2.50	0	0
C. Males 611	0	0	0	0	0	0	0	0
612	0	0	0	0	0	0	0	0
613	0	0	0	0	0	0.50	0	0
614	0	0	0	0	0	0	0	0

Analysis of variance

Source of variation	SS	DF	MS	F	SS	DF	MS	F
Between subjects								
Treatment	9.03	1	9.03	41.05^{**}	14.45	1	14.45	40.14^{**}
Error	1.32	6	0.22		2.16	6	0.36	
Within subjects								
Familiarity females	7.51	1	7.51	44.18^{**}	15.82	1	15.82	43.94^{**}
Trt x Fam	7.51	1	7.51	44.18^{**}	14.45	1	14.45	40.14^{**}
Error	1.02	6	0.17		2.16	6	0.36	
Number females	1.32	1	1.32	10.15^{*}	0.00	1	0.00	-
Trt x Num	1.32	1	1.32	10.15^{*}	0.03	1	0.03	0.43
Error	0.76	6	0.13		0.43	6	0.07	
Fam x Num	2.00	1	2.00	10.53^{*}	0.00	1	0.00	-
Trt x Fam x Num	2.00	1	2.00	10.53^{*}	0.03	1	0.03	0.43
Error	1.16	6	0.19		0.43	6	0.07	

Table IV.12 Social displays down-up and total major displays

		Down-up				Total major displays			

Summary of data

Females present		Familiar		Strange		Familiar		Strange	
		One	Four	One	Four	One	Four	One	Four
T.P. Males	Male 601	0.50	0.25	0	0	7.00	2.75	0	0.50
	602	0.25	0.50	0	0	5.75	5.25	0	0.00
	603	0.50	1.25	0	0	7.00	5.00	0	0.00
	604	0.00	0.00	0	0	4.50	4.25	0	0.25
C. Males	611	0	0	0	0	0	0	0	0
	612	0	0	0	0	0	0	0	0
	613	0	0	0	0	0	0.50	0	0
	614	0	0	0	0	0	0	0	0

Analysis of variance

Source of variation	SS	DF	MS	F	SS	DF	MS	F
Between subjects								
Treatment	0.33	1	0.33	5.50	54.47	1	15.47	259.88**
Error	0.38	6	0.06		1.24	6	0.21	
Within subjects								
Familiarity females	0.33	1	0.33	5.50	53.17	1	53.17	161.12**
Trt x Fam	0.33	1	0.33	5.50	50.63	1	50.63	153.42**
Error	0.38	6	0.06		1.97	6	0.33	
Number females	0.02	1	0.02	1.00	1.03	1	1.03	2.78
Trt x Num	0.02	1	0.02	1.00	1.42	1	1.42	3.84
Error	0.14	6	0.02		2.19	6	0.37	
Fam x Num	0.02	1	0.02	1.00	1.64	1	1.64	3.22
Trt x Fam x Num	0.02	1	0.02	1.00	2.13	1	2.13	4.18
Error	0.14	6	0.02		3.06	6	0.51	

Figure IV.1

Experiment 6. Analysis of variance, interaction profile.
Grunt-whistle display; interaction of familiarity of females x
number of females for the T.P. Group only.
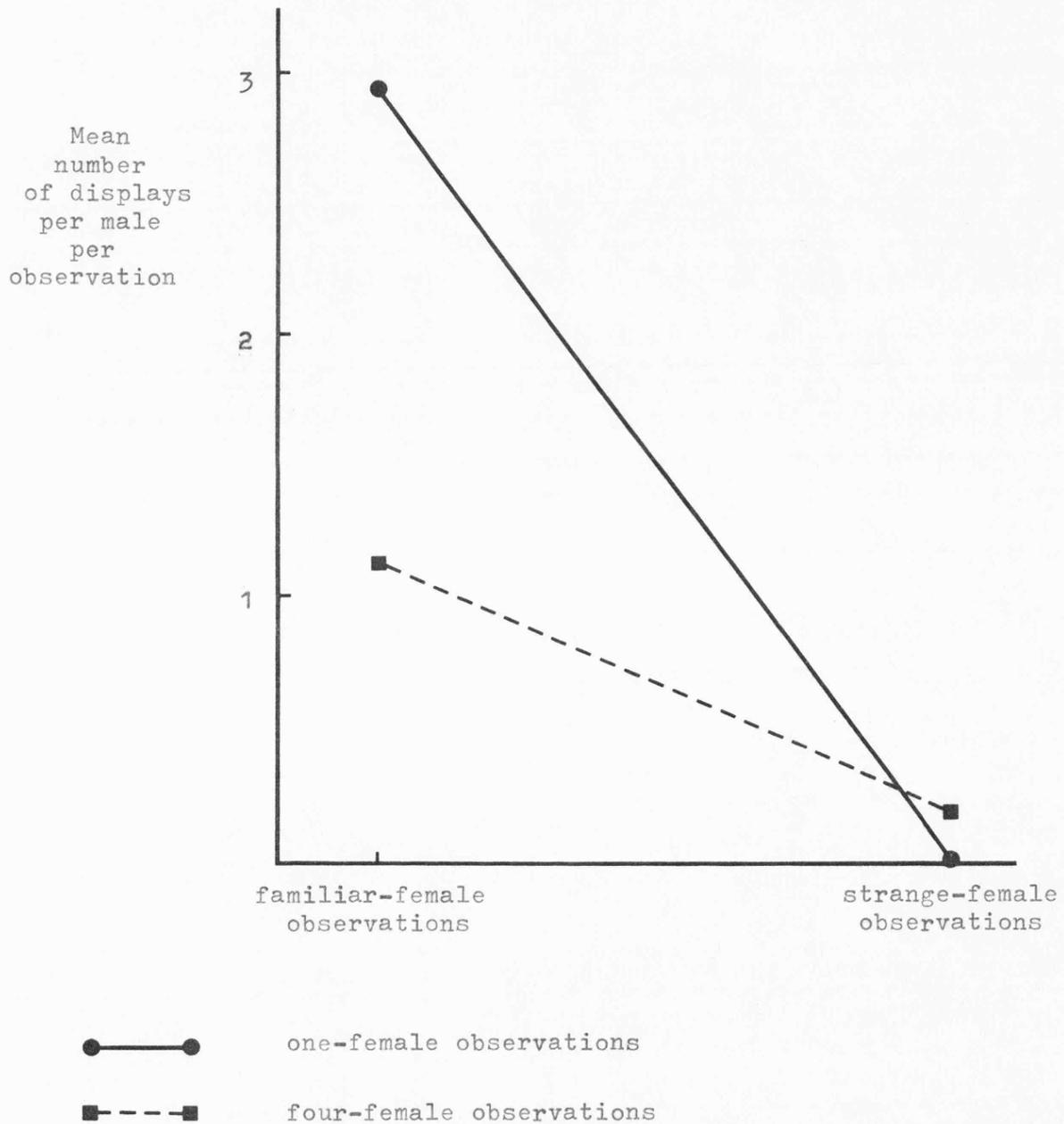
in the case of the down-up (Table IV.12), although a similar trend was apparent for this display. Down-ups were seen only in the familiar-female observations of the T.P. group, but only in three of the four males, and down-ups occurred at a lower frequency than the other display movements.

The analysis of the grunt-whistle frequencies revealed interactions, at a lower level of significance, of the other factors, i.e. treatment x number of females, familiarity of females x number of females, and also the three way interaction. Grunt-whistles were not given at all by the C. males, and so the profile of the only remaining meaningful interaction, that of familiarity of females x number of females for the T.P. group only is shown in Fig. IV.1. The figure shows that the frequency of grunt-whistles was very low in the strange-female observations, in both the one-female and four-female situations, but in the familiar-female observations the display was given more frequently with one female than with four females present.

Most of the displays were comparable in form to those given by adult mallards, but as in the previous experiments some of the grunt-whistles lacked the whistle vocalisation. The details of the head-up-tail-up sequence were not recorded consistently, but it was noted that the head-up-tail-up was often followed by nodswimming and sometimes by turn-back-of-head as well.

The addressees of the grunt-whistles and head-up-tail-ups are shown in Table IV.19. Most of the displays were addressed to females, and only one male (Male 603) addressed an appreciable number of displays to males.

Pair displays

The occurrences of the turn-back-of head movement as a discrete behaviour pattern outside the context of the head-up-tail-up are recorded in Table IV.13. The ANOVA revealed no significant main effects or inter-

Table IV.13   Pair display turn-back-of-head

Summary of data

Females present		Familiar		Strange	
		One	Four	One	Four
	Males				
	601	0.25	1.25	0	0
T.P. Males	602	0.00	0.50	0	0
	603	0.25	1.00	0	0
	604	0.25	5.75	0	0
	611	0	0	0	0
C. Males	612	0	0	0	0
	613	0	0	0	0
	614	0	0	0	0

Analysis of variance

Source of variation	SS	DF	MS	F
Between subjects				
Treatment	2.67	1	2.67	3.42
Error	4.66	6	0.78	
Within subjects				
Familiarity females	2.67	1	2.67	3.42
Trt x Fam	2.67	1	2.67	3.42
Error	4.66	6	0.78	
Number females	1.88	1	1.88	2.65
Trt x Num	1.88	1	1.88	2.65
Error	4.26	6	0.71	
Fam x Num	1.88	1	1.88	2.65
Trt x Fam x Num	1.88	1	1.88	2.65
Error	4.26	6	0.71	

actions, but it may be noted that turn-back-of-head was seen only in the familiar-female observations of the T.P. males.

The addressees of the turn-back-of-head displays are indicated in Table IV.19. Three of the males addressed their displays to the introduced (only familiar) females, whilst Male 603 addressed his turn-back-of-head to a fellow male.

The second pair display, mock-preen, was rarely observed. It was performed just twice by T.P. Male 603, who addressed the display to a male.

Sexual behaviour

Sexual behaviour, too, was uncommon. Only the pre-copulatory head-pumping display was seen; one bout of head-pumping was given by a C. male and several bouts by T.P. Male 604.

Aggressive behaviour

The agonistic behaviour of the males is summarised in Tables IV.14 - IV.18. As usual, aggressive actions directed against males and females were counted separately.

There was a significant main effect of number of females for the total female-directed aggressive actions (Table IV.18). Thus, not surprisingly, more female-directed aggressive acts occurred (in both T.P. and C. groups) when a larger number of females was present, although the difference was not significant when the individual actions (threat, peck chase and fight) were analysed separately.

The males also showed a significantly higher frequency of total female-directed aggression in the strange-female observations compared with the familiar-female observations (Table IV.18). In this case the total was made up chiefly by pecks; for female-directed pecks the main effect of familiarity was significant at the 1% level (Table IV.15). Although the treatment x familiarity interaction was not quite significant, it may be

Table IV.14 Aggressive behaviour: threats

		Male-directed threats				Female-directed threats			

Summary of data

Females present		Familiar		Strange		Familiar		Strange	
	Males	One	Four	One	Four	One	Four	One	Four
T.P. Males	601	0	0	0	0	0	0	0	0.25
	602	0	0	0	0	0	0	0	0
	603	0	0	0	0.25	0	0	0.25	0
	604	1.50	0.25	0	0	0	0	0	0
C. Males	611	0	0.25	0	0	0	0	0	0
	612	0	0	0	0	0	0	0	0
	613	0	0	0	0	0.25	0	0.25	0.33
	614	0	0	0	0	0	0	0	0

Analysis of variance

Source of variation	SS	DF	MS	F	SS	DF	MS	F
Between subjects								
Treatment	0.10	1	0.10	1.11	0.00	1	–	–
Error	0.54	6	0.09		0.15	6		
Within subjects								
Familiarity females	0.10	1	0.10	0.91	0.02	1	0.02	–
Trt x Fam	0.05	1	0.05	0.45	0.00	1	–	–
Error	0.65	6	0.11		0.04	6	–	
Number females	0.02	1	0.02	0.33	0.00	1	–	–
Trt x Num	0.05	1	0.05	0.83	0.00	1	–	–
Error	0.35	6	0.06		0.04	6	–	
Fam x Num	0.05	1	0.05	1.00	0.00	1	–	–
Trt x Fam x Num	0.10	1	0.10	2.00	0.00	1	–	–
Error	0.28	6	0.05		0.06	6	–	

Table IV.15 Aggressive behaviour: pecks

| | | Male-directed pecks | | | | Female-directed pecks | | | |

Summary of data

Females present		Familiar		Strange		Familiar		Strange	
		One	Four	One	Four	One	Four	One	Four
	Males								
	601	0	1.25	0	0.25	0	0	0	0.50
T.P.	602	0	0.00	0	0.00	0	0	0	0.00
Males	603	0	0.50	0	0.00	0	0	0	0.00
	604	1.00	0.50	0	0.25	0	0	0	1.25
	611	0	0	0	0	0	0	0.25	0.67
C.	612	0	0	0	0	0	0.25	1.25	1.33
Males	613	0	0	0	0	0.25	0	1.25	1.67
	614	0	0	0	0	0	0	0.50	0.33

Analysis of variance

Source of variation	SS	DF	MS	F	SS	DF	MS	F
Between subjects								
Treatment	0.44	1	0.44	4.89	1.12	1	1.12	4.67
Error	0.52	6	0.09		1.41	6	0.24	
Within subjects								
Familiarity females	0.24	1	0.24	6.00*	2.26	1	2.26	14.13**
Trt x Fam	0.24	1	0.24	6.00*	0.78	1	0.78	4.88
Error	0.24	6	0.04		0.93	6	0.16	
Number females	0.10	1	0.10	1.43	0.20	1	0.20	4.00
Trt x Num	0.10	1	0.10	1.43	0.03	1	0.03	0.60
Error	0.44	6	0.07		0.31	6	0.05	
Fam x Num	0.02	1	0.02	0.29	0.20	1	0.20	2.86
Trt x Fam x Num	0.02	1	0.02	0.29	0.03	1	0.03	0.43
Error	0.42	6	0.07		0.40	6	0.07	

Table IV.16   Aggressive behaviour: chases

| | | Male-directed chases | | | | Female-directed chases | | | |

Summary of data

| Females present | | Familiar | | Strange | | Familiar | | Strange | |
		One	Four	One	Four	One	Four	One	Four
	Males								
	601	0	0.00	0.00	0	0	0	0	0.25
T.P.	602	0	0.00	0.00	0	0	0	0	0
Males	603	0	1.25	0.50	0.75	0	0	0	0
	604	0.50	1.75	0.25	0	0	0	0	0
	611	0	0	0.25	0	0	0	0.00	0.00
C.	612	0	0	0.00	0	0	0	0.25	0.67
Males	613	0	0	0.25	0	0	0	0.50	2.67
	614	0	0	0.00	0	0	0	0.00	1.67

Analysis of variance

Source of variation	SS	DF	MS	F	SS	DF	MS	F
Between subjects								
Treatment	0.63	1	0.63	2.42	0.95	1	0.95	4.13
Error	1.58	6	0.26		1.36	6	0.23	
Within subjects								
Familiarity females	0.07	1	0.07	0.54	1.13	1	1.13	4.91
Trt x Fam	0.20	1	0.20	1.54	0.95	1	0.95	4.13
Error	0.77	6	0.13		1.36	6	0.23	
Number females	0.13	1	0.13	1.86	0.64	1	0.64	4.92
Trt x Num	0.28	1	0.28	4.00	0.50	1	0.50	3.85
Error	0.43	6	0.07		0.79	6	0.13	
Fam x Num	0.28	1	0.28	4.00	0.64	1	0.64	4.92
Trt x Fam x Num	0.13	1	0.13	1.86	0.50	1	0.50	3.85
Error	0.43	6	0.07		0.79	6	0.13	

Table IV.17   <u>Aggressive behaviour; fights</u>

| | Male-directed fights | | | | Female-directed fights | | | |

Summary of data

Females present	Familiar		Strange		Familiar		Strange	
	One	Four	One	Four	One	Four	One	Four
Males								
T.P. Males 601	0	0.25	0	0	0	0	0	0.25
602	0	0.00	0	0	0	0	0	0.00
603	0	0.25	0	0	0	0	0	0.00
604	0	0.00	0	0	0	0	0	0.25
C. Males 611	0	0	0	0	0	0	0	0
612	0	0	0	0	0	0	0	0
613	0	0	0	0	0.25	0.50	0	0.33
614	0	0	0	0	0	0	0	0

Analysis of variance

Source of variation	SS	DF	MS	F	SS	DF	MS	F
Between subjects								
Treatment	0.01	1	0.01	3.33	0.01	1	0.01	0.25
Error	0.02	6	0.00		0.23	6	0.04	
Within subjects								
Familiarity females	0.01	1	0.01	3.33	0	1	-	-
Trt x Fam	0.01	1	0.01	3.33	0.03	1	0.03	3.00
Error	0.02	6	0.00		0.05	6	0.01	
Number females	0.01	1	0.01	3.33	0.04	1	0.04	4.00
Trt x Num	0.01	1	0.01	3.33	0	1	-	-
Error	0.02	6	0.00		0.08	6	0.01	
Fam x Num	0.01	1	0.01	3.33	0.01	1	0.01	3.33
Trt x Fam x Num	0.01	1	0.01	3.33	0.01	1	0.01	3.33
Error	0.02	6	0.00		0.02	6	0.00	

Table IV.18   Total all aggressive actions

Summary of data

		All male-directed aggression				All female-directed aggression			
Females present		Familiar		Strange		Familiar		Strange	
		One	Four	One	Four	One	Four	One	Four
	Males								
T.P. Males	601	0	1.50	0.00	0.25	0	0	0	1.25
	602	0	0.00	0.00	0.00	0	0	0	0.00
	603	0	2.00	0.50	1.00	0	0	0.25	0.00
	604	3.00	2.50	0.25	0.25	0	0	0	1.50
C. Males	611	0	0.25	0.25	0	0	0.00	0.25	0.67
	612	0	0	0.00	0	0	0.25	1.50	2.00
	613	0	0	0.25	0	0.75	0.50	2.00	5.00
	614	0	0	0.00	0	0	0.00	0.50	2.00

Analysis of variance

Source of variation	SS	DF	MS	F	SS	DF	MS	F
Between subjects								
Treatment	3.45	1	3.45	4.16	4.82	1	4.82	3.68
Error	4.96	6	0.83		7.85	6	1.31	
Within subjects								
Familiarity females	1.32	1	1.32	2.03	7.43	1	7.43	12.81*
Trt x Fam	1.53	1	1.53	2.35	2.77	1	2.77	4.78
Error	3.87	6	0.65		3.45	6	0.58	
Number females	0.38	1	0.38	1.52	1.96	1	1.96	8.52*
Trt x Num	0.50	1	0.50	2.00	0.27	1	0.27	1.17
Error	1.52	6	0.25		1.37	6	0.23	
Fam x Num	0.28	1	0.28	2.15	1.96	1	1.96	5.76
Trt x Fam x Num	0.07	1	0.07	0.54	0.27	1	0.27	0.79
Error	0.75	6	0.13		2.01	6	0.34	

Figure IV.2

Experiment 6. Analysis of variance, interaction profile.
Male-directed pecks; interaction of treatment x familiarity of
females.
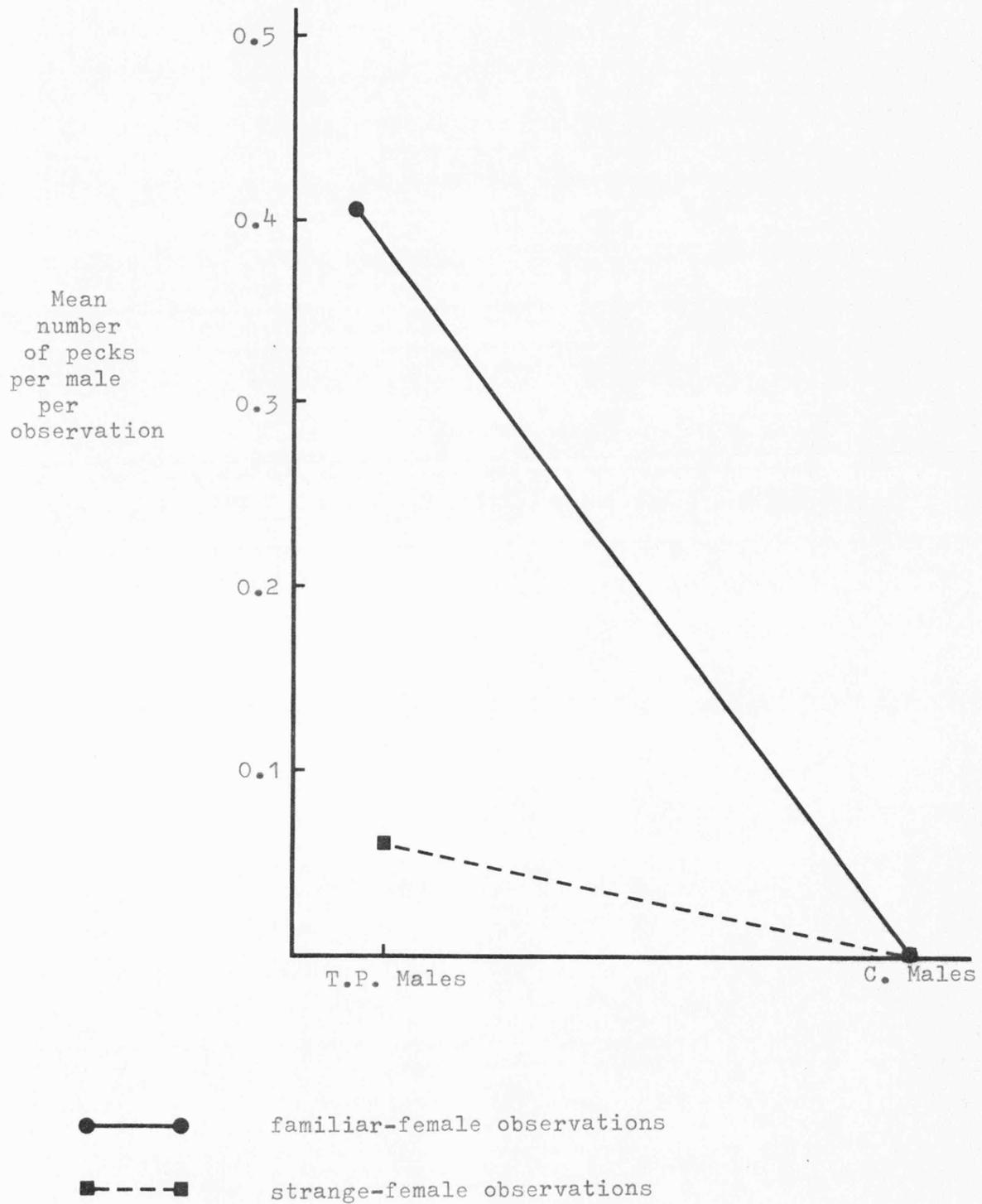
Table IV.19

Experiment 6. Addressees of the social displays grunt-whistle and head-up-tail-up, and the pair display turn-back-of-head, given by the T.P. males.

The table shows the number of displays addressed to a female (F), to a male (M) and the number for which the addressee was not determined (X).

Display	Grunt-whistle			Head-up-tail-up			Turn-back-of-head		
	F	M	X	F	M	X	F	M	X
Male									
601	11	2	7	14	2	2	5	0	1
602	5	0	4	27	2	3	2	0	0
603	6	6	8	10	7	4	0	2	3
604	9	1	9	14	0	3	24	0	0
Total	31	9	28	65	11	12	31	2	4

noted from the data in Table IV.15 that the C. males contributed on the whole more female-directed pecks than the T.P. males.

The only male-directed aggressive behaviour to provide a result of significance was pecks, for which there was an interaction of treatment and familiarity of females (Table IV.15). From the profile of this interaction (Figure IV.2) it can be seen that the T.P. males pecked each other more often in the familiar-female observations than in the strange-female observations, whilst the C. males did not peck each other at all.

A difference in the behaviour of the T.P. and C. males which is not described by the ANOVA may be found in a comparison of the total male-directed and total female-directed aggression exhibited by each male in the experiment as a whole, that is in all sixteen observations taken together. This information may be assessed from the data presented in Table IV.18. The four C. males were all more aggressive towards females than towards males, whereas three T.P. males were more aggressive towards each other than towards females (T.P. Male 602 exhibited no aggressive behaviour at all).

Behaviour of the females

The females used in the introductions engaged in very little social behaviour. No sexual behaviour or inciting was seen, but some of the females directed a few aggressive actions to the males, and one of them gave a little nodswimming. No differences could be discerned in the behaviour of the females in the different experimental situations.

4.4. Discussion

This experiment has demonstrated that although the testosterone treatment may encourage the performance of certain adult behaviour patterns in juvenile males, the expression of the behaviour is influenced by the familiarity of the males with the females who are present.

This was exemplified most clearly in the case of the social dis-

plays. The testosterone-injected birds displayed in the presence of familiar females, but not when strange females were introduced. A similar effect was found for the pair display turn-back-of-head.

It also appears that some of the precocious behaviour which is facilitated by the treatment depends on factors other than familiarity with females. The persistent chasing of females and grasping-neck-feathers which characterised the behaviour of the males in experiment 4 did not occur in the present experiment, in either the familiar-female or the strange-female observations. It is therefore likely that the occurrence of these behaviour patterns in the earlier experiment was promoted not by the fact that strange females were used, but by the period of monosexual isolation of the males during the injection period (see Section 3.4).

From a similar deduction it seems likely that the absence of an extended period of monosexual separation in the present experiment prevented, by and large, the development of homosexual behaviour in the injected males. However, in view of the fact that the males are now known to respond differently to strange and familiar females, it may be important that the males are kept with familiar females during the injection period (as was the case in the present experiment) to inhibit the development of homosexuality.

There was no general enhancement of aggressive behaviour by the testosterone treatment, but there were some differences in the aggressive responses of the testosterone-injected and control males which were, again, related to the strangeness or familiarity of the females.

These results can be interpreted in terms of conflicting interests of the resident males to behave aggressively towards an introduced bird, and to compete with each other for the attentions of an unpaired female.

Sexual rivalry is generally thought to be the cause of inter-male aggression within a flock. WEIDMANN & DARLEY (1971a) observed that a resident group of adult male mallards were aggressive towards one another

when a female was introduced to them, but not when a strange male was introduced. The female introductions were also accompanied by intense courtship activity, and the authors suggested that the aggression was due to competition between the males in attracting the females.

The following argument postulates that in the juvenile males of the present experiment inter-male aggression, and female-directed social displays and turn-back-of-head, are all behavioural manifestations of a situation where the males are competing for the attention of the females.

Thus the data suggest that the testosterone-injected males were in active competition for the familiar females (the highest frequency of male-directed pecking occurred in these observations, together with social displays and turn-back-of-head), but they were not sexually interested in the strange females. In the strange-female observations there was less pecking between males, little or no social display and turn-back-of-head, and more aggressive acts against females than in the familiar-female observations.

There appeared to be no sexual competition between the control males, as indeed would be anticipated in birds of juvenile status. The frequency of male-directed aggression was lower in this group, and the males did not perform social display or pair displays. The control birds in fact presented a predominantly aggressive response to the introduced females, particularly to the strange ones.

The testosterone-injected males did not give more social displays in the four-female observations than in the single-female observations, although studies of social display in adults have established that male displays are elicited partly by stimuli provided by the behaviour of females. The females used here were juveniles so, perhaps by virtue of their developmental immaturity or inexperience, the appropriate stimuli were not forthcoming. There were, for instance, hardly any cases of nodswimming, which is one female behaviour which certainly does facilitate displaying in adult

males (WEIDMANN & DARLEY, 1971a). One of the male displays, the grunt-whistle, occurred more often in the single-female observations than in the four-female tests. This might suggest that this particular display was promoted by the increased competition between males created by the unequal sex ratio in the single-female observations.

The testosterone-treated males were seen to give social displays in the very first familiar-female introduction, which was made after a single 5 mg injection had been administered to each male, two days earlier. ANDREW (1975a) noted a response to testosterone propionate injections in young chicks, in the form of precocious sexual behaviour, eighteen hours after the onset of treatment, but the literature includes no evidence for the minimum latency to a behavioural response to testosterone in ducks. In most of the published studies the first behavioural observations were made several days after the initiation of treatment. BALTHAZART (1976a) however mentions that juvenile male Rouen ducks give social displays only after one or two weeks of testosterone injections. The apparent latency to response found in different experiments will probably depend on a variety of factors, such as dosage and experimental conditions (see Section IV.6).

In view of the fact that the testosterone-injected males addressed social displays to the familiar females, it was hoped that the females might show some response. In fact very little social behaviour was exhibited by the females, certainly no inciting or sexual behaviour by which they might have demonstrated preferences for the males. The juvenile females may not have reached the stage of developmental maturity required for these behaviour patterns; to observe the effect of precocious male displays on females it is probably better to use adult females so that this possibility may be excluded.

IV.5. EXPERIMENT SEVEN

5.1. Introduction

It has now been established that juvenile male mallards can be induced to give social displays in the presence of familiar females by the administration of testosterone propionate. If the experimental males are not separated from females at any stage it is likely that they will address their displays to the females, and they will not develop homosexual behaviour or engage in persistent chasing of the females.

Bearing these points in mind, this experiment was designed to investigate the effect of hormone-induced displays on the behaviour of females, particularly on the development of their sexual preferences.

In this experiment groups of males were presented with an equal ratio of initially unfamiliar adult females. The males and females were kept together for several days to allow mutual familiarity to develop, and the social behaviour of the birds was sampled at intervals.

It was decided to use mature, initially strange females, rather than the juvenile females from the males' own rearing group, for two reasons:

1) Any preferences shown by the females could be attributed to events which occurred since the experiment (and injection regime) was begun. If the rearing-group females were used any relationships which were observed during the experiment might have originated during the previous months. SHERROD (1974) has demonstrated that, in mallards raised in captivity, early experience is important in determining later social and sexual companion preferences.

2) If a particular behaviour pattern was not shown by the females, this could not be explained in terms of their developmental immaturity.

5.2. Methods

The experiment was conducted immediately after experiment 6, using the same males as subjects (they were now about three and a half months old). The injections were continued without a break, the T.P. males each receiving 5 mg of testosterone propionate every other day. The two groups of males were kept in the same pens they had occupied for the previous three weeks. The original resident females were removed and were kept apart from the males for the duration of the experiment.

There were two parts to the experiment:

Part A.   Day 1 to Day 7

The original resident females were removed on the morning of day 1. That afternoon four adult females were introduced to each group, and they were kept with the males continually for six days.

Every day two or three observations were made of each group, between 08.30 and 16.00 hours. Each observation was initiated at a predetermined time, with no prior disturbance of the birds, and lasted 30 minutes. The observations were made in pairs; one group was watched for 30 minutes, immediately followed by an observation of the other group. The group to be observed first was alternated on successive occasions.

The social behaviour patterns recorded were the same as those recorded in the previous experiment, with the addition that the approximate duration in seconds of each burst of female nodswimming or inciting was measured. In all 14 observations were made of each group in part A.

Part B.   Day 7 to Day 11

On day 7 the first batches of females were removed, and another four females were introduced to each group. These females were kept with the males until day 11 when the study was ended prematurely by the escape of some birds from the observation pens. Observations were continued in

the manner described above.

The sixteen females used in the experiment were adults, one year older than the males, and they had not been in visual contact with the males before. They were selected at random from a large group of mallards which was kept on the main pond of the field station. The females were caught on the day before they were required, and were kept overnight in a separate pen.

5.3. Results

The data are presented in two sections:

(1) Global differences in the behaviour of the T.P. and C. males, and in the behaviour of the females introduced to the two groups.

(2) Detailed analysis of the oriented displays of the birds in the T.P. group.

(1) Comparison of the T.P. and C. groups

As stated above, both groups were observed for two or three 30 minute sessions each day. Some of the sessions were characterised by a low level of social activity, whereas in some observation periods the birds, especially those in the T.P. group, exhibited high levels of activity. This finding corresponds with those of other workers (e.g. RAITASUO, 1964) who have reported a polyphasic daily activity rhythm in wild mallards, with activity sessions alternating with rest periods.

In order to reduce the variation in the results caused by this phenomenon, the observations on each day were combined, and a daily mean score of each recorded behaviour pattern (frequency per 30 minutes) was determined.

The behaviour of the T.P. and C. males was compared by the Mann-Whitney U-test, using the median of the daily scores of each bird.

Behaviour of the males

The T.P. males gave considerably more social displays than did the C. males, in both Part A and Part B (Table IV.20). Significant differences were found for total displays, grunt-whistles and head-up-tail-ups in both parts and for down-ups in Part B. Very few displays were given by the control males, and those which were recorded were mainly head-up-tail-ups. Three of the T.P. males addressed their displays to females in both parts, but Male 603 displayed mainly to one of the other males.

The T.P. males also gave significantly more turn-back-of-head displays than the controls (Table IV.21), but mock-preen was very rare in both groups.

Sexual behaviour, too, was seldom observed. Pre-copulatory head-pumping was exhibited accasionally by the T.P. males, but never by the control males (Table IV.21). Male 601 was once seen to mount a female, but the other behaviour patterns associated with copulation were not recorded. The sexual behaviour and pair displays given by three of the T.P. males were always addressed to females, but Male 603 again addressed his behaviour to a male.

The aggressive behaviour of the males is summarised in Tables IV.22 and IV.23 respectively. There were no significant differences between the median scores of the T.P. and C. males, but an examination of the total frequencies reveals some very obvious trends.

Male-directed aggressive behaviour was almost entirely confined to the T.P. males. Threats, pecks, chases and fights were seen between the T.P. males, but only a single male-directed threat was delivered by a control male.

In contrast the T.P. and C. males performed roughly equal frequencies of female-directed aggressive behaviour. The only difference here was that the control males threatened, pecked, chased and occasionally

Table IV.20

Experiment 7. Social displays given by the males. The table shows the total frequency (T) and the median of the daily scores (M) in each observation series (Part A and Part B observations). The median scores of the T.P. and C. males were compared by the Mann-Whitney U-test. The significance levels of the probabilities associated with the U-values are expressed as N.S. = not significant (p > 0.05)
  * = p < 0.05

	Display	Grunt-whistle		Head-up-tail-up		Down-up		Total major displays	
		T	M	T	M	T	M	T	M
Part A (14 observations)	Male								
	601	17	0.7	13	0.3	16	0.8	46	2.0
T.P. Males	602	12	0.5	53	2.3	3	0.1	68	3.3
	603	16	1.0	21	0.7	8	0.5	45	2.7
	604	9	0.3	25	0.5	4	0.0	38	1.3
	Total	54		112		31		197	
C. Males	611	0	0.0	4	0.0	0	0.0	4	0.0
	612	1	0.0	5	0.0	0	0.0	6	0.0
	613	0	0.0	3	0.0	0	0.0	3	0.0
	614	0	0.0	0	0.0	0	0.0	0	0.0
	Total	1		12		0		13	
	U =		0		0		2		0
	P:		*		*		N.S.		*
Part B (9 observations)	601	10	0.7	6	0.3	10	1.2	26	2.4
T.P. Males	602	10	1.3	31	3.0	5	0.4	46	4.1
	603	17	2.0	8	1.1	7	0.8	32	3.0
	604	2	1.3	20	2.3	4	0.3	36	4.0
	Total	49		65		26		140	
C. Males	611	0	0.0	0	0.0	0	0.0	0	0.0
	612	1	0.0	3	0.0	0	0.0	4	0.0
	613	0	0.0	0	0.0	0	0.0	0	0.0
	614	1	0.0	0	0.0	0	0.0	1	0.0
	Total	2		3		0		5	
	U =		0		0		0		0
	P:		*		*		*		*

Table IV.21

Experiment 7.   Pair displays and pre-copulatory head-pumping.

For explanation of table see Table IV.20

	Display	Mock-preen		Turn-back-of-head		Head-pumping	
		T	M	T	M	T	M
Part A (14 observations)	Male 601	0	0.0	78	4.2	1	0.0
	T.P. 602	2	0.0	29	1.8	0	0.0
	Males 603	1	0.0	7	0.4	1	0.0
	604	0	0.0	20	1.2	0	0.0
	Total	3		134		2	
	611	0	0.0	0	0.0	0	0.0
	C. 612	0	0.0	0	0.0	0	0.0
	Males 613	0	0.0	0	0.0	0	0.0
	614	0	0.0	0	0.0	0	0.0
	Total	0		0		0	
	U =	8		0		8	
	P:	N.S.		*		N.S.	
Part B (9 observations)	601	0	0.0	24	2.8	2	0.0
	T.P. 602	0	0.0	48	5.7	0	0.0
	Males 603	4	0.0	26	1.9	1	0.0
	604	0	0.0	10	1.3	12	1.3
	Total	4		108		15	
	611	0	0.0	0	0.0	0	0.0
	C. 612	0	0.0	2	0.0	0	0.0
	Males 613	1	0.0	0	0.0	0	0.0
	614	0	0.0	0	0.0	0	0.0
	Total	1		2		0	
	U =	8		0		6	
	P:	N.S.		*		N.S.	

Table IV.22

Experiment 7. Aggression directed against males

For explanation of table see Table IV.20

	Display		Threat		Peck		Chase		Fight		Total	
			T	M	T	M	T	M	T	M	T	M
Part A (14 observations)	T.P. Males	Male 601	3	0.0	2	0.0	56	2.5	2	0.0	63	3.0
		602	1	0.0	4	0.0	0	0.0	2	0.0	7	0.0
		603	12	0.7	5	0.2	5	0.2	2	0.0	24	1.9
		604	9	0.0	6	0.0	3	0.0	0	0.0	18	0.0
		Total	25		17		64		6		112	
	C. Males	611	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
		612	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
		613	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
		614	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
		Total	0		0		0		0		0	
	U =		6		6		4		8		4	
	P:			N.S.		N.S.		N.S.		N.S.		N.S.
Part B (9 observations)	T.P. Males	601	3	0.3	0	0.0	1	0.0	0	0.0	4	0.5
		602	3	0.3	3	0.0	6	0.8	0	0.0	12	1.3
		603	7	0.8	5	0.5	22	1.6	0	0.0	34	3.2
		604	2	0.0	1	0.0	0	0.0	0	0.0	3	0.0
		Total	15		9		29		0		53	
	C. Males	611	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
		612	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
		613	1	0.0	0	0.0	0	0.0	0	0.0	1	0.0
		614	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
		Total	1		0		0		0		1	
	U =		2		6		4		8		2	
	P:			N.S.		N.S.		N.S.		N.S.		N.S.

Table IV.23

Experiment 7.   Aggression directed against females.

Only the total frequencies are shown;   most of

the median scores were zero

			Display	Threat	Peck	Chase	Fight	Total
Part A (14 observations)	T.P. Males	Male						.
		601	4	1	0	0	5
		602	0	0	0	0	0
		603	1	2	0	0	3
		604	2	2	0	0	4
		Total	7	5	0	0	12
	C. Males	611	1	0	1	0	2
		612	6	0	2	0	8
		613	4	1	10	0	15
		614	2	0	0	0	2
		Total	13	1	13	0	27
Part B (9 observations)	T.P. Males	601	1	3	0	0	4
		602	2	1	0	0	3
		603	1	8	0	0	9
		604	2	1	0	0	3
		Total	6	13	0	0	19
	C. Males	611	1	0	1	1	3
		612	2	4	0	0	6
		613	5	0	2	0	7
		614	3	1	0	1	5
		Total	11	5	3	2	21

fought with the females, whilst the T.P. males gave threats and pecks only.

Behaviour of the females

The most common displays given by the females, nodswimming and inciting, are recorded in Table IV.24. The total durations of these displays are shown, and also the median daily durations. The median scores of the eight females introduced to the T.P. group were compared with those of the eight females kept with the C. group.

Nodswimming was given by only a few of the females, and was performed regularly (i.e. median daily duration >0 secs) by just one bird in each group in each part of the experiment.

Inciting was shown by most of the females, and several of the females introduced to both groups addressed inciting displays to other females. Inciting addressed to a male, however, was significantly more common in the females presented to the T.P. group. Five females addressed a substantial amount of inciting to testosterone-injected males, but male-directed inciting was very rare in the control group.

Very few sexual and aggressive actions were given by the females, just a few head-pumping bouts and a few threats and pecks, with no noticeable differences between the females kept with the two groups.

(2) The orientation of displays in the T.P. group

The orientation of the displays of the males (grunt-whistles, head-up-tail-ups and turn-back-of-head) and of the females (inciting) are recorded in Appendix 5. In both parts of the experiment each of the T.P. males was found to display almost exclusively to a particular individual, and each male addressed his social displays and his turn-back-of-head to the same bird. Male 603 addressed Male 602 in both parts of the experiment, but fortunately the other three males exhibited no homosexual behaviour.

Each of the females, too, incited almost exclusively to a parti-

Table IV.24

Experiment 7. Nodswimming and inciting given by the females.

The table shows the total duration, in seconds (T) of the displays of

each female, and the median of the daily scores (M).

Display			Nodswimming		Inciting addressed to			
					Males		Females	
			T	M	T	M	T	M
	Female	Expt. Part						
Females introduced to the T.P. males	621	A	0	0.0	167	6.0	0	0.0
	622	A	2	0.0	0	0.0	86	7.3
	623	A	20	0.8	283	23.0	8	0.0
	624	A	6	0.0	316	17.5	0	0.0
	631	B	13	1.3	345	44.5	0	0.0
	632	B	0	0.0	0	0.0	146	13.8
	633	B	0	0.0	98	2.0	11	0.2
	634	B	0	0.0	0	0.0	374	42.8
	Total		41		1,209		625	
Females introduced to the C. males	625	A	0	0.0	0	0.0	14	0.0
	626	A	0	0.0	0	0.0	31	2.1
	627	A	9	0.2	22	0.0	364	8.5
	628	A	0	0.0	0	0.0	5	0.0
	635	B	0	0.0	0	0.0	146	13.7
	636	B	8	0.8	7	0.0	332	23.8
	637	B	0	0.0	0	0.0	4	0.0
	638	B	0	0.0	0	0.0	3	0.0
	Total		17		29		899	
	U =		31.5		12		32	
	P:		N.S.		*		N.S.	

Figure IV.3

Experiment 7.   T.P. Group, sexual preferences of the females, and females addressed by the males with social displays and turn-back-of-head.

An arrow 601 ⟶ 624 indicates that Male 601 addressed most or all of his social displays and turn-back-of-head to Female 624.
An arrow 601 ←---- 624 indicates that Female 624 addressed most or all of her inciting to Male 601.

Part A   MALES   FEMALES

601 ⇄ 624

604   621

602 ⇄ 623

603   622

Part B   MALES   FEMALES

601 ⇄ 633

604   631

602   632

603   634
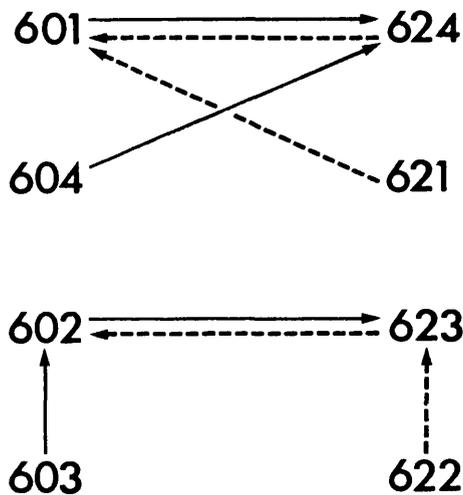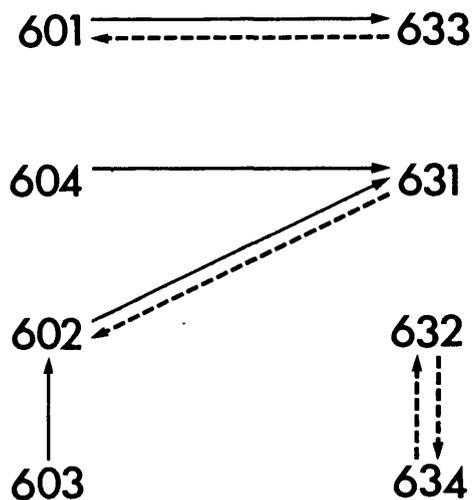
cular companion, thus the sexual preferences of the females could be determined. This information is summarised in Figure IV.3.

Three of the females showed homosexual preferences; in Part B Females 632 and 634 appeared to form a homosexual 'pair', addressing inciting to each other. Of the other five females, four developed preferences for a male who displayed to them. These were Females 623 and 624 in Part A and Females 631 and 633 in Part B. The remaining female, Female 621 in Part A, addressed inciting to a male who displayed to a different female. None of the males displayed to Female 621 anyway.

5.4. Discussion

The hormone treatment resulted, as expected, in a facilitation of social display in the males, whilst there was a non-significant increase in the frequency of turn-back-of-head, but no substantial effect on sexual or aggressive behaviour (see Section IV.6 for further discussion of the hormonal control of these behaviour patterns).

Unfortunately the homosexual problem was not entirely eradicated. One of the testosterone-injected males showed homosexually-oriented displays; this was the same male who showed a slight tendency in this direction in experiment 6. Although the males were not subjected to monosexual isolation or to repeated introductions of strange females, the females used were not as familiar to them as the other males in the group. In future studies it would probably be wise to separate males which had been reared together before stimulating them with testosterone. The homosexual problem was somewhat worse with the females, but it appeared that the behaviour of the testosterone-injected males was effective in reducing this abnormality (see below).

Three of the males did display to the initially unfamiliar females, and there were indications of competition between the testosterone-injected males as were found in experiment 6. Aggressiveness between

males was enhanced compared with the control males, who behaved aggressive-
ly towards the females only. Although the overall frequency of female-
directed aggression was unchanged by the hormone treatment, it might be
argued that the testosterone-injected males were less hostile to the fe-
males in that they did not chase or fight with them.

So what differences could be found in the behaviour of the fe-
males introduced to the two groups of juvenile males? The only female
behaviour to occur more frequently in one group than in the other was
male-directed inciting, which was facilitated by some factor specific to
the testosterone-injected males.

This inciting behaviour was unseasonal; the experiment was con-
ducted in early August, a period when inciting and other displays do not
normally occur. Inciting addressed to other females was seen in both
groups, so the inciting display itself may have been released by an effect
of crowding, or perhaps by the experimental procedure of introducing fe-
males who were partly familiar with each other to a group of totally un-
familiar birds. Homosexually-oriented inciting as a response of females
introduced to a new group has now occurred several times in this investi-
gation. There was, however, clearly some aspect of the behaviour of the
testosterone-injected males which promoted the release of heterosexual
inciting behaviour in the moulting females. This factor may well have
been the social displays - the only behaviour to occur significantly more
frequently in the testosterone-injected males than in the controls.

The five females who developed sexual preferences for the young
males provide circumstantial evidence in favour of the hypothesis that
social display promotes pair formation. From the present results, though,
it is not possible to distinguish between relative importance of the true
'social displays' (grunt-whistle, head-up-tail-up, and down-up) and the so-
called pair display or directed courtship display turn-back-of-head, which
was also given by the testosterone-injected males. It should be mentioned,

however, that many authors nowadays (e.g. STANDEN, 1976; SCHOMMER, 1978)
regard the distinction between the two forms of display as misleading.
It is now apparent in many duck species that the 'social' displays do in
fact bear components which are directed specifically towards a female.
This is certainly true of the grunt-whistle and head-up-tail-up displays
of the mallard, which in itself must surely argue in favour of a courtship
function of this behaviour.

It was hoped in this experiment to show that a female would
develop a specific preference for a male who addressed displays to her.
Each of the males (except the homosexual individual) did display pre-
dominantly to a particular female, and in most cases the female apparently
preferred the male who displayed to her.   Unfortunately it was not possible
to determine the primary factor in this relationship.   The male's dis-
playing and the female's inciting were usually both recorded for the first
time in the same observation session.

IV.6.   DISCUSSION: THE EFFECTS OF TESTOSTERONE ON THE BEHAVIOUR OF
        JUVENILE MALE MALLARDS

6.1.   Social displays

(a)   General

        The data presented in this study have established that exogenous
testosterone will facilitate the performance of social displays by juvenile
male mallards, but the expression of the behaviour usually depends upon the
presence of familiar females.   The testosterone-injected males of experi-
ments 6 and 7 did not exhibit social display during a fifteen minute intro-
duction of a strange female, but they did display to females who were
initially strangers to them, when these females were allowed to remain with
them for a longer period.

In experiment 4 the testosterone-injected males did display in the presence of strange females, but the situation here was different because the males were strongly homosexual. Their social displays were addressed not to the introduced females but to the other males in the group; familiar birds with whom they had established homosexual bonds.

It has often been shown that the expression of behaviour which may be facilitated by testosterone varies according to certain external conditions (e.g. SCHEIN & HALE, 1959; ANDREW, 1975a). In adult mallards social behaviour patterns, particularly social display, can be markedly different when males are observed with strange or with familiar females (see experiment 2), and the same is true of courtship patterns in male ring doves (ERICKSON & MORRIS, 1972; ERICKSON, 1973; SILVER & BARBIERE, 1977).

The reluctance of the testosterone-injected males in experiment 6 to display to strange females may have been due to their limited social experience. The males had been confined to their own rearing-groups since hatching, and the introductions during the hormone treatment represented their first contact with other conspecifics. Early social experience was shown to modify the behavioural responses of androgen-injected turkey poults to certain stimuli (SCHEIN & HALE, 1959).

The conclusion that exogenous testosterone will promote social display in mallard ducklings is in agreement with many earlier reports (see Section IV.1), but injections of testosterone propionate have repeatedly failed to facilitate such a response in Rouen ducklings (BALTHAZART & STEVENS, 1975; 1976; DEVICHE & BALTHAZART, 1976). These negative results have been used by the authors as support for an hypothesis that social display is not controlled by testosterone alone, but that other hormonal factors are important (see Section IV.1). An alternative explanation, in terms of experimental procedure, can now be advanced for the absence of social display in these studies.

In the experiments of BALTHAZART & STEVENS (1975, 1976), the experimental males were individually isolated during the early injection period. The observations were made by introducing several birds simultaneously to a separate observation pen for fifteen or thirty minutes, after which they were returned to their isolation pens. The birds were therefore always tested in the presence of strangers only, a factor which could have inhibited social display. A similar criticism can be applied to the third paper which was mentioned, that of DEVICHE & BALTHAZART (1976). The ducklings in this experiment were housed in groups, but the groups were kept separate, and each observation was made by taking a single male from each group for introduction to the observation pen.

It is also possible that in these experiments the expression of social display was inhibited because the males were unfamiliar with their surroundings, as the observations were made by introducing the birds to a novel environment. This would certainly have been a significant factor limiting the behaviour of mallards. I have noted on several occasions that the ducks at the field station will not exhibit their full range of social behaviour, especially the social displays, when they are first placed in a strange pen. A similar phenomenon has been recorded in the green-winged-teal (McKINNEY, 1965c) and in gadwall (SCHOMMER, personal communication).

The suggestion that one or both of these factors prevented the expression of displays in the testosterone-injected Rouen ducklings is strengthened by the result of a second experiment conducted by DEVICHE & BALTHAZART (1976). Immediately after their first series of observations described above, DEVICHE & BALTHAZART resumed the hormone treatment but carried out the observations of the males in a different way. A group of males was placed in the observation pen and left there overnight, and on the following day a female was introduced to the males. Under these conditions the males performed social displays!

It seems, then, that there is no reason to reject the hypothesis of an androgenic control of social display on the basis of negative results obtained from some testosterone-injection experiments.

BALTHAZART and co-workers have suggested that social display may be regulated not by androgen but by the gonadotrophin,follicle-stimulating hormone (F.S.H.). They have been unable to obtain quantitative differences in display frequencies as a result of injecting mammalian gonadotrophins (DEVICHE & BALTHAZART, 1976; BALTHAZART & DEVICHE, 1977; BALTHAZART, 1978), but the hypothesis rests mainly on correlation analyses. These are the absence of positive correlations of plasma testosterone concentration and display rates in individual birds (BALTHAZART, DEVICHE & HENDRICK, 1977a), and the correlation of the seasonal cycle of social display with circulating levels of F.S.H. rather than of testosterone (BALTHAZART & HENDRICK, 1976).

BEACH (1975), however, has emphasised that the presence (or absence) of a correlation between endocrinological and behavioural measures cannot be taken to imply causation, without the availability of more direct evidence. BALTHAZART et al. (1977a) mention themselves several reasons why the apparent lack of individual correlations of testosterone levels and behaviour frequencies might be misleading. For instance, the hormone levels were measured in blood samples which were collected several hours after the behavioural observations were made. These measurements may not reflect accurately the hormone concentrations which were present during the behavioural tests, since there are substantial daily variations in both testosterone (BALTHAZART, 1976a) and gonadotrophin (BALTHAZART, HENDRICK & DEVICHE, 1977b) levels in the plasma of individual drakes.

Evidence drawn from correlations of seasonal fluctuations in hormone levels and behaviour frequencies should also be treated with some reserve, in view of the possibility of a variation in the hypothalamic sensitivity to testosterone throughout the annual cycle (HUTCHINSON, 1976).

It may therefore be concluded that there is no strong evidence against the hypothesis which is supported by the present study, that social displays are controlled by endogenous androgen.

(b) **Effect of the testosterone treatment on the different display movements**

The three major displays were not affected equally by the hormone treatment. The head-up-tail-up was, on the whole, the most common display, and the down-up was the least (see Table IV.25).

In most of the observation series, one or more of the testosterone-injected birds failed to perform the down-up. In the POST-INJECTION observations of experiment 4, which were conducted 3-4 days after the termination of injections, the down-up did not occur at all, although grunt-whistles and/or head-up-tail-ups were still given by four of the six experimental males.

The total frequencies and relative proportions of the major displays given by each of the ten males which were injected with testosterone are shown in Table IV.25. These data may be compared with the display proportions of adult mallards observed in an undisturbed group in autumn and in spring (Table III.13), and in a residential all-male group subjected to repeated introductions of a female (Tables III.16 & III.17; 'four-male observations'). The comparison will confirm that the adult males under all three conditions performed relatively more down-ups and fewer head-up-tail-ups than were given by the testosterone-injected juveniles.

The study of BALTHAZART (1974) is also relevant to this discussion; juvenile Rouen males injected with testosterone did not perform a single down-up, although the frequencies of the other major displays, and also of introductory shakes and head-flicks, were significantly increased by the treatment.

One possible explanation of these results is that the various

Table IV.25   Social displays of the 10 testosterone-injected males

used in experiments 4 to 7.

The table shows the number of the three major displays grunt-whistle (GW), head-up-tail-up (HU) and down-up (DU), given by each of the testosterone-injected males. The relative proportions of the three displays performed by each male are expressed as percentages of the total displays.

Male	Experiments in which male was used	Frequencies				Percentages		
		GW	HU	DU	Total	GW	HU	DU
01	4 and 5	2	31	20	53	4	59	38
02	4 and 5	25	28	10	63	40	44	16
03	4 and 5	58	30	13	101	57	30	13
04	4 and 5	9	70	3	82	11	85	4
05	4 and 5	10	14	5	29	35	48	17
06	4 and 5	5	23	0	28	18	82	0
601	6 and 7	47	37	29	113	42	33	26
602	6 and 7	31	116	11	158	20	73	7
603	6 and 7	53	50	22	125	42	40	18
604	6 and 7	40	62	8	110	36	56	7
Total		280	461	121	862	33	54	14

social display movements are activated by different threshold concentrations of testosterone, or by different durations of treatment.

In domestic chicks (ANDREW, 1975a,b) and in young turkeys (SCHLEIDT, 1970), some sexual behaviour patterns required a higher dosage, or a longer duration of testosterone injections, than others. In mallard ducklings the various copulatory behaviours appear with different latencies after the initiation of testosterone treatment (see below). HUTCHISON (1970) was able to show that in the male ring dove different courtship displays were activated by different hypothalamic concentrations of testosterone. In the case of the mallard social displays it might be postulated that the down-up requires a higher daily or cumulative dose, or a longer duration of treatment, than the other two displays.

The delayed appearance of the down-up in the testosterone-treated birds, and the relatively high frequency of head-up-tail-ups, correspond with the development of social display in the ontogeny of untreated birds. According to deLANNOY (1967) the first major display to appear in juveniles males is the head-up-tail-up, followed by the grunt-whistle, and the down-up is the last. Notably the first displays of the control males in experiment 7 were mainly head-up-tail-ups, with a few grunt-whistles but no down-ups.

Possibly the physiological mechanisms which activate the down-up display require a longer duration of hormonal stimulation for their maturation or functional activation compared with the mechanisms underlying the head-up-tail-up and grunt-whistle. This might apply both to untreated birds undergoing normal rates of growth and development, and also to ducklings in which the maturation process is accelerated by the administration of exogenous testosterone.

The possible importance of absolute threshold concentrations of testosterone, rather than the duration of hormonal stimulation, in specifying the different displays, should not be excluded. The measurement of

plasma hormone concentrations, in both testosterone-injected and normally maturing birds, would be valuable. If, for instance, the sequential appearance of the different displays was parallelled by a steady increase in circulating testosterone levels, this might argue in favour of the threshold hypothesis.

It should be mentioned that DEVICHE & BALTHAZART (1976) found slight differences in the proportions of the displays of Rouen males subjected to different hormone treatments (see Section IV.1). These authors tentatively suggest that the different displays depend on different hormonal states, specifically that the down-up may be controlled by testosterone alone whereas the head-up-tail-up may require the synergistic action of testosterone and F.S.H. The evidence cited for this hypothesis, however, remains unconfirmed.

An entirely different explanation can be advanced for the abundance of head-up-tail-ups and the relatively uncommon occurrence of down-up in the present series of experiments. It may be that the hormonal priming of the males was sufficient to enable them to give all of the displays, but the appropriate behavioural releasing stimuli were not always present. It has already been noted that the down-up depends partly if not entirely on male-male interactions. It is conceivable that interactions of the appropriate nature occurred less frequently in the juvenile males than they would in a group of adult birds.

(c)   Effect of the treatment on the definition of the display movements

It has already been remarked that some of the grunt-whistle displays of the testosterone-injected males were of noticeably poor definition, in both postural and vocal aspects, compared with the characteristic adult display. In adult males the social display movements have sometimes been ascribed a 'typical intensity' (e.g. WEIDMANN, 1956), although JOHNSGARD (1960a) noted that some of the grunt-whistles seen very early and late in the season lacked the characteristic whistle call.

A poor definition of the grunt-whistle display in testosterone-injected ducklings has also been reported in wild mallards (ETIENNE, 1964) and in Rouens (P. DEVICHE, personal communication). Again, this corresponds with the early ontogenetic development of social display. The first display movements of young mallards are often indistinct in form (deLANNOY, 1967), and this is also true in other species, for instance goldeneye (DANE & van der KLOOT, 1964) and wood duck (KORSCHGEN & FREDRICKSON, 1976). It is not known if this is due to the inexperience of the young birds, or to immaturity of their neural or endocrine systems.

The head-up-tail-up display complex, as exhibited by the testosterone-injected males, was often truncated, lacking nodswimming and turn-back-of-head. It was noted, however that the males observed in experiments 4 and 5 gave nodswimming and turn-back-of-head more frequently in the latter experiment. Hence it may be postulated that the completion of the display sequence requires a longer total duration of hormone treatment than the head-up-tail-up movement itself. Alternatively, the difference in the execution of the head-up-tail-up complex may have been an indirect result of other behavioural aspects of the two experiments. Perhaps as a result of a reduction in the time spent chasing females in experiment 5, the males may simply have been allowed more time and space in which to complete the head-up-tail-up sequence.

6.2. Pair displays

The literature includes no information on the effect of testosterone injections on the pair displays.

In the present study mock-preen was rare in the testosterone-injected ducklings and the control birds alike. This is not a common display in captive groups of adult mallards (experiments 1 to 3, also DES-FORGES & WOOD-GUSH, 1976) so any conclusions relating to the hormonal control of the display would be premature.

The turn-back-of-head display was facilitated by the testosterone treatment; it occurred frequently in experiment 7 and occasionally in experiment 6. Why, then, was turn-back-of-head not recorded in the earlier experiments? It is not likely that the display requires a particularly high testosterone threshold or a long period of treatment; the daily dose (in experiments 4 and 5) and total duration of injections (experiments 4 and 5 combined) was greatest in the experiments in which the display did not occur.

The variable occurrence of turn-back-of-head is more likely to be explicable from behavioural considerations. There is no doubt that the turn-back-of-head of the male is partly facilitated by the behaviour of the female. The 'pair-palaver', involving a mutual display by the male and the female of turn-back-of-head and inciting, is well documented. WEID-MANN & DARLEY (1971a) have examined in some detail the intimate relation-ship of these two displays.

Similarly, in the testosterone-injected ducklings it seems that turn-back-of-head is more likely to occur if the females are responsive. Turn-back-of-head was seen most frequently in experiment 7, when the fe-males were showing their interest in the males by inciting. In experi-ment 5 the only two males to give turn-back-of-head were the ones to whom inciting displays were addressed.

In the testosterone-injected ducklings turn-back-of-head was facilitated not only by inciting, but also by the mere presence of familiar females. In experiment 6 the males addressed some turn-back-of-head to the familiar females, but none at all to the strange females. All of the females used in the experiment were largely unresponsive to the males; certainly no inciting was recorded, even by the familiar females.

6.3. Sexual behaviour

In contrast to the social displays, the displays and behaviour

associated with mating did not often occur in the testosterone-injected ducklings. The only significant effect was recorded in experiment 4, when the injected males performed frequent grasping-neck-feathers. Precopulatory head-pumping displays were seen occasionally in some of the experiments, but mounting, copulation and post-copulatory displays were never recorded.

Other authors have reported a strong stimulatory effect of testosterone on copulatory behaviour in ducklings (see Section IV.1), so why was so little precocious sexual behaviour seen in the present experiments?

In two domestic breeds it has been demonstrated that the various sexual patterns appear with different latencies after the initiation of testosterone injections. The order in which the behaviours appear correspond with their order of occurrence in the normal mating sequence of adults.

In one of these studies, DESFORGES (1974) gave newly hatched Aylesbury ducklings daily injections of testosterone propionate. The dosage rate was 1 mg per day for the first week, rising to 5 mg per day after two weeks. Head-pumping was seen in these birds after 7-9 days of treatment, grasping-neck-feathers after 12-14 days and mounting attempts after 14-16 days.

In the second investigation (BALTHAZART & STEVENS, 1976), one-month old ROUEN ducklings injected with 5 mg of testosterone propionate per day gave head-pumping and grasping-neck-feathers with a median latency of 6 days after the onset of injections. Mounting attempts appeared with a latency of $7\frac{1}{2}$ days and mounting at 10 days. The birds performed copulation and post-copulatory bridling and nodswimming displays only after a second course of injections at two months of age.

The dosage regimes used in the present study were as follows:

Experiment.	Daily dose (mg. test.prop. per bird).	Duration of treatment (days).	Days after initiation of treatment that observations were conducted.
4	10	12	10-13
5	5	9	8-9
6	5/2	12	2-11
7	5/2	22	13-22

The figures for experiment 7 include the days of treatment under experiment 6 since there was no intervening break in the injection schedule.

The dosage rate and length of observation period were in some of these experiments less than those of the studies cited above. The exact latencies which may be expected are likely to depend on factors such as breed, age of subjects and testing conditions, but the general principle may partly account for the absence of mounting, copulation and post-copulatory displays in the present study.

Alternatively, the paucity of sexual displays may have been due to a lack of the appropriate releasing stimuli. In adult mallards mating typically occurs between mutually 'consenting' birds, and a male will generally not proceed further than a few head-pumps if the female does not respond. Indeed the mounting attempts of the testosterone-injected Aylesbury ducklings (DESFORGES, 1974) usually occurred when a female was addressing sexual behaviour to the male concerned.

In the present experiments the females, although they sometimes incited the males, very seldom performed sexual behaviour, and hence were not 'sexually receptive' to the males.

In the experiments on the Rouen ducklings the injected males addressed sexual displays to, and sometimes mounted, females who did not

show reciprocal sexual behaviour (BALTHAZART & STEVENS, 1976), and sexual behaviour was even given by testosterone-injected males tested without females present (BALTHAZART & STEVENS, 1975). As mentioned earlier, however, the birds in these experiments were kept individually isolated between observations, so this isolation might have increased their sexual motivation and the likelihood of sexual behaviour occurring more spontaneously. It has already been suggested that the chasing and grasping-neck-feathers performed by the testosterone-injected mallards in experiment 4 was promoted by the monosexual isolation of the birds between observations.

In addition, sexual behaviour after testosterone treatment might be more likely to occur in domestic ducklings than in mallards. This is because copulations in wild mallard are usually restricted to paired birds, but domestic ducks do not form pair bonds and mating is promiscuous at all times (DESFORGES & WOOD-GUSH, 1976).

6.4. Aggressive behaviour

In several avian species aggressive behaviour is believed to depend upon high androgen concentrations (see CREWES & SILVER, 1979, for review). The evidence for the effect of testosterone on the aggressive behaviour of ducks, however, is inconclusive.

ETIENNE (1964) and ETIENNE & FISCHER (1964) reported an increase in the aggressivity of mallard ducklings and adult castrates after the administration of testosterone propionate. Exogenous testosterone also increased the frequency of some aggressive responses in male gadwall ducklings (SCHOMMER, 1978). There are conflicting reports concerning the effect of testosterone on the aggressivity of male Rouen ducklings. The ducklings injected by BALTHAZART (1974) and DEVICHE & BALTHAZART (1976) did not show more aggressive behaviour than the control birds. A similar treatment did, however, facilitate the occurrence of some agonistic

patterns in male Rouen ducklings observed in monosexual groups (BALTHAZART
& STEVENS, 1975) and in the presence of females (BALTHAZART & STEVENS,
1976).

In the present investigation the aggressive responses of the
testosterone-injected males differed substantially in the different experi-
mental conditions. In experiment 4 the testosterone-injected males chased
the females much more often than the controls did, but female-directed
threats, pecks and fights, and all measures of male-directed aggression,
were comparatively rare. The same males gave very low frequencies of all
aggressive actions in experiment 5 when they were kept with females be-
tween observations.

In experiments 6 and 7 the males were also kept with females,
and there was a tendency for the testosterone-injected males to show en-
hanced aggressiveness towards males whilst the control males were slightly
aggressive towards the females only.

It is probably better not to attempt to describe an effect of
testosterone on aggression per se, but rather to relate these findings to
the other aspects of the social behaviour of the males in the different
experimental conditions.

The predominantly male-directed aggressive behaviour of the testo-
sterone-injected males in experiments 6 and 7 has already been discussed,
in terms of competition (promoted by testosterone) between the males for
the attention of the females.

This inter-male rivalry was obviously not present in experiment 4,
when the injected males exhibited clear homosexual preferences and did not
display to the strange females which were introduced. It is not clear,
however, if the persistent chasing of the females represented an accentuated
aggressive response to a newcomer, as was shown to a lesser degree by the
control males in the later experiments. As previously mentioned the
chasing might have been sexually motivated. Further information on this

point could be provided by observing the behaviour of males kept in a

monosexual group on the introduction of a strange male. If an introduced

male was chased less vigorously than an introduced female, this would

possibly argue for a sexual motivation underlying the pursuits of the

females.

CHAPTER V

THE ROLE OF MALE AGGRESSION AND DOMINANCE IN PAIR FORMATION

The experiments described in the preceding chapters have concentrated on the role of social display in pair formation, but there were one or two indications that the aggressive behaviour of drakes might also be involved in this process.

These last two experiments were designed to investigate the role of male dominance and aggressiveness in pairing success. The experiments utilised a basic unit of two males and one female. The key behavioural parameters of interest were (i) the dominance relationship between the two males, and (ii) the sexual preference of the female.

V.1. EXPERIMENT EIGHT

1.1. Introduction

In pilot experiments with the one female-two males situation the following observations were made:

(a) When a male and female who are initially strangers to one another are kept together in a pen, and a male who was previously paired with the female is introduced to the pen, the female will generally exhibit a preference for her old mate over the strange male.

(b) When a male is introduced to a pen containing a male and a female, there will nearly always be aggressive interactions between the males. If the aggressive encounters are all in one direction, i.e. one of the males is always the aggressor, this male can be said to be dominant over the other.

It was decided to make use of this information in investigating whether the preference of a female for one of two males is related to the dominance relationship between the males in question.

A female and a male who were initially strangers to one another were housed together in a pen. Every day, or every few days, a second male who was either familiar with or had been paired with the female was introduced to the pen for a brief period. It was expected that for the first few days the female would prefer the introduced male, at least if it was her old mate.

The first question to arise is, would the introduced male also be dominant over the resident male? If so, one may ask if the relationships would change with time. For instance, would the resident male later become dominant over the other, and would this change be followed by a change in the female's allegiance?

1.2. Methods

The experiment was conducted between 25th October and 17th December. The pens used for the observations were L. pen, E. pen and W. pen (see Figure II.1).

The birds used were selected from two rearing-groups, which had been maintained intact since the individuals hatched in the spring of that year. The birds in one rearing-group were not familiar with those of the other group. One of the groups was observed closely for several days, and several monogamous pair bonds within the group were identified.

The experiment was conducted in two stages.

(a) Two of the stable pairs were selected; one pair was placed in E. pen and one pair in W. pen. A couple of days were allowed for the birds to familiarise themselves with the surroundings. Then, on October 25th the males were removed, and each was replaced by one of the 'strange' males from the other rearing-group, who was thereafter referred to as the resident male.

On the following day the introductions were begun. Three males were used for repeated introductions to each pen. One of these males was

the previous mate of the resident female, the other two were males from the same rearing-group, with whom the female was obviously familiar although she had not been paired with either of them.

On each observation day three introductions were made to each pen, one introduction of the 'previous mate' and one introduction of each 'familiar' male. Each introduction lasted fifteen minutes, during which time the displays and interactions of the birds were recorded, and after this period the introduced male was removed.

During the experimental period the males used for the introductions were housed in small pens, each with a female with whom he was initially unfamiliar, i.e. from the other rearing group.

(b) The resident birds were all removed, and the procedure was repeated with three more stable pairs (and three different 'resident' males), using E. pen, W. pen and L. pen.

Data were thus collected from fifteen experimental cases. Five cases involved repeated introductions to a male and female of the previous mate of the female, the other ten involved repeated introductions of a male who was familiar with the female.

1.3.   Results

The data obtained from the fifteen cases are summarised in Tables V.2 - V.16, and will be described shortly. The tables show the relevant social and aggressive behaviour which occurred in each observation period. The main characteristics of the cases are summarised in Table V.1.

General

Female preferences

In four cases (cases 8, 11, 12 and 14) the female exhibited a preference for the resident male in the first or second observation period, and her preference remained unchanged throughout the experiment. Some

inciting, always addressed to the resident male, was recorded in nearly every observation to confirm the female's constant preference for the resident male.

In the other 11 cases the female initially preferred the introduced male; for two or more observations she addressed inciting only to the introduced male, but she later switched her preference to the resident male. The preference-change cases included all those in which the introduced male was previously paired with the female.

In most of these cases the female's preference changed abruptly, either (a) she addressed inciting only to the introduced male in one observation, but on the next introduction she incited exclusively to the resident, or (b) the abrupt switch in inciting orientation occurred during the course of a single observation period.

In some of the cases the preference change was preceded by a few days when the female addressed inciting mainly to the introduced male, but she also addressed a few seconds of inciting to the resident male. After the preference change, however, the female no longer incited to the introduced male.

Male dominance

In six of the cases one male (in five cases it was the resident) dominated the other throughout the experiment. The dominant male performed some overt aggressive behaviour during each observation to confirm his constant dominance.

In the other nine cases (including all five in which the introduced male was the old mate of the female) the introduced male was initially dominant, but later the resident male became dominant. As with the preference changes, the dominance changes were abrupt, occurring either during the course of a single observation period or between two observation periods. After the resident male had become dominant (sometimes after a

fight) the introduced male showed no further aggressive behaviour.

The individual cases are now described, with particular reference to the preference and dominance changes, and giving some information additional to that provided in the tables. Each case is placed in one of three categories on the basis of the relationships of the individuals concerned (Table V.1).

Category A

Initially the female preferred the introduced male and the introduced male dominated the resident male. Both preference and dominance changed during the course of the experiment. Table V.1 shows which of the two was the first to change, and how much time elapsed before the second change. ('Sessions' indicates that the two changes occurred in different observation sessions.) For this purpose the time of the dominance change was defined as the moment of the first threat, peck or chase directed by the resident male towards the introduced male. There was a preceding period of variable duration following the last aggressive action performed by the introduced male, during which no aggressive encounters were recorded.

The time of the preference change was defined as the time of the first inciting display addressed to the resident male after which no further inciting was addressed to the introduced male.

Category B

The resident male was preferred by the female and also dominant over the other male throughout the experiment.

Category C

The female initially preferred the introduced male, and later changed her preference to the resident male. The initial dominance relationship between the males, however, did not change.

Table V.1

Experiment 8   Summary of cases

An explanation of the three right-hand columns is given in the text.   R = Resident Male

I = Introduced Male

Case No.	Identity of resident male	Previous relation- ship of introduced male to female	Male initially preferred by female	Did the female's prefe- rence change?	Male initially dominant	Did the dominance change?	Cate- gory	Did dominance or pre- ference change first?	Time lag bet- ween changes
1	840	Paired	I	Yes	I	Yes	A	Dom.	Ses- sions
2	840	Familiar	I	Yes	I	Yes	A	Dom	11 min.
3	840	Familiar	I	Yes	I	Yes	A	Dom.	10 min.
4	843	Paired	I	Yes	I	Yes	A	Pref.	8 sec.
5	843	Familiar	I	Yes	I	Yes	A	Pref.	1 min.
6	843	Familiar	I	Yes	I	No	C	-	
7	844	Paired	I	Yes	I	Yes	A	Pref.	Ses- sions
8	844	Familiar	R	No	R	No	B	-	
9	844	Familiar	I	Yes	I	Yes	A	Pref.	Ses- sions
10	848	Paired	I	Yes	I	Yes	A	Pref.	1 min.
11	848	Familiar	R	No	R	No	B	-	
12	848	Familiar	R	No	R	No	B	-	
13	850	Paired	I	Yes	I	Yes	A	Dom.	Ses- sions
14	850	Familiar	R	No	R	No	B	-	
15	850	Familiar	I	Yes	R	No	C	-	

CASE 1 (Category A)

For the first seven observations the female exhibited a consistent preference for her previous mate, and also directed some aggressive behaviour towards the resident male. There was a fight between the males within seconds of the first introduction, in which the victor was the introduced male, and he subsequently dominated the resident male. A second fight occurred early in the eighth observation, which was won by the resident male. After this fight the resident male delivered a large number of aggressive actions at the introduced male. The female performed no more aggressive behaviour, but she continued to address inciting to the introduced male for the rest of the observation period.

In the following observation period the female changed her preference; she addressed inciting to the resident male as soon as her old mate was introduced. The resident male chased the introduced male persistently throughout much of the fifteen minute period. This persistent chasing continued for some days, but had declined by the final observation session.

CASE 2 (Category A)

The female preferred the familiar, introduced male throughout the first seven observation periods. The introduced male was dominant from the first session, and the female also directed some aggressive actions towards the resident male.

During the eighth observation both the male dominance relationship and the female's preference changed. One and a half minutes after the introduction there was a fight, won by the resident male, who was afterwards very aggressive towards the introduced male. After the fight the female performed no more aggressive actions, but she addressed inciting to the introduced male for a further 11 minutes. She then switched her preference and incited only to the resident male.

Experiment 8   Explanation of Tables V.2 - V.16

Each table summarises the behaviour of the three birds in one 'case'.

Aggression

R→I, I→R;   Number of aggressive actions (threats, pecks and chases com-
bined) directed by the resident male (R) towards the intro-
duced male (I), and directed by the introduced male towards
the resident male respectively.   In some observation periods
the resident male spent most of the time persistently chasing
the other male.   In these instances the individual chases
were too numerous to count, and the entry 'PC' denotes per-
sistent chasing.

Fights;   Number of fights between males.

Dom.Male;   The resident (R) or introduced male (I) was designated as
dominant on the basis of the direction of their aggressive
encounters.

Female→R, Female→I;   Number of aggressive actions directed by the female
towards the resident male and the introduced male respectively.

Preference

Inciting R, Inciting I;   Duration in seconds of the female's inciting dis-
play addressed to the resident male and to the introduced male
respectively.

Pref. Male;   The male to whom the female's inciting displays were addressed
was designated the preferred male.   The entry 'I,R' indicates
that during the course of the observation period the female's
initial preference for the introduced male changed to a pre-
ference for the resident male.

Display

Female NS;   Duration in seconds of nodswimming displays given by the female.

Displays R, Displays I;   Number of major social displays given by the resi-
dent male and the introduced male respectively.

Notes   Where neither male was identified as the dominant or the pre-
ferred male, the cell in the table was left blank.   Where the
frequency or duration of a behaviour pattern was zero, the cell
was also left blank for clarity.

Table V.2   CASE 1.   Resident Male (R) No. 840

Introduced Male (I) previously paired with female

	Oct. 26	27	28	29	Nov. 1	3	5	9	10	12	.16	26
Date / Obsn. No.	1	2	3	4	5	6	7	8	9	10	11	12
Aggression												
R→I								46	PC	PC	PC	5
I→R	5	1	3		4	1	3					
Fights	1							1				
Dom. Male	I	I	I		I	I	I	R	R	R	R	R
Female→R	10	12	15	14	13	18	7					
Female→I												
Preference												
Inciting R									18	21	16	4
Inciting I	150	72	102	105	135	119	121	42				
Pref. Male	I	I	I	I	I	I	I	I	R	R	R	R
Display												
Female NS	1	1			3	6	5	37	4			
Displays R						1		3	2			
Displays I					4	7	1	9				

Table V.3   CASE 2.   Resident Male (R) No. 840

Introduced Male (I) familiar with female

	Oct. 26	27	28	29	Nov. 1	3	5	9	10	12	16	26
Obsn. No.	1	2	3	4	5	6	7	8	9	10	11	12
Aggression												
R→I								62	PC	PC	PC	3
I→R	7	2	1	4	2	4	1					
Fights								1				
Dom.Male	I	I	I	I	I	I	I	R	R	R	R	R
Female→R	4	9	4	11	3	6	15	1				
Female→I												
Preference												
Inciting R								10	51	21	16	5
Inciting I	64	102	73	170	201	152	118	68				
Pref. Male	I	I	I	I	I	I	I	I,R	R	R	R	R
Display												
Female NS		3	1		4	1	6	37	2			
Displays R							2	12	4			
Displays I							2	1				

In subsequent observations, as in CASE 1, the resident male chased the introduced male persistently. The female's preference for the resident did not alter.

CASE 3 (Category A)

The female demonstrated a clear preference for the introduced male from the first observation to the seventh, and directed some aggressive behaviour towards the resident male from the second session.

There were no aggressive encounters between the males on the first day, but from the second session onwards the introduced male appeared to be dominant.

Both preference and dominance changed during the eighth session. There were no aggressive interactions during the first minute, but then the resident pecked and chased the introduced male. There was no fight, but the dominance had irreversibly changed; all aggressive behaviour was subsequently performed by the resident male.

The female addressed inciting to the introduced male for the first 10 minutes of the eighth session, then she switched per preference and all subsequent inciting was addressed to the resident. She was no longer aggressive towards the resident. The resident male exhibited persistent chasing during the following two sessions.

CASE 4 (Category A)

The female preferred the introduced male (her previous mate) for the first eleven sessions. After a fight early in the first session, the introduced male was dominant throughout this period.

Both dominance and preference changed during the twelfth session, although in earlier observations the female had addressed very brief bursts of inciting to the resident male. Two seconds after the twelfth introduction the female began inciting to the resident, and eight seconds later there was a fight between the males which was won by the resident.

Table V.4   CASE 3.   Resident Male (R) No. 840

Introduced Male (I) familiar with female

	Oct. 26	27	28	29	Nov. 1	3	5	9	10	12	16	26
Date												
Obsn. No.	1	2	3	4	5	6	7	8	9	10	11	12
Aggression												
R→I								80	PC	PC	17	20
I→R		2		4	7	1	2					
Fights												
Dom. Male		I		I	I	I	I	R	R	R	R	R
Female→R		6	11	6	20	16	17					
Female→I												
Preference												
Inciting R								9	72	44	15	36
Inciting I	13	156	63	121	107	175	138	39				
Pref. Male	I	I	I	I	I	I	I	I,R	R	R	R	R
Display												
Female NS	1	1		2	2	2	10	3				
Displays R						4		2		1	2	1
Displays I				6	8	8	3	2				

Table V.5   CASE 4.   Resident Male (R) No. 843

Introduced Male (I) previously paired with female

Date / Obsn. No.	Oct. 26 / 1	27 / 2	28 / 3	29 / 4	Nov. 1 / 5	3 / 6	5 / 7	9 / 8	10 / 9	12 / 10	16 / 11	22 / 12	24 / 13	26 / 14
Aggression														
R→I												21	18	16
I→R	19	5	5	7	9	10	5	5	8	14	7			
Fights	1											1		
Dom.Male	I	I	I	I	I	I	I	I	I	I	I	R	R	R
Female→R	2	1												
Female→I														
Preference														
Inciting R							1	1		1	1	34	32	13
Inciting I	276	200	206	120	196	127	80	.111	156	206	130			
Pref. Male	I	I	I	I	I	I	I	I	I	I	I	R	R	R
Display														
Female NS		3		1										
Displays R	28	3	2		1	4	1	5	1	7	5	3		
Displays I					2			1		5	3			

In subsequent observations all aggression was directed by the resident male to the introduced male, and the female's inciting was addressed exclusively to the resident.

CASE 5 (Category A)

Once again the female's preference for the introduced male and the dominant status of this male were apparent for the early part of the experiment, and the female was occasionally aggressive towards the resident male.

During the ninth, tenth and eleventh sessions the female addressed a little inciting towards the resident, along with a great deal of inciting addressed to the introduced male. During the twelfth observation, both preference and dominance changed. The female began inciting to the resident male two seconds after the introduction, and this time she continued to incite to the resident. A minute later the males fought, the resident won and chased the other away. Aggressive behaviour performed by the resident reached a high frequency during that session, became persistent in the thirteenth session and declined in the fourteenth.

CASE 6 (Category C)

This was one of the only two cases (the other was case 15) in which the preferred male failed to dominate the other for a substantial period.

The female demonstrated her preference for the introduced male in the second session, which persisted until the eighth. In the ninth session her preference finally changed, although she had addressed a little inciting to the resident male in the preceding three observations.

The resident male, however, never became dominant. No aggressive encounters between the males were recorded until the fifth observation, but after that the introduced male remained dominant.

Table V.6   CASE 5.   Resident Male (R) No. 843

Introduced Male (I) familiar with female

	Oct. 26	27	28	29	Nov. 1	3	5	9	10	12	16	22	24	26
Date / Obsn. No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Aggression														
R→I												65	PC	34
I→R	2	2		7	6	4	8	3	4	7	8			
Fights												1		
Dom.Male	I	I		I	I	I	I	I	I	I	I	R	R	R
Female→R		4	2	3										
Female→I														
Preference														
Inciting R									2	1	3	33	35	17
Inciting I	431	442	175	234	388	235	235	28	164	114	67			
Pref. Male	I	I	I	I	I	I	I	I	I	I	I	R	R	R
Display														
Female NS					8	3	1							
Displays R	32	30	9	24	24	12	8		4	2		1		1
Displays I				7			9	4	2	6	10			

Table V.7 CASE 6. Resident Male (R) No. 843

Introduced Male (I) familiar with female

	Oct. 26	27	28	29	Nov. 1	3	5	9	10	12	16	22	24	26
Date														
Obsn. No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Aggression														
R→I														
I→R					1	1	5	4	14	8	2	6	7	8
Fights														
Dom. Male					I	I	I	I	I	I	I	I	I	I
Female→R				3	3									
Female→I														
Preference														
Inciting R						1	2	6	10	5	11	8	96	30
Inciting I		3	68	114	203	40	49	25						
Pref. Male		I	I	I	I	I	I	I	R	R	R	R	R	R
Display														
Female NS														
Displays R			7	5	21	3	5	4		1			5	4
Displays I														

CASE 7 (Category A)

The female preferred the introduced male (her previous mate), and directed occasional aggressive actions towards the resident male, throughout the first nine observations. During the early part of the tenth session she addressed a little inciting to the introduced male, but then her preference suddenly changed and she incited only to the resident.

The dominance relationship between the males changed more gradually. The introduced male was dominant until the eighth observation period. During the next two sessions the males appeared to be even; in the ninth session each pecked the other once, and in the tenth no aggressive encounters were recorded. By the eleventh observation period, however, the resident male had become dominant.

CASE 8 (Category B)

After a fight on the first day, all aggressive actions were performed by the resident male, who thus remained dominant. The female gave no inciting on the first day, but from the second observation period onwards she preferred the resident male.

CASE 9 (Category A)

During the first two sessions the introduced male dominated the resident, the female preferred the introduced male and she was occasionally aggressive towards the resident. During the third observation session the female changed her preference, but the introduced male was still dominant. Five seconds into the next session saw a fight between the males; the resident male was victorious and remained dominant thereafter.

CASE 10 (Category A)

For the first four sessions the female preferred the introduced male (her old mate), who was also dominant. During each observation, however, there were fights between the males; the introduced male was

Table V.8   CASE 7.   Resident Male (R) No. 844

Introduced Male (I) previously paired with female

Date	Nov. 30	Dec. 1	2	3	6	8	9	10	12	15	17
Obsn. No.	1	2	3	4	5	6	7	8	9	10	11
Aggression											
R →I									1		12
I →R	2	4		1	2	6	1	2	1		
Fights											
Dom.Male	I	I		I	I	I	I	I			R
Female →R	3	1	4	1		1		1			
Female →I											
Preference											
Inciting R										29	71
Inciting I	205	600	800	318	214	113	64	39	27	8	
Pref.Male	I	I	I	I	I	I	I	I	I	I,R	R
Display											
Female NS		2	3	36	21	3	3				
Displays R			2	5	11		1		3		
Displays I		1	7	27	17	3	11		2		

Table V.9   CASE 8.   Resident Male (R) No. 844

Introduced Male (I) familiar with female

Date	Nov. 30	Dec. 2	6	9	12	15
Obsn. No.	1	2	3	4	5	6
Aggression						
R→I	4	9	3	6	3	6
I→R						
Fights	1					
Dom. Male	R	R	R	R	R	R
Female→R						
Female→I						
Preference						
Inciting R		44	83	91	136	125
Inciting I						
Pref. Male		R	R	R	R	R
Display						
Female NS		68	29	2	4	
Displays R		8	4	13	10	
Displays I		3		5		

Table V.10   CASE 9.   Resident Male (R) No. 844

Introduced Male (I) familiar with female

Date	Dec. 1	3	8	10	15	17
Obsn. No.	1	2	3	4	5	6
Aggression						
R→I				17	12	16
I→R	3	4	6			
Fights				1		
Dom.Male	I	I	I	R	R	R
Female→R	2	2				
Female→I						
Preference						
Inciting R			61	156	87	68
Inciting I	400	365				
Pref. Male	I	I	R	R	R	R
Display						
Female NS	20	122		1		
Displays R	2	4		9	2	
Displays I	4	35	2			

Table V.11   CASE 10.   Resident Male (R) No. 848

Introduced Male (I) previously paired with female

Date / Obsn. No.	Nov. 30 / 1	Dec. 1 / 2	2 / 3	3 / 4	6 / 5	8 / 6	9 / 7	10 / 8	12 / 9	15 / 10
Aggression										
R→I					5	1	5	20	1	3
I→R	6	15	7	7						
Fights	2	1	1	1						
Dom.Male	I	I	I	I	R	R	R	R	R	R
Female→R										
Female→I							1	3		
Preference										
Inciting R					50	37	67	64	28	17
Inciting I	70	95	48	46						
Pref.Male	I	I	I	I	R	R	R	R	R	R
Display										
Female NS	7	6	4	9	3					
Displays R				3		3				
Displays I										

victorious each time and the resident male did not give any pecks, threats or chases.

During the fifth observation both preference and dominance changed. Two seconds after the start of the observation the female began inciting to the resident male. One minute later the resident male pecked and chased the introduced male; there was no fight but in subsequent encounters between the males the resident was always the aggressor. The female was sometimes aggressive towards the introduced male in later observations.

CASE 11 (Category B)

The female preferred the resident male from the first day. After a fight on the first day, the resident male asserted his dominance.

CASE 12 (Category B)

As in CASE 11, the resident male was both preferred and dominant throughout.

CASE 13 (Category A)

The introduced male was both preferred and dominant during the first five observation periods. There were fights between the males on most days, but each time the introduced male won.

After the sixth introduction there was an immediate fight, this time the resident male was victorious and he spent much of the next fifteen minutes chasing the other male. The female still preferred the introduced male during this time. During the following observation the resident male chased the other persistently, and the female's preference was not detectable. During the eighth session the female began inciting to the resident male. The persistent chasing declined in the ninth session, but the resident male remained both dominant and preferred by the female.

Table V.12   CASE 11.   Resident Male (R) No. 848

Introduced Male (I) familiar with female

Date	Nov. 30	Dec. 2	6	9	12	15
Obsn. No.	1	2	3	4	5	6
Aggression						
R→I	5	11	6	7	7	5
I→R						
Fights	1					
Dom.Male	R	R	R	R	R	R
Female→R						
Female→I						
Preference						
Inciting R	69	74	48	48	6	31
Inciting I						
Pref. Male	R	R	R	R	R	R
Display						
Female NS	17	25	3			
Displays R	10	9	1	2	1	
Displays I						

Table V.13   CASE 12.   Resident Male (R) No. 848

Introduced Male (I) familiar with female

	Dec.				
Date	1	3	8	10	15
Obsn. No.	1	2	3	4	5
Aggression					
R→I	12	8	5	5	7
I→R					
Fights					
Dom.Male	R	R	R	R	R
Female→R					
Female→I					
Preference					
Inciting R	115	104	105	51	81
Inciting I					
Pref. Male	R	R	R	R	R
Display					
Female NS	62	17	2		
Displays R	9	11	9	1	
Displays I					

Table V.14   CASE 13.   Resident Male (R) No. 850

Introduced Male (I) previously paired with female

Date Obsn. No.	Nov. 30 1	Dec. 1 2	2 3	3 4	6 5	8 6	9 7	10 8	12 9	15 10
Aggression										
R→I						PC	PC	PC	14	6
I→R	11	6	7	3	2					
Fights	1	1		2	1	1				
Dom.Male	I	I	I	I	I	R	R	R	R	R
Female→R										
Female→I										
Preference										
Inciting R								20	6	48
Inciting I	50	41	98	15	11	6				
Pref. Male	I	I	I	I	I	I		R	R	R
Display										
Female NS		2			1					
Displays R										
Displays I			1							

Table V.15 CASE 14. Resident Male (R) No. 850

Introduced Male (I) familiar with female

Date	Nov. 30	Dec. 2	6	9	12	15
Obsn. No.	1	2	3	4	5	6
Aggression						
R→I	7	13	15	8	6	6
I→R						
Fights						
Dom.Male	R	R	R	R	R	R
Female→R						
Female→I						
Preference						
Inciting R	9	15	8	17	13	10
Inciting I						
Pref. Male	R	R	R	R	R	R
Display						
Female NS						
Displays R	2	8		3		2
Displays I						

Table V.16   CASE 15.   Resident Male (R) No. 850

Introduced Male (I) familiar with female

Date	Dec. 1	3	8	10	15
Obsn. No.	1	2	3	4	5
Aggression					
R →I	24	29	PC	PC	12
I→R					
Fights					
Dom.Male	R	R	R	R	R
Female→R					
Female→I					
Preference					
Inciting R				6	15
Inciting I	19	67	3		
Pref. Male	I	I	I	R	R
Display					
Female NS	4	7			
Displays R		3			
Displays I					

CASE 14 (Category B)

The resident male was preferred by the female and dominant over the other male throughout the experiment.

CASE 15 (Category C)

The female initially preferred the introduced male, but later changed her allegiance. The resident male was dominant during every observation, and he chased the introduced male persistently on the day the female first preferred him, and during the preceding session.

Social display

The frequencies of social displays and female nodswimming are recorded in Tables V.2 - V.16. Some of the resident males and some of the introduced males gave many displays, but others gave very few. There was no obvious relationship between display frequencies and changing female preferences. The display frequencies were probably affected considerably by the time spent in other activities, for instance chasing.

1.4. Summary of the cases and discussion

The five females utilised in this experiment showed a clear preference for their original mate over the resident male, for 4, 9, 13, 15 and 22 days respectively after they were separated from their mates. This demonstrates a striking persistence of the pair bond, despite the fact that the mates were only together for a fifteen minute period once every couple of days. The auditory channel of communication, of course, was always open, and it has already been noted (experiment 1) that this is probably important in maintaining a bond between birds which are visually isolated.

In many cases the females also preferred a 'familiar' male to the resident male for several days. In these instances the primacy of the female's familiarity with the introduced male was apparently more important

than the recency of her familiarity with the resident male in determining her preference. SHERROD (1974) studied the development of social and sexual preferences in juvenile mallards, but she was unable to demonstrate a predominant role of either primacy or recency of experience in determining preferences. The importance of familiarity in the formation of pair bonds in adults is discussed further in Chapter VI.

In the present study the females in most cases changed their preference during the course of the experiment. These changes were usually abrupt and were also unambiguous and irreversible; this might not have been so if several males had been present in each group (see experiment 1, also WEIDMANN, 1956).

The changes in male dominance were also abrupt; there were no records of continuous alternation in the direction of aggressive encounters between two males, which was very convenient for the main purpose of the experiment.

There was a strong positive relationship between female preference and male dominance; in almost every observation the female preferred the dominant drake. In four cases the resident male was preferred by the female and also dominant over the introduced male throughout the experimental period. In the other eleven cases the female initially preferred the introduced male but later changed her preference to the resident drake. In nine of these cases there was a comparable change in dominance, such that the resident male became dominant at the same time as the female changed her sexual preference.

The important question here is the following; which variable is the primary factor, a change in which precipitated a change in the other variable? Both possibilities would seem to be feasible, either
(a) females tend to prefer dominant drakes, so in the experimental situation the preference changes followed the changes in the dominance relationships of the males, or

(b) the support of a mate tends to help a drake dominate other males, so the dominance changes would have followed the preference changes.

It is also possible for both these factors to operate and to complement one another. The data from the present experiment do not establish either one of these alternatives for certain. In four cases (involving two of the females) the dominance change was recorded before the alteration of the female's preference, and in five cases, concerning the other three females, it was the preference which apparently changed first.

In some cases it is possible that the dominance or preference might have effectively changed, and that the change might have been evident to the ducks themselves, some time before the change became apparent to the observer (by the expression of overt aggression or inciting behaviour).

Some indirect evidence for the two alternatives mentioned above can be suggested. In ten of the eleven cases in which there was a preference change, the male who was initially dominant was the introduced male. This contrasts with the usual aggressiveness of a resident male towards a newcomer. Clearly the 'prior residence' effect was superseded in these cases, one possible reason being the preference of the resident female, thus favouring alternative (b) above.

The same argument cannot be used for the instances of the changes in preference and dominance which occurred in favour of the resident male later on. These changes are certainly compatible with alternative (b), but on the other hand the dominance relationship of males might have been the first variable to change, perhaps as a result of a gradual strengthening in the position of the resident male as the occupant of the pen. If this were true then alternative (a) is justified. Further experiments are obviously required to test the two alternatives.

It should be mentioned that in two cases the correlation of female preference and male dominance did not hold. Possibly in these cases one of the males was considerably more aggressive than the other, or the pre-

ference of the female was particularly strong, to cause a departure from the usual dominance-preference relationship.

It is also possible that the observed behaviour of the three birds in any particular group was affected by certain extraneous factors, for instance the behaviour of the resident pair during the preceding introductions on the same day. In cases 1, 2 and 3, which involved the same resident pair, the resident male became dominant over all three introduced males on the same day. A second factor which may have influenced the results was the behaviour and relationship of the introduced males with their own new females, i.e. the females they were kept with between observation sessions.

Some additional features of the aggressive interactions recorded in the experiment require some comment.

Fights between males did not occur in a haphazard manner, but they appeared to be associated with the establishment or reversal of dominance. In most cases the fights, if they occurred at all, were recorded either on the first day, when the dominance relationship was established, or on the day when the dominance changed. In two cases the males fought on several days prior to (but not after) the dominance change, perhaps indicating that the resident was repeatedly (and at first unsuccessfully) 'challenging' the dominance of the introduced male.

In several cases the resident male chased the introduced male persistently during one or more observations. This 'victimisation' of one drake by another has been noticed before (e.g. DESFORGES, 1974), but in the present experiment this behaviour appeared to be associated with the dominance/preference changes. The persistent chasing occurred for one or more observation sessions immediately after the resident male had first become dominant and/or secured the preference of the female.

Much more aggressive behaviour was shown by the females compared with previous experiments. Four of the five females showed overt

aggression, always against the male who was both subordinate and non-
preferred at the time. It is open to question whether the dominant status
of a female's mate facilitates the expression of overt aggressive behaviour
by the female, or whether the converse is true, i.e. the aggressiveness of
a female increases the likelihood of her mate dominating the other male
(see alternative (b) above).

V.2.   EXPERIMENT NINE

2.1.   Introduction

As a result of the findings of experiment 8 two hypotheses were
made, (a) that a female is more likely to prefer a dominant male than a
subordinate male, (b) that a male who is favoured by a female is likely to
become dominant over another male.

Unfortunately there was time only for a pilot experiment to test
the former hypothesis, which produced inconclusive results. The second
hypothesis was tested in this experiment.

The experimental unit was, again, two males and one female, and
the behavioural parameter under study was the dominance relationship of the
two drakes. The preference of the female was known in advance, as only
firmly paired birds were used.

Several dyads of males were tested. A given two males were ob-
served together on two occasions, once in the presence of the mate of one
of the males, and once with the mate of the other. The hypothesis to be
tested was that the male whose mate was present would always be dominant,
so the dominance relationship between the two males would be different in
the two situations.

By using only firmly established pairs, and a short observation
period, a possible confounding effect of 'a female tending to prefer a

dominant drake' could be excluded. It was fairly certain that the female would prefer her own mate, regardless of whether or not he might be dominant over the other male.

Since stable dominance hierarchies occur in small groups of captive mallards (experiment 1), it was also of interest to see if long-standing dominance relationships between males would impede or enhance any tendency for a dominance reversal in the three-bird situation described above.

2.2. Methods

The experiment was conducted in March. The birds used were 8 firmly established pairs, four pairs from one rearing-group and four pairs from another. Birds in different groups were not familiar with each other before the experiment.

The groups were observed for a few days prior to the start of the experiment, and the birds selected for use were those which were obviously firmly paired.

The experimental observations were carried out in E. pen and W. pen. All birds had some experience of both pens, but during the experiment the two groups were kept in two of the other large pens.

The observations took seven days to complete. At 9.00 a.m. each day the sixteen birds were caught up. Each male was isolated in a small pen (see Figure II.1), and the females were kept in a monosexual group in another pen.

A female was then placed in one of the experimental pens, and she was allowed one hour to settle down. Two males were selected, one of which was the mate of the female. The two males were introduced simultaneously into the experimental pen, and the behavioural interactions of the birds were followed for fifteen minutes. The three birds were then removed; each male was returned to his isolation pen and the female was returned to

the all-female group. This procedure was then repeated using three different birds. Several such observations were made during the course of the day. At the end of the day the birds were replaced in their respective home groups.

A total of 56 observations was made. Each male was tested twice with each of the other males. The first time Male X and Male Y were introduced to a pen with the mate of Male X already present. On the second occasion Male X and Male Y were introduced to the mate of Male Y. If the first observation of these two males was in E. pen, the second would be in W. pen. The two observations were approximately three hours apart, and the two males were not used in any other tests in the intervening period. The 8 males used yielded 28 dyads (= 'pairs' of males); 12 of these were dyads of familiar males (i.e. members of the same group) and 16 were of unfamiliar males (members of different groups).

The tests were balanced so that each male was first tested with his mate present in approximately half of the dyads in which he was used. Each male was tested with his mate present an approximately equal number of times in E. pen and in W. pen.

2.3. Results and discussion

In all observations the female gave intermittent bursts of inciting, always addressed to her mate. In 32 of the 56 observations the female began inciting within five seconds of the introduction of the males, and in all but four tests inciting was recorded during the first minute. The females rarely showed overt aggression (only three instances were noted; each time the female threatened the 'rival' male), but aggressivee encounters between males were common.

There was generally no question over which male was dominant. In 49 observations aggressive behaviour was performed by only one of the males, who was of course designated the dominant male. The other 7 cases

were characterised by an early reversal in the initial dominance, i.e. one male showed aggressive behaviour at the start of the observation, but the second male soon asserted his dominance, often after a fight, and directed numerous aggressive actions towards the other male for the remainder of the observation period. The dominance reversals occurred in six observations within one minute from the start, and within four minutes in the other observation. In all these cases the male who latterly became dominant was designated the dominant male.

The dominance relationships between the males were highly dependent on the identity of the female present. The data presented in Table V.17 show that in all but six observations the dominant male was the one who was paired with the female. Thus in the 28 dyads, the dominance was reversed in 22 cases according to the identity of the female, whilst in six dyads the same male was dominant in both observations.

The dominance reversals occurred in 8 of the 12 dyads of familiar males and in 14 of the 16 dyads of strange males. The difference between familiar and strange dyads is no greater than would be expected by chance ($\chi^2 = 0.0379$, d.f. = 1, $p > 0.5$, 2 tailed). There is, therefore, no evidence that familiarity of males, and hence a history of aggressive encounters between them, has any modifying effect on the dominance reversal which is facilitated by the extreme conditions of the present experiment, i.e. the presence of the mate of one but not of the other.

The dyads in which dominance reversals did not occur might be explained by strong individual differences between the males concerned. Male A2, for instance, who failed to be dominant in three observations with his own mate present, might have been a particularly non-aggressive or otherwise weak individual. Alternatively, the pair bond between Male A2 and his mate may not have been very strong compared with the other pairs, in which case the presence of his mate would not have had such a large effect.

Table V.17

<u>Experiment 9</u>.   Dominance relationships of the males

Each cell shows the dominance relationship between the two males in a single observation.

D = The male whose mate was present was dominant

S = The male whose mate was present was subordinate

Identity of male whose mate was present

	A1	A2	A3	A4	B1	B2	B3	B4
A1		D	S	D	D	D	D	D
A2	D		D	D	D	D	D	D
A3	D	D		D	D	D	D	D
A4	S	S	D		D	D	D	D
B1	D	S	D	D		D	D	D
B2	D	D	D	D	D		D	S
B3	D	D	D	D	D	D		D
B4	D	S	D	D	D	D	D	

Identity of male whose mate was absent

Males A1, A2, A3 and A4 were members of one rearing-group,

Males B1, B2, B3 and B4 were members of the other group.

It was apparent, however, that in most cases the female had a strong influence on the ability of her mate to dominate a male to whom he had been subordinate only three hours earlier. As stated above, the females did not contribute directly to the aggression directed against the 'rival' male. The means by which their influence was brought to bear is a matter for conjecture, but the inciting display may be important. Many authors consider that inciting contains a ritualised aggressive component directed against a rival male, and an inciting female will occasionally swim close to the rival and stretch her neck in the threatening gesture.

In the present experiment the female performed inciting before her mate first showed aggression towards the rival male in 38 cases, whilst the male's aggressive behaviour appeared in advance of the inciting in 12 cases (this excludes the 6 cases in which the mated male never became dominant). This difference is statistically significant ($x^2 = 13.52$, d.f. = 1, $p < 0.001$), from which it might be speculated that the inciting display of the female promotes 'dominant' behaviour in her mate. Presumably this effect may operate either by facilitating subordinate behaviour in the rival male or by encouraging the expression of aggressive behaviour by the paired male. The latter function is that which is regarded as the evolutionary origin of the display (LORENZ, 1941), and according to LEBRET (1961) inciting "increases the aggression and intolerance of the drakes".

It is also possible that inciting has no such direct effect at all. The primacy of inciting over aggression may simply reflect a stronger motivation in paired birds to engage in the pair palaver when meeting after a temporary separation than to express direct interest in other birds who may be nearby.

Social display was not recorded in any observations. Copulations with associated pre- and post-copulatory displays occurred in several observations, and the females copulated willingly only with their mates.

Nineteen rape attempts were seen, where the rival male chased, mounted and sometimes actually copulated with the female. Rape attempts occurred with equal frequency in observations where the male and female involved were familiar and in observations in which they were strangers ($\chi^2 = 0.019$, d.f. = 1, p >0.8). Most attempted rapes occurred as soon as the males were introduced, and were initiated before any aggressive interactions between the males had been seen. On only four occasions was a rape attempt made by a male much later in the observation session when he was clearly subordinate to the paired male.

CHAPTER VI

DISCUSSION: PAIR FORMATION AND BREEDING BEHAVIOUR

In this chapter the results of the study are assessed, and a discussion is presented of some aspects of the behaviour of the mallard relating to pair formation and breeding.

The account is divided into three parts,

1. The formation and maintenance of monogamous pair bonds within the structure of the flock.

2. The initial breeding attempts of the pairs, and the aggressive behaviour of paired drakes.

3. Subsequent breeding attempts; re-pairing and promiscuity.

VI.1.   THE PAIR BOND WITHIN THE FLOCK

1.1.   Social display

(a) Social display and courtship

Some general points arising from the present investigation suggest that social display is related to pair formation.   The resident group of males (experiment 2) did not display in the spring when they were observed in the presence of their mates, but they did display to strange females when their mates had been removed.   This experimental procedure did not produce such a dramatic difference in the autumn (experiment 1), as social display did occur in the group of paired birds, but display frequencies did increase when the resident females were removed and the males were presented with unfamiliar females.

These findings are consistent with the view that social display is involved in courtship, but it is recognised that the experimental procedure of changing the females, which presented the males with the opportunity to resume courtship behaviour, may also have altered other aspects of the social organisation of the group.   There was also a large daily variation in the incidence of social display in these experiments, so ob-

viously display frequencies are affected by factors other than the intensity of pair formation pressure. It is noteworthy, however, that in the autumn experiment the unpaired females gave much more nodswimming than the females which had been stably paired with the males for several months. Possibly this indicated a need in the unpaired females to stimulate courtship from the males, in order to select a mate from the displaying drakes (c.f. McKINNEY, 1975a).

The finding that a single drake will display to a female (experiment 3) suggests that social display is more likely to be based on courtship than on say, inter-male hostility, as postulated by LEBRET (1961). The grunt-whistle and head-up-tail-up displays obviously do not depend on male-male interactions, though the same does not apply to the down-up.

Additional evidence supporting the hypothesis that social display is effective in courtship was provided by the precocious display behaviour of the juvenile males injected with testosterone. In experiment 7 adult females were more responsive, in their demonstration of sexual preferences by inciting, to the testosterone-injected males than to the non-displaying control birds.

The orientation of the male social displays and female preferences were examined in detail in adults (experiments 1 and 2) and in testosterone-injected juveniles (experiment 7) when pair formation was studied in groups in which the males and females were initially unfamiliar with each other. There was some degree of agreement between these two measures; in many cases a female demonstrated her preference for a male who displayed to her. This relationship did not always hold, and the displaying of some of the males was apparently 'unsuccessful' in eliciting a favourable response from the female to whom the displays were addressed. This is not very surprising, however, particularly in the rather small groups utilised in these experiments. Some males (and also some females) are bound to be more attractive as potential mates than others, and WEIDMANN (1956) reported that

unpaired birds would address courtship behaviour to several individuals before finalising their choice of mate.

On the whole the data support the hypothesis of a courtship function of social display. The occurrence of social display in a group of stably paired birds (experiment 1) might appear to be inconsistent with this view, and the persistence of display activity in the wild long after most of the flock members are paired was taken by LEBRET (1961) as eviddence that social display is not involved directly in pair formation. An explanation for the extended period of social display can, however, be found within the framework of the courtship hypothesis (e.g. SCHOMMER, 1978). Survival rates in the wild are low (HOCHBAUM, 1944; SOWLS, 1955), so males and females must be in a continual state of readiness to perform courtship displays (or, in the case of females, to stimulate males to display) in case their first mate is lost. This is likely to be particularly important in migratory populations, where mates may be lost during migration, so that pair formation can occur on either the wintering or the breeding grounds (WEIDMANN, 1956). The persistence of social display in paired birds may suggest that the behaviour is involved in maintenance of the bond, or that the males were attempting to form personal liaisons with females other than their mate (see Section VI.3).

(b) Pairing, social display and competition

According to SIEGFRIED (1974) and McKINNEY (1975a) the conspicuous nuptial plumage and elaborate epigamic displays of male ducks have probably evolved as a result of sexual selection, promoted by competition between males for mates.

RAMSAY (1956) and LEBRET (1961) were unable to detect evidence of competition between males during pairing, but in accordance with HOCHBAUM (1944) and McKINNEY (1975a) it seems inevitable that there will be competition as the members of a flock sort themselves out into pairs. The

competition is of course, likely to be accentuated by the unbalanced sex ratio in favour of males in winter flocks.

Expanding on the early views of HEINROTH (1910), McKINNEY (1975a) sought to explain the evolution of the communal aspect of social display in terms of the competitive interests of the courting males. He proposed that it would be advantageous to unpaired males to join in ongoing courtship activities, since there will presumably be a female present whom other males consider to offer possibilities as a potential mate. McKINNEY emphasised that social display should be regarded not as an organised activity with a raison d'etre of its own, but rather as the simultaneous efforts of individual males to court females.

In the same way McKINNEY considered that the pronounced synchronisation of male displays into discrete bursts was due to competition between males for the attention of females. A single male performing a major display is likely to catch the undivided attention of a female, but this may be countered by the other males present if they display at the same time, even though this may necessitate displaying from a sub-optimal spatial position. A similar argument has been propounded by WHITNEY & KREBS (1975) and PARTRIDGE & KREBS (1978) to account for the evolution of group calling in Pacific tree frogs, i.e. the synchronised calling by male frogs will enable each frog to reduce the female-attracting properties of the calls of rival males.

As a consequence of the view that social display is promoted by competition between males, one would expect inter-male hostility to be common in display sessions. NILSSON (1969) interpreted the flock display of the goldeneye duck in this way, and he pointed out a number of correlations between courtship activity and inter-male aggression in this species.

In the course of the present investigation it has already been noted that social display appears to be enhanced by competition between males. For instance, the introduction of females to groups of one, two

or four males (experiment 3) demonstrated that display frequencies increased when more males were present.   In the testosterone-injected ducklings, the experimental conditions which allowed the expression of social display activity were also characterised by an enhancement of male-directed aggression (experiments 6 and 7).

It should, however, be emphasised that the three major displays of the mallard drake are not equivalent in their dependence on the competitive aspect of courtship.

The grunt-whistle appears to be the commonest display given by a male in a 'non-competitive' situation, when he is displaying to a female with no other males present (experiment 3).   The head-up-tail-up is possibly the most important display in the initial competitive courtship of unpaired males, since the relative frequency of head-up-tail-ups was increased when the resident males in the autumn experiment (experiment 1) were presented with unfamiliar females in place of their established mates.

The down-up, however, is clearly more dependent than the other two displays on interactions between males.   It is the most highly synchronised of the three major displays (McKINNEY, 1975a) and is not used by a single male displaying to a female (experiment 3).

McKINNEY (1975a) believes that in the green-winged-teal the down-up contains two signal components;   the display simultaneously conveys courtship towards a female and threat towards a nearby male.   The linkage of these two messages, threat and courtship, in a single display is not uncommon in birds, a well known example being the territorial song of many passerines (see MOYNIHAN, 1955).   Sometimes the two functions may be distinguished by differences in form or orientation of the display in different behavioural contexts.   For instance WILEY (1975) was able to detect slight differences in certain components of the song-spread display of the carib grackle when the display was used as either courtship or threat.   As a second example, the 'bubbling' display is used by the male North American

ruddy duck in both threat and courtship, but the body orientation of the
drake is different according to whether he is addressing a male or a female
(SIEGFRIED, 1976).

The rab-rab display of the mallard drake is one which may convey
entirely different messages to other birds depending on the context in
which it is performed. When rab-rabs are given by a male in close proxi-
mity to his mate or potential mate, the display presumably functions in
reinforcement of the pair bond or in courtship. When several males engage
in a rab-rab palaver the displays are probably based on an aggressive in-
tent. The rab-rab display is also commonly given when a paired male and
female meet another pair or a single drake, and in this context the rab-
rab calling of the paired drake may fulfil both functions simultaneously.

To return to the down-up, in the gadwall this display is usually
linked in temporal sequence with the head-up-tail-up, but occasionally the
down-up is given on its own (SCHOMMER, 1978). The combined display is al-
ways performed by a male with his body oriented in a specific way with res-
pect to a nearby female and also to a second male, but the isolated down-
up is oriented only towards a rival male. This suggests that the down-up
may have threat and courtship functions when it is linked to the head-up-
tail-up, but threat only when it is performed alone. The lone down-up is,
in fact, the only gadwall display studied by SCHOMMER in which she did not
detect a female-oriented component.

In the mallard, there is no conclusive evidence that the down-up
is functional in courtship. Unlike the grunt-whistle and head-up-tail-up
displays, the down-up has no visual aspect which is directed specifically
towards a female, nor is the body of the performing male oriented with res-
pect to the position of the female (see Section I.3.4). Added to this is
the recent evidence that the down-up is not included in the repertoire of
a single male displaying to a female.

It may be postulated that the down-up might be effective in

attracting the attention of a female despite the absence of a specific female-oriented element, indeed SCHOMMER (1978) considers that any display performed in a social context is likely to relate signal information both to females and to rival males. It is, however, conceivable that the occurrence of down-ups in social display sessions is due solely to aggressive interactions between males. The constant jostling for position of the drakes would provide plentiful opportunities for aggressive displays, and it should be born in mind that down-ups are also seen in supposedly aggressive encounters between males at times other than during social display.

1.2. **Familiarity**

Social display is undoubtedly not the only behaviour involved in courtship. A male addresses social displays, 'directed courtship' displays and sexual behaviour towards a potential mate, and as a bond develops the two birds keep closer together and their activities become more synchronised.

Thus it seems that the development of a pair bond involves not only specific courtship displays on the part of the male, but also a gradual familiarisation of the partners and tolerance of close proximity. McKINNEY (1975a) and MARLER (1976) have emphasised that an important function of a male's courtship must be to reduce the aggressive tendencies of the female towards him, and thus to enable him to approach her more closely.

The process of familiarisation is probably as important as the displays themselves in many species, including estrildine finches (BUTTER-FIELD, 1970), ring doves (ERICKSON, 1973), common grackles (WILEY, 1976) and gadwall (SCHOMMER, 1978).

In the mallard, KLINT (1975) argued that individual recognition and prolonged familiarity could modify innate and imprinted preferences in situations where wild-stock mallards were reared with and subsequently

allowed to choose between wild-type or white-coloured conspecifics. The importance of familiarity in determining sexual preferences was demonstrated in experiment 8, when females which were kept with an initially strange male preferred an introduced male with whom they were familiar (although not actually paired) for several days or even weeks before switching their preference to the resident male.

It has been suggested that conspicuous displays may be important in the process of familiarisation by affording the performer the capacity to impress his identity on those who witness the display (MARLER, 1976; SCHOMMER, 1978). The post-copulatory displays of male ducks may well be important in this respect, by enabling the drake to impress his identity on his mate (McKINNEY, 1975a). In the mallard, however, copulations do not usually occur in a social context. In an active social group, especially when potential rivals may be present, the key function of assertion of the identity of a drake to his mate or potential mate might be served by the social displays.

This function would presumably be assisted if the form of each display was slightly different in different individuals but was consistent within the same individual. The social displays of the goldeneye (DANE & van der KLOOT, 1964) and the Chilean teal (STANDEN, 1976) do in fact show more inter-individual than intra-individual variation. This also appears to be the case in the mallard; some individual idiosyncrasies in the form of the displays have been found, and individuals differ in the duration of their displays (U. WEIDMANN, J. DARLEY & K.E.L. SIMMONS; unpublished observations).

The persistence of social display in paired birds (e.g. experiment 1) may in fact be due to a constant requirement of the drakes to affirm their identity to their mates, thus helping to maintain a close attachment. This is believed to be an important function of social display in the Chilean teal (STANDEN, 1976), and MARLER (1976) has speculated that

the maintenance of individual familiarity may be the ultimate function of many time-consuming social rituals in animals.

1.3. Plumage characters

Presumably the conspicuous plumage of male ducks, as well as the elaborate display, is the result of selection pressure. It is not certain, however, just how important plumage characters are in determining the pairing success of mallard drakes. There are reports of pairs seen in the wild in early autumn whilst the drake was still wearing the eclipse plumage (RAITASUO, 1964), but these may be instances of a pair bond persisting from the preceding breeding season.

PALMER (1976) suggested that females might preferentially pair with males with certain plumage features, such as a wide white band at the collar. JOHNSGARD (1960a) reported that in a free-flying population of mallards a small number of adult males with plumage aberrations were unable to obtain mates. These drakes performed a disproportionately high number of social displays, which led JOHNSGARD to speculate that they were forced to compete more strongly for mates than the wild-type drakes. Controlled experiments on the importance of male plumage characters in determining sexual preferences of females were not conclusive (KLINT, 1973).

The present investigation, however, makes it clear that the nuptial plumage is by no means essential for a drake to attract a female's preference. In experiment 7 the juvenile testosterone-injected males which attracted unseasonal inciting displays from females were still wearing juvenile plumage. There is, of course, no evidence here for the relative importance of displays and plumage characters in pairing success. It would be interesting to observe the preference shown by a female who was allowed to choose between a non-displaying adult drake in nuptial plumage and a juvenile male displaying under the influence of exogenous testosterone.

1.4. The role of aggression and dominance in pair formation

There was no doubt that in the undisturbed groups the males formed a stable dominance hierarchy; this was found both in the autumn and under certain circumstances in the spring. The hierarchy was analysed using directed threats, pecks and chases, and as one might expect in a peck order full scale fighting between males was very rare. In those experiments in which fighting was recorded (experiments 8 and 9) the conflicts did not seem to occur at random, but the fights were nearly always associated with a change in the dominance relationship of the two drakes involved.

In all experiments the females directed very little aggression towards each other or towards the males. This is compatible with the frequently cited argument that females should remain relatively passive in order to facilitate pairing (e.g. CASTORO & GUHL, 1958; WOOLFENDEN & FITZPATRICK, 1977).

It should be noted that WEIDMANN (1956) and PULLIAINEN (1963) were unable to detect a dominance hierarchy in wild mallard flocks. This does not necessarily mean, however, that the behaviour associated with the hierarchy in captivity is abnormal and cannot be related to the natural situation, for two reasons:

a) Hierarchies may in fact exist in the wild, based not so much on overt aggression by dominant birds, but rather on avoidance by subordinate birds of higher ranking individuals. Avoidance is more difficult for the human observer to detect. In an intensive study of social behaviour in the gadwall SCHOMMER (1978) noted that although overt aggression was not common, even in captive flocks, avoidance was very important in social interactions.

b) In a large, mobile flock repeated encounters between the same two birds may be fairly rare, and so a peck order may not become apparent. But the factors (behavioural or otherwise) which enable one drake to be dominant over another when they are placed in crowded captive conditions may still

be present in wild birds, and these factors may be evident to the ducks themselves although possibly not to the human observer.

In any case, in the present experiments the dominance hierarchy was not simply an artifact brought about by excessive crowding, since in experiment 2 the hierarchy of the males was clearly dependent upon their reproductive status (see below).

It is, therefore, probably worthwhile to speculate on the possible adaptive functions of dominance in the mallard, and to attempt to extra-polate from the behaviour observed in the captive situation to the inter-actions of birds in the wild state.

Dominance hierarchies have been demonstrated in many avian species, and the potential advantages to a dominant bird are diverse. It has been suggested that a high ranking bird might be more successful than subordinates in feeding (KREBS et al., 1972), or might be more likely to obtain a breeding territory or might obtain a better territory (GOFORTH & BASKETT, 1971; WILEY, 1973; SMITH, 1976; KNAPTON & KREBS, 1976). Male dominance is often related to success in obtaining a mate; this occurs in many lek species (e.g. BALLARD & ROBEL, 1974) and also in captive pigeons (CASTORO & GUHL, 1978). WOOLFENDEN & FITZPATRICK (1977) studied the com-plex dominance relationships which are found in Florida scrub jay families, and sought to explain their findings in terms of the reproductive interests of the individuals involved.

In the present investigation several observations indicated that inter-male aggression and dominance relationships were related in some way to pair formation.

(i)   In experiment 1 some peaks in the frequency of male-directed aggres-sion were coincident with the establishment of or changes in the mating preferences shown by the females.

(ii)   In experiment 2 there was a marked change in the nature of male-male aggressive encounters when the resident females were removed and the males

were presented with strange females, (and social display activity was resumed). That is to say, there was an immediate termination of territorial-type aggression and a reversion to the dominance hierarchy.

(iii) In the experiment involving repeated introductions of a male to a resident male and female (experiment 8), in most cases a change in the sexual preference of the female was coincident with a change in the dominance relationship of the two males.

The unconfirmed hypothesis that a dominant drake would have greater success in pairing is attractive for a number of reasons. It was suggested earlier (Section I.3) that the attention-catching properties of a drake's displays might be enhanced if he is able to achieve, through his dominance over the other drakes in the displaying group, the optimal spatial position relative to the female for performing displays. According to WEIDMANN & DARLEY (1971a) the dominant male in a group does usually maintain the best displaying position. It has been suggested that the overt hostility between drakes during social display is due to competition between the males for displaying positions (CRAMP & SIMMONS, 1977), and the constant manoeuvring of the drakes might in fact be partly due to repeated avoidance by subordinate males of dominant drakes.

A more direct role of male dominance in pairing success can be put forward; that a female might positively select a mate on the basis of his ability to dominate other drakes. There well may be advantages for a female to pair with a dominant male; if her mate is able to repel other drakes she will possibly suffer less harassment later in the season as males begin pursuit and raping behaviour. A female paired to a subordinate drake may have to spend a greater amount of her own time and energy in evading and fighting strange drakes.

The potential advantages accruing to a female who is paired with a dominant male might be realised in an alternative way, if a female is able to enhance the social status and/or aggressiveness of her mate after

pairing. This effect was shown to operate in experiment 9, where the dominant status of a drake was clearly dependent upon the presence of his mate. This experiment was conducted during the breeding period, when one would expect a drake to have a selfish interest in chasing other males away from his mate (to prevent rape). It is not known if the dominant status of a male is enhanced by the presence of a mate earlier in the season.

VI.2. THE BREEDING PERIOD: PAIR BREEDING, AGGRESSION AND TERRITORIALITY

The paired birds observed at the start of the breeding season (experiment 2) seemed to be behaving in a territorial manner. Each pair remained for most of their time within a particular area of the pen, their nest was within this area and the resident male was aggressive towards all other males who encroached upon his 'territory'.

It is possible that these manifestations of territoriality were in part artifacts of the high population density in the pen. In the wild home ranges of mallard pairs are much larger than those allowed by the confinement of the birds in the present study, and the ranges of neighbouring pairs may overlap considerably. A paired drake does not usually defend an area around his mate's nest, but HOCHBAUM (1944), DZUBIN (1955) and SOWLS (1955) believed that the small part of the home range embracing the waiting areas of the male constituted a territory or defended area, from which the male would chase other conspecifics. Certainly the so-called three-bird-flights, in which a drake chases the female of an intruding pair, are reportedly often initiated from the waiting area of the resident male, who generally returns to the same area after the chase (CRAMP & SIMMONS, 1977).

BEZZEL (1959), LEBRET (1961), HORI (1963) and RAITASUO (1964) considered that the term 'territory' was inappropriate as applied to the mallard, and RAITASUO (1964) stated that breeding mallard drakes do not

repel strange males. According to CRAMP & SIMMONS (1977), the extent to which a mallard male defends an area as a true territory depends on such factors as local population density and habitat characteristics. Similarly McKINNEY (1973, 1975a), has sought to explain the differences in the breeding behaviour of different dabbling ducks, including the degree of apparent territoriality, in terms of species-specific ecological constraints such as food requirements and availability, features of nesting habitat and predation pressure (see below).

Whether or not terms like 'territorial' can be rightly used to describe the breeding behaviour of the mallard, the biological function of the chasing behaviour of the males, other than those chases which are clearly associated with attempted rape, has not been satisfactorily resolved. According to McKINNEY (1965c), DZUBIN (1969a) and BARCLAY (1970) chasing results in the spacing of nests, since a pair, particularly the female, would tend to avoid nesting in an area from which they were chased. This view was supported by GILMER et al. (1975), who conducted a telemetry study of a number of mallards breeding on a Manitoba marsh, and were convinced that the aggressive behaviour of the drakes influenced the movements of adjacent pairs. Furthermore GILMER (1971) observed that when a drake left his mate after she had begun incubation the site he vacated was rapidly utilised by other pairs.

The potential adaptive advantages of spacing in ducks which have commonly been cited are a reduction in predation risks (McKINNEY, 1965c) and the establishment of an exclusive feeding area for the female during the laying and incubation periods when her energy requirements are high. The latter function has been suggested to be the basis of the aggressive behaviour of breeding males in the gadwall (DWYER, 1975), the shoveller (SEYMOUR, 1974a; McKINNEY, 1973; 1975a, see below) and the eider, in which ASHCROFT (1976) was able to show that the feeding rate of a female increased when her mate was nearby.

As a result of intensive studies of breeding shovellers, both
in the wild (SEYMOUR, 1974a,b) and in captivity (McKINNEY, 1967), it
appears that this species exhibits breeding behaviour which closely
approaches territoriality in the classical sense.   For instance, the home
ranges of shoveller pairs are smaller and have less overlap than those of
other species (see also GILMER et al., 1975), the drake stays almost con-
stantly within an area surrounding his mate's nest, he utilises a long-
range threat signal if other males approach and he always chases away con-
specifics who enter his territory.   Shoveller males who occupy adjacent
territories engage in ritualised fighting at the common boundary, and
pursuit flights are characterised by the reversal of roles of the pursuer
and pursued male as the territorial boundary is crossed.   The shoveller
utilises a specialised feeding method and requires a rich supply of food
(plankton) in relatively permanent ponds throughout the breeding season.
Thus McKINNEY (1973) and SEYMOUR (1974a) consider it likely that the func-
tion of the aggressive behaviour and territoriality of male shovellers is
the protection of an adequate supply of food for their mates.

This is less likely to be the basis of the chasing and spacing
of breeding mallards, since their food requirements are much less specia-
lised.   The observations that mallard drakes do not attempt to repel ducks
of other species, and that several nests of other ducks may be made close
to each mallard nest (HOCHBAUM, 1944; McKINNEY, 1965c) might also be cited
as evidence against the argument that spacing is caused by pressure of
predation or food availability.   Despite intensive field study (e.g.
DZUBIN, 1969a; DZUBIN & GOLLOP, 1972; POSPHALANA et al., 1974) the
breeding success of the mallard in relation to population density and food
availability is not clear.

A second possible adaptive function of the aggressive behaviour
of mallard drakes is one which has been described loosely as 'defen$\overset{c}{\cancel{s}}$e of
the mate'.   Certainly the aggressive behaviour of males during the breeding

season is directly related to the presence of their mates.   It was demonstrated conclusively in experiment 2 that the territorial structure of the group broke down immediately when the females were taken out of the pen. This differs dramatically from the case of the shoveller, in which a genuine site attachment has been observed.   SEYMOUR (1974c) showed that a shoveller drake initially became territorial when he secured a mate, but that he still defended the site they occupied from other males after his mate had been removed.   Furthermore, SEYMOUR reported a clear example of a reversal of the dominance relationship between two drakes according to ownership of the site of their encounter, in which the presence of the mate was not important.   The converse was demonstrated in the captive mallards in experiments 8 and 9;   clearly the presence of a mate is of great importance in determining the dominant status of a male.   In accordance with this observation, PALMER (1976) stated that a mallard drake defends an invisible area around his mate, and may attack other drakes from any location if he is accompanied by the female.

So, in the case of the mallard, what exactly is meant by 'defense of the mate'?   HOCHBAUM (1944) suggested that a mallard drake repels other drakes from the vicinity of his mate to prevent interference in their copulations.   An alternative possibility is that the aggressive behaviour of males and the resultant spacing of nests reduces the opportunities for the female to be raped by strange males.   The aggressive behaviour of paired males in experiment 2 did not appear to have this effect, since the frequency of rape attempts was just as high in the second half of the experiment when the paired females were replaced by the 'new' females who were not protected by the males.   It is quite likely that the artificially high density of the pairs in the experimental pen precluded an effective control of rape attempts.   The 'home range' of each pair was smaller than that quoted by GILMER et al. (1975) for mallards breeding in Manitoba by a factor of 10^5, and TITMAN & LOWTHER (1975) reported that the incidence of rape

was particularly high in a crowded breeding population.

A paired male would appear to have three lines of defenc̨e against the fertilisation of his mate by other drakes (i.e. rape). Apart from the postulated preventative measure of spacing he may attempt to repel would-be rapists by physically fighting them off. It is not uncommon, however, for several drakes to chase and attempt to rape a female simultaneously. In this event the paired male would probably be less likely to prevent the rape by direct intervention, and he might also risk injury to himself in doing so. According to BARASH (1977) the mate of a rape victim may adopt an alternative strategy to reduce the chance of his mate laying eggs fertilised by 'foreign' sperm, which entails no risk of injury and less energy expenditure than fighting. This strategy is for the male to copulate with his mate immediately or very soon after the rape, to ensure that his own sperm compete with those of the rapist. BARASH argued that it would be to the advantage of the male in such circumstances to force a copulation on his own mate, that is to rape her himself, if she is not prepared to mate with him willingly. Such 'forced pair copulations', which are distinguished from ordinary copulations between the members of a pair by the absence of the pre-copulatory ritual, have been recorded in wild populations (BEZZEL, 1959; RAITASUO, 1964) and also in captive mallard (BARRETT, 1973). GOODWIN (1956) reported that females who have just been raped by strange males are sometimes raped by their own mates soon afterwards, but he did not elaborate on the significance of this behaviour.

In a small urban population of mallard BARASH (1977) observed 39 forced pair copulations, of which 30 occurred within ten minutes of a rape attempt on the female concerned; a highly significant association. Furthermore BARASH noted that a forced pair copulation was more likely to follow a successful rape attempt (judged by the performance of post-copulatory displays by the rapist) than an unsuccessful one. In a group of captive mallards BARRETT (1973) also reported that forced pair copulations

tended to follow rape attempts; 11 out of 15 forced pair copulations came within one hour of an attempted rape.

VI.3.   THE BREEDING PERIOD: DESERTION, RE-PAIRING AND PROMISCUITY

Incubation and care of the young in the mallard are accomplished by the female alone, and in the wild the pair bond breaks soon after the hen has begun incubating.   In a wildlife reserve population in Idaho ORING (1964) reported that in ten of thirteen mallard pairs the drake left his mate on the first day of incubation.   The concensus of a number of authors (see McKINNEY, 1965c for references) is that mallard pair bonds generally break during the first week of incubation.

Adaptive advantages can be envisaged for both the male and the female in terminating their relationship once incubation has commenced. From the point of view of the female, the presence of the colourful and conspicuous drake near the nest might attract predators (SIBLEY, 1957; SCHAMEL, 1977).   From the point of view of the drake, his reproductive success will be enhanced by deserting his mate if he is able to father more progeny by addressing his attention towards other females.

Mate desertion as an evolutionary adaptation to maximise repro- ductive success is a topic which has received a great deal of attention in recent years.   Breeding strategies and mate desertion in particular have been discussed in terms of the theory of parental investment (TRIVERS, 1972; DAWKINS, 1976; DAWKINS & CARLISLE, 1976; MAYNARD SMITH, 1977; GRAFEN & SIBLEY, 1978), and PARKER (1974) analysed mate desertion from the specific approach of time expenditure on different reproductive activities. From an evolutionary standpoint the basic point, emphasised by TRIVERS (1972), is that if one member of a pair is able to raise the young unaided, then the other partner will desert to pursue secondary breeding attempts

with other conspecifics.

Comparative studies of mating systems in birds and mammals in general (ORIANS, 1969; SELANDER, 1972; EMLEN & ORING, 1977), and specifically in the Anatidae (McKINNEY, 1973, 1975a; SIEGFRIED, 1974, 1976), have argued that the breeding strategy (for instance mate fidelity, or early desertion and subsequent promiscuity) found in a given species depends on a range of ecological factors like abundance of food and predation pressure, as well as availability of mates.

The shoveller and the pintail, for instance, both members of the genus Anas, have strikingly different mating systems, which have been studied in depth by McKINNEY (1973, 1975a). The shoveller drake, due to a requirement to secure a rich localised food source for his mate, behaves in a territorial manner, vigorously defending his mate and their food supply against other conspecifics. The pair bond remains intact until the end of incubation, and the male invests very little time and energy in attempting to rape strange females. Presumably the female shoveller would be unable to raise the brood successfully if she was deserted or neglected by her mate earlier on. Pintail, on the other hand, range widely throughout the breeding season, utilising locally abundant food sources as they become available. It is clearly not economically feasible for each pair to protect an exclusive food supply, hence there is no territorial defenᶜe, the pair bond breaks early and the drake is free to spend much of his time pursuing and raping other females (both during the time he is paired and afterwards).

The strategy of the mallard appears to be intermediate between these two types. The drake may defend his mate vigorously during egg laying, but deserts to invest a greater amount of time in rape later on (see below).

Although the pair bond breaks early in incubation, in the wild many female mallards are in a position to make a second nesting attempt some

time after their mate has departed. This situation can arise in a number of ways:

a) Loss of the first clutch or brood by predation,

b) Desertion of the clutch by the incubating hen. According to BELLROSE (1976) some ten to fifteen per cent of nest loss in mallards is due to desertion by the female. This may occur as a result of harassment by predators or by other mallards, and abandoning of nests may be particularly prevalent where the breeding density is high (TITMAN & LOWTHER, 1975). Although mallards are well known for their adaptability to man, HUNT & ANDERSON (1966) reported that wild mallard hens abandon their nests more readily than ducks of other species as a result of human disturbance.

c) It has even been reported that a mallard female may lay a second clutch after successfully rearing a first brood (BJÄRVALL, 1969).

Re-nesting attempts are by no means exceptional; more than 50 per cent of mallard hens with destroyed nests made second nesting attempts according to the observations of KEITH (1961), COULTER & MILLER (1968), and DZUBIN & GOLLOP (1972).

A female who makes a second breeding attempt after her mate has left will obviously require fertilisation by a drake. It has been suggested (LEBRET, 1961) that a female in this situation might renew the pair bond with her old mate, but there is little evidence that this is a regular occurrence in the wild. If the observations of GILMER et al. (1975) are typical, that mallard drakes leave their home range soon after the female has begun incubating, then subsequent reunions of old mates would be rather unlikely.

If her old mate is not available a re-nesting female could try to form a pair bond with another drake, but it might alternatively be suggested that fertilisation could be achieved adequately by rapes alone.

Instances of a male or female pairing with a second partner after the dissolution of their first bond have been cited (SOWLS, 1955; WEIDMANN,

1956; LEBRET, 1961). The data from experiment 2 suggested that the males, after their original mates had been removed, were interested in forming bonds with 'strange' females, in as much as the drakes displayed to the new females and the daily frequency of rape chases did not increase. Social display does not normally occur as late as May in a dispersed breeding population, but the artificial situation of a 'flock' of unpaired birds presumably allowed the unseasonal expression of social behaviour involved in courtship.

In this experiment the original females were removed before any of them had begun incubation. It would be interesting to repeat this type of experiment during the incubation phase, that is to separate the paired birds at the time at which bonds would break under natural conditions. Would the drakes show the same interest in courting new females if they already had one 'successful' breeding attempt behind them? A study of breeding behaviour in the pintail (SMITH, 1968) showed that during the nesting season paired males spent more time raping strange females than did unpaired males, and the latter performed more courtship displays than the paired males. These results could be interpreted to suggest that pintail drakes do not invest heavily in promiscuous reproductive efforts until they have accomplished or at least begun an initial breeding attempt through a monogamous bond.

It is possible that some of the activities of mallard earlier in the year, during the flock period, may have some relevance to the re-nesting situation. Many workers have reported that paired males may address social displays to females other than their own mate. McKINNEY (1975a) speculated that these males may be trying to establish personal liaisons with a number of females, in order to facilitate future pairing attempts should they become necessary. This might arise through the death of the original mate, but as we have seen a second pairing might also become possible after the drake has deserted his incubating mate. It is also conceivable that a

drake who had familiarised himself with a female by displaying to her might be more successful in raping her than other drakes with whom the female was completely unfamiliar. These suggestions have not been tested but they are attractive because, if true, they would help to account for the persistence of social display in winter flocks long after most of the individuals are paired.

In contrast to the behaviour of the males in experiment 2, the 'new' females did not show a corresponding interest in pair formation. None of the females performed nodswimming and only one of them established a personal relationship with a resident drake. The duration of the experiment (5 days) was probably too short to enable any firm conclusions to be made regarding the motivation of the females.

Rapes are quite common during the breeding season, and McKINNEY (1975a,b) and TITMAN & LOWTHER (1975) consider that rapes contribute significantly to the fertilisation of eggs. From studies of wild populations of unmarked birds (LEBRET, 1961; RAITASUO, 1964; McKINNEY, 1965c) it is said that rapes occur more frequently during the latter part of the breeding season, when many of the drakes have deserted their incubating mates, than during the earlier period when most of the females are laying first clutches. In a captive group of breeding mallards, however, BARRETT (1973) recorded the highest frequency of rape attempts during the period that the females were laying, as did SMITH (1968) in the pintail, and she concluded that the primary stimulus for a male to engage in rape is provided by the presence or behaviour of a laying female.

In the view of McKINNEY (1975a) forced copulations or rapes are only of benefit to males, and females are 'victims of the system'. On the other hand, it is arguable that females trying to re-nest may benefit from being raped, if they have been deserted by their original mates. Some authors have speculated that re-nesting hens in need of fertilisation might actually encourage males to chase them.

SOWLS (1955), studying ducks breeding on prairie marshland, was convinced that many aerial pursuits in which a female was chased by a number of males were initiated by the female herself. SOWLS wrote that re-nesting females 'teased' drakes to chase them by uttering a call he referred to as the 'incitement' call. Watching the behaviour of marked females whose nests he had deliberately destroyed during incubation, SOWLS concluded that only females who had already been deserted by their mates initiated pursuit flights; the teasing behaviour was not shown by those females whose mate was still present.

SOWLS observed the teasing behaviour, which he termed 're-nesting courtship', in pintail, mallard and gadwall, but notably not in the shoveller or blue-winged teal. The latter two species both have long pair bonds; the drake does not leave his mate until late incubation.

It is not clear if the 'incitement' calls mentioned by SOWLS were really inciting calls; PHILLIPS and van TIENHOVEN (1962) and ABRAHAM (1974) considered that the behaviour in question was in fact the repulsion display. Repulsion displays are commonly given by incubating and post-incubating females, and the usual interpretation of the behaviour is that it functions in discouraging males from chasing the performer. PHILLIPS and van TIENHOVEN, however, believe that repulsion calls have a strong attracting effect upon drakes, and they described female pintails giving repulsion displays and not attempting to escape from the males who approached them,but rather enticing the males by making short runs and slow, hovering flights.

It has proved difficult to obtain direct evidence for these suggestions. If females do indeed entice males to chase them, is it for the purpose of initiating a rape or is it perhaps to stimulate courtship behaviour with a view to selecting a second mate? It might seem unlikely that a female would actively precipitate a rape chase in which she might be fertilised by a male not of her choosing. If, however, rape is un-

avoidable due to the persistence of the males, or if this is the only way in which she will be able to lay a second clutch, then by encouraging several males to chase her a female might at least be able to ensure that it is the strongest and quickest drake who succeeds.

SUMMARY

Despite considerable work on the behaviour of ducks, many questions remain over the behavioural basis of pair formation. One controversial topic has been the functional importance of the group activity known as 'social display'. Social behaviour was studied here in individually marked captive mallards of wild stock. Particular attention was paid to the roles of social display and of male aggressive behaviour in pair formation.

In the autumn social display was more frequent in a group of unpaired birds than in a group comprising paired individuals only. At the beginning of the nesting season in spring paired males did not display to their mates, but they did display to unpaired females when their mates had been removed. In many cases a female paired with a drake who had addressed displays to her. In another experiment social displays were given by a male to a female in the absence of other males. These data suggest that social display is more likely to be based on courtship than on, say, hostile interactions between males, except possibly in the case of the 'down-up' display. This was the only display movement which was not given by a male displaying to a female on his own.

Dominance hierarchies were formed amongst the males during the autumnal courtship period. In the spring the 'territorial' pattern of aggression between paired males changed to a dominance hierarchy as soon as the resident females were replaced by strange females and display activity was resumed. In an experiment involving groups of one female and two males the pairing preference of the female was closely associated with the dominance relationship between the males. In many of these groups the dominance relationship of the males and the mating preference of the female changed at the same time, such that the female was always paired with the dominant drake.

Social behaviour was studied in juvenile male mallards injected with testosterone propionate. This treatment facilitated the occurrence of many adult behaviour patterns, including social display, although the expression of the behaviour was dependent on the conditions under which the birds were observed. Social display, for instance, occurred only if the males were familiar with the females who were present, unless the males had become homosexual. The findings of these experiments were compared with those of other studies, including those in which testosterone treatment has failed to facilitate social display in domestic ducks.

The displays of the young males in the present study were effective in attracting the sexual interest of adult females during the summer post-breeding period, thus supporting the conclusion that social display is functional in courtship.

The social behaviour of the mallard was discussed in terms of pair formation within the flock, territorial responses and other aspects of the breeding behaviour of pairs, and secondary pairing and promiscuity during the latter part of the nesting season.

APPENDICES

Appendix 1. English and latin names of species mentioned in the text

English name	Latin name
Blue-winged teal	Anas discors
Budgerigar	Melopsittacus spp.
Carib grackle	Quiscalus lugubris
Chilean teal	Anas flavirostris flavirostris
Common grackle	Quiscalus quiscula
Eider duck	Somateria mollissima
Florida scrub jay	Aphelocoma coerulescens coerulescens
Gadwall	Anas strepera
Goldeneye duck	Bucephala clangula
Green-winged teal	Anas crecca
Japanese quail	Coturnix coturnix japonica
* Mallard	Anas platyrhynchos
Mandarin duck	Aix galericulata
North American ruddy duck	Oxyura jamaicensis jamaicensis
Pacific tree frog	Hyla regilla
Pintail	Anas acuta
Pochard	Netta rufina
Redhead	Aythya americana
Ring dove	Streptopelia risoria
Shoveller	Spatula clypeata
Starling	Sturnus vulgaris
Turkey	Meleagris gallopavo
Weaver bird	Quelea quelea
Wood duck	Aix sponsa
Wood pigeon	Columba livia
Zebra finch	Poephila guttata

* Includes domestic breeds; Aylesbury, Khaki-Campbell, Pekin, Rouen.

<u>Appendix 2</u>.   Experiment 1, Behaviour frequencies

        The following tables show the numbers of various displays

and other behaviour patterns performed by each of the birds in a

3-hour observation period on each of the dates indicated.

        In the cases of the female displays nodswimming and inciting

the values are the total duration (in seconds) of the displays given by

each female during the observation period.   All inciting recorded in

the tables was addressed to a male.   In addition, Female 22 addressed

inciting displays to a female, on the following dates:

        Nov. 15th: 11 seconds

        Nov. 16th: 35 seconds

        Nov. 17th: 28 seconds

        Nov. 18th: 4 seconds

        Nov. 19th: 1 second

a. Male behaviour: social displays

	Display	Grunt-whistle				Head-up-tail-up				Down-up				Total major displays			
	Male	01	02	03	04	01	02	03	04	01	02	03	04	01	02	03	04
Date																	
	Oct. 21st	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	22nd	7	5	4	3	3	2	0	3	2	3	2	2	12	10	6	8
With	25th	6	4	5	4	3	3	0	2	6	6	5	8	15	13	10	14
'old'	27th	3	2	0	1	1	2	0	1	2	2	1	1	6	6	1	3
females	29th	5	3	4	1	0	1	1	1	2	2	3	4	7	6	8	6
	Nov. 1st	5	2	1	1	3	2	0	1	1	0	0	1	9	4	1	3
	5th	4	0	4	2	0	0	1	2	3	3	1	2	7	3	6	6
	8th	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
	9th	15	0	0	2	7	0	0	0	0	0	0	0	22	0	0	2
	11th	5	1	3	1	3	4	2	4	4	6	3	6	12	11	8	11
	12th	5	1	1	2	7	1	1	5	2	0	1	2	14	2	3	9
With	15th	13	7	10	7	14	13	14	7	13	13	15	20	40	33	39	34
'new'	16th	5	1	7	8	2	2	3	3	4	3	4	5	11	6	14	16
females	17th	2	1	1	1	0	1	0	1	3	2	3	4	5	4	4	6
	18th	14	4	7	4	7	4	5	2	5	4	6	7	26	12	18	13
	19th	3	1	0	0	1	0	1	1	1	1	0	1	5	2	1	2
	22nd	12	6	5	2	4	2	5	4	6	4	6	4	22	12	16	10
	24th	11	1	11	5	3	1	4	3	3	1	3	4	17	3	18	12
	26th	11	17	10	6	9	19	8	7	9	4	13	11	29	40	31	24
	29th	3	3	3	2	1	2	1	1	1	1	1	1	5	6	5	4
	Dec. 6th	4	2	4	5	4	2	6	3	2	3	1	1	10	7	11	9

b. **Male behaviour: sexual behaviour**

Behaviour		Pre-copulatory head-pumping				Copulation			
Male		01	02	03	04	01	02	03	04
Date									
	Oct. 21st	7	0	1	1	4	0	1	0
	22nd	3	0	4	1	2	0	1	0
With	25th	0	1	0	0	0	0	0	0
'old'	27th	1	1	0	1	0	1	0	0
females	29th	0	1	0	4	0	0	0	0
	Nov. 1st	3	0	0	3	0	0	0	0
	5th	3	1	0	1	1	0	0	1
	8th	0	0	0	5	0	0	0	0
	9th	15	0	0	0	3	0	0	0
	11th	2	0	0	2	0	0	0	2
	12th	6	0	0	2	2	0	0	0
With	15th	5	0	0	3	1	0	0	1
'new'	16th	7	0	1	4	2	0	0	1
females	17th	0	0	0	3	0	0	0	0
	18th	16	0	0	3	3	0	0	1
	19th	5	0	0	8	2	0	0	2
	22nd	0	0	3	2	0	0	1	1
	24th	1	0	3	3	0	0	1	1
	26th	5	9	9	0	0	2	1	0
	29th	0	4	4	1	0	2	0	0
	Dec. 6th	0	2	2	5	0	0	0	1

c. **Male behaviour; aggression directed towards males**

Behaviour		Threats				Pecks				Chases				Total			
Male		01	02	03	04	01	02	03	04	01	02	03	04	01	02	03	04
Date																	
Oct.	21st	6	1	1	0	0	0	0	0	6	1	0	0	12	2	1	0
	22nd	2	0	8	0	1	0	0	0	0	0	1	0	3	0	9	0
With	25th	2	2	5	0	0	0	0	0	0	0	2	0	2	2	7	0
'old'	27th	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2	0
females	29th	3	0	2	0	0	0	2	0	1	0	2	0	4	0	6	0
Nov.	1st	1	0	2	0	0	0	1	0	0	0	0	0	1	0	3	0
	5th	3	0	2	0	0	0	0	0	0	0	0	0	3	0	2	0
	8th	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
	9th	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0
	11th	2	0	0	0	0	1	1	0	0	0	1	0	2	1	2	0
	12th	1	0	0	0	1	0	0	0	2	0	0	0	4	0	0	0
With	15th	1	0	5	0	2	1	0	0	0	0	0	0	3	1	5	0
'new'	16th	1	0	1	0	1	3	0	0	0	0	0	0	2	3	1	0
females	17th	0	0	4	0	2	0	0	0	0	0	0	0	2	0	4	0
	18th	0	0	3	0	0	0	0	0	1	0	0	0	1	0	3	0
	19th	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0
	22nd	5	0	17	0	7	1	0	0	2	0	7	0	14	1	24	0
	24th	0	0	10	0	1	0	2	0	1	0	7	0	2	0	19	0
	26th	4	16	14	0	2	1	0	0	1	10	8	0	7	27	22	0
	29th	3	2	8	0	2	1	2	0	2	0	3	0	7	3	13	0
Dec.	6th	2	2	8	0	1	0	0	0	0	1	3	0	3	3	11	0

d. **Male behaviour; aggression directed towards females**

Behaviour	Threats				Pecks				Chases				Total			
Male	01	02	03	04	01	02	03	04	01	02	03	04	01	02	03	04
Date																
Oct. 21st	0	0	0	0	0	0	0	0	4	0	0	0	4	0	0	0
22nd	0	0	1	0	0	0	0	0	7	0	0	0	7	0	1	0
With 25th	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
'old' 27th	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
females 29th	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nov. 1st	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5th	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8th	9	1	2	1	4	0	0	0	0	0	0	0	13	1	2	1
9th	1	2	0	0	0	3	0	0	0	2	0	0	1	7	0	0
11th	0	0	0	1	2	0	0	0	0	0	0	0	2	0	0	1
12th	0	0	0	0	0	3	2	2	0	0	0	0	0	3	2	2
With 15th	0	0	0	0	2	1	1	1	0	0	0	0	2	1	1	1
'new' 16th	0	0	0	1	0	3	0	3	0	0	0	0	0	3	0	4
females 17th	0	0	0	0	0	2	0	2	0	0	0	0	0	2	0	2
18th	0	1	0	1	1	0	1	0	0	0	0	0	1	1	1	1
19th	0	0	0	0	0	8	0	1	0	0	0	0	0	8	0	1
22nd	0	0	0	0	4	1	0	0	3	0	0	0	7	1	0	0
24th	0	0	0	1	1	0	2	0	0	0	0	0	1	0	2	1
26th	0	1	2	0	3	5	3	0	0	0	0	0	3	6	5	0
29th	1	0	0	0	3	3	0	1	0	0	0	0	4	3	0	1
Dec. 6th	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0

e. <u>Female behaviour</u>

Behaviour	Nod-swimming				Pre-copulatory head-pumping				Copulation				Inciting			
Female	11	12	13	14	11	12	13	14	11	12	13	14	11	12	13	14
Date																
Oct. 21st	0	0	0	0	7	0	1	1	4	0	1	0	45	0	3	11
22nd	0	0	0	10	3	0	3	0	2	0	1	0	26	11	21	49
'old' 25th	1	0	0	0	0	1	0	0	0	0	0	0	14	4	24	7
females 27th	1	0	0	0	0	1	0	1	0	1	0	0	20	12	5	42
29th	0	0	0	0	0	1	0	4	0	0	0	0	1	0	0	7
Nov. 1st	5	0	0	0	3	0	0	3	0	0	0	0	21	4	5	34
5th	0	0	0	0	2	1	0	1	1	0	0	1	18	6	9	46

Behaviour	Nod-swimming				Pre-copulatory head-pumping				Copulation				Inciting			
Female	21	22	23	24	21	22	23	24	21	22	23	24	21	22	23	24
Date																
Nov. 8th	8	2	14	17	0	0	0	5	0	0	0	5	33	59	57	308
9th	25	0	19	22	0	0	9	0	0	0	9	0	115	30	79	61
11th	0	0	38	40	0	0	1	2	0	0	1	2	10	34	43	112
12th	8	0	5	16	2	0	4	2	0	0	4	2	74	10	35	84
'new' 15th	43	0	26	40	2	0	2	3	0	0	2	3	112	31	57	135
females 16th	26	0	0	16	5	0	1	4	1	0	1	4	55	9	20	74
17th	2	0	22	1	0	0	0	3	0	0	0	3	7	3	21	14
18th	30	0	3	2	3	0	5	3	1	0	5	3	131	0	34	46
19th	1	0	1	2	4	0	1	8	2	0	1	8	25	2	15	23
22nd	6	0	14	0	0	0	2	1	0	0	2	1	8	13	28	98
24th	3	0	2	1	1	0	3	3	0	0	3	3	29	2	44	62
26th	10	25	10	4	4	10	9	0	0	2	9	0	102	550	68	44
29th	0	0	1	0	0	4	4	1	0	2	4	1	12	36	20	14
Dec. 6th	2	0	1	3	0	2	2	5	0	0	2	5	5	21	14	65

<u>Appendix 3</u>.   Experiment 1, orientation of displays

         The first table shows the number of social displays (grunt-

whistles and head-up-tail-ups combined) addressed by each male to each

of the females, on each observation date of the 'old female' observa-

tions.   The table also shows the number of displays for which the

identity of the addressee was not determined (notation 'X').   The

second table gives the same information for the 'new female' observa-

tions.

         The third table shows the duration (in seconds) of inciting

displays addressed by each of the 'new' females to each of the males,

in each observation period.

a. **Social displays of the males in the 'old female' observations**

Performer	Male 01					Male 02					Male 03					Male 04				
Addressee	Females 11	12	13	14	X	Females 11	12	13	14	X	Females 11	12	13	14	X	Females 11	12	13	14	X
Date																				
Oct.21st																				
22nd	7				2	2	3			2			3		1				4	2
25th	8				1		4			3	1		2		2	1		2	1	2
27th	2				2		1			3									1	1
29th	3				2	1	1			2			2		3				1	1
Nov. 1st	6				2		2			2			1							2
5th	3				1								3		2			1	3	
Total	29	0	0	1	10	3	11	0	0	12	1	0	11	0	8	1	0	3	10	8

Performer	Male 01					Male 02					Male 03					Male 04				
Addressee	\ 21	22	23	24	X	21	22	23	24	X	21	22	23	24	X	21	22	23	24	X
Date																				
Nov. 8th		1																		
9th	18	3			1														1	1
11th		5			3				1	4				3	2				3	2
12th	1	1	7		3					2				2					5	2
15th	9		2	2	14	3			2	15	6			3	15				5	9
16th	3			2	2				1	2	5				5	1			6	4
17th					2					2					1				2	
18th	10	4			7					8	6		1		5				3	3
19th	3		1						1		1								1	
22nd	6	1			9	1				7	4		1		5				3	3
24th	9	3			2					2	9		1		5				4	4
26th	10				10	30				6	4				14				5	8
29th					4	2				3	1				3				1	2
Dec. 6th	4				4	2				2	3				7				4	4

c. Inciting performed by the 'new' females

Performer	Female 21				Female 22				Female 23				Female 24			
Addressee (Male No.)	01	02	03	04	01	02	03	04	01	02	03	04	01	02	03	04
Date																
Nov. 8th	33				59				56			1				308
9th	115				30				78			1				61
11th	10				9			25	43							112
12th	74				10				35							84
15th	112				31				57							135
16th	55				9				20							74
17th	7				3				8		13					14
18th	121		10						33			1				46
19th	25							2	15							23
22nd	8				13				3		25					98
24th	18		11				2				44					62
26th	85		17			550					68					44
29th	10		2			36					20					14
Dec. 6th			5			21					14					65

<u>Appendix 4.</u>   Experiment 4, behaviour of the males in the POST-INJECTION

   observations

      These tables show the total (T) and median (M) frequency of

each behaviour pattern performed by the males in the POST-INJECTION

observations.   The tables also show the results of a comparison of the

median frequencies of the testosterone-injected and control males by

Mann-Whitney U-test (N.S. = not significant).

a. **Social displays**

(The abbreviations are given in Table II.1)

Display		HF T	HF M	IS T	IS M	GW T	GW M	HU T	HU M	NS T	NS M	DU T	DU M	Total major displays T	Total major displays M
	Male														
	01	24	3.5	3	0.0	0	0	2	0	1	0	0	0	2	0
	02	11	2.5	8	0.5	2	0	2	0	1	0	0	0	4	0
T.P. Males	03	5	1.0	4	0.5	1	0	1	0	0	0	0	0	2	0
	04	18	4.5	0	0.0	1	0	8	1.0	2	0.5	0	0	9	1.5
	05	3	0.5	2	0.5	0	0	0	0	0	0	0	0	0	0
	06	2	0.5	2	0.5	0	0	0	0	0	0	0	0	0	0
Total		63		19		4		13		4		0		17	
	11	3	0.5	0	0.0	0	0	0	0	0	0	0	0	0	0
	12	3	0.0	4	0.0	0	0	0	0	0	0	0	0	0	0
C. Males	13	5	1.0	5	1.0	0	0	1	0	0	0	0	0	1	0
	14	2	0.0	0	0.0	0	0	0	0	0	0	0	0	0	0
	15	3	1.0	2	0.5	0	0	1	0	1	0	0	0	0	0
	16	1	0.0	1	0.0	0	0	0	0	0	0	0	0	0	0
Total		17		12		0		2		1		0		2	
U =		6		14		18		15		15		18		15	
P		N.S.		N.S.		N.S.		N.S.		N.S.		N.S.		N.S.	

b. Sexual and aggressive behaviour

Behaviour pattern	Grasping-neck-feathers		Total male-directed aggressive actions		Female-directed aggressive actions									
					Threats		Pecks		Chases		Fights		Total	
	T	M	T	M	T	M	T	M	T	M	T	M	T	M
T.P. Males Male 01	3	0.5	0	0	0	0	2	0	6	1.0	1	0	9	2.0
02	1	0	2	0.5	0	0	2	0	5	0.5	0	0	7	1.5
03	1	0	0	0	0	0	1	0	4	0.0	0	0	5	0.5
04	3	1.0	0	0	0	0	4	0.5	16	3.5	0	0	20	4.5
05	0	0	1	0	0	0	1	0	12	1.5	0	0	13	2.0
06	1	0	0	0	0	0	0	0	1	0.0	1	0	2	0.5
Total	9		3		0		10		44		2		56	
C. Males 11	4	0	1	0	0	0	11	2.0	2	0.5	0	0	13	2.5
12	5	0	1	0	0	0	8	0.5	0	0	1	0	9	0.5
13	1	0	0	0	1	0	3	0	2	0	3	0	9	1.0
14	0	0	0	0	0	0	0	0	1	0	0	0	1	0.0
15	1	0	1	0	4	0.5	4	0	1	0	0	0	9	2.0
16	1	0	0	0	0	0	1	0	0	0	1	0	2	0.0
Total	12		3		5		27		6		5		43	
U =	12		15		15		14.5		7.5		18		12	
P:	N.S.		N.S.		N.S.		N.S.		N.S.		N.S.		N.S.	

The first table shows the orientation of the displays of the males and females in Part A, the second in Part B.

Male displays

The tables show the number of social displays (grunt-whistles and head-up-tail-ups combined) and the number of turn-back-of-head displays (TBH) addressed by each male to each of the other birds in the group. The column 'X' indicates the number of social displays for which the identity of the addressee was not determined.

Female inciting displays

The total duration (in seconds) of inciting displays addressed by each female to each of the other birds is recorded.

Male displays

Performing male	Display	Addressee								x̄
		Males				Females				
		601	602	603	604	621	622	623	624	
601	Soc.Disps.					1			18	11
	TBH					14			64	
602	Soc.Disps.							47	3	15
	TBH							29		
603	Soc.Disps.		24							13
	TBH		7							
604	Soc.Disps.							2	21	11
	TBH								20	

Female inciting displays

Performing female	Addressee							
	Males				Females			
	601	602	603	604	621	622	623	624
621	167							
622					6		79	1
623		282		1	1	2		5
624	315			1				

Part B

Male displays

Performing male	Display	Addressee males 601	602	603	604	Females 631	632	633	634	X
601	Soc.Disps.					2		12		2
	TBH					3		21		
602	Soc.Disps.					33		2		6
	TBH					48				
603	Soc.Disps.		12			1				11
	TBH		26							
604	Soc.Disps.					22		2		8
	TBH					8		2		

Female inciting displays

Performing female	Males 601	602	603	604	Females 631	632	633	634
631	4	327	9	5				
632								146
633	98							11
634						373	1	

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Social behaviour, pair formation, and the behavioural effects of testosterone in the mallard (Anas platyrhynchos). (Abstract). By Arthur R. Goldsmith.

Despite considerable work on the behaviour of ducks, many questions remain over the behavioural basis of pair formation. Social behaviour was studied here in individually marked captive mallards of wild stock. Particular attention was paid to the roles of 'social display' and of male aggressive behaviour in pair formation.

In the autumn social display was more frequent in a group of unpaired birds than in a group comprising paired individuals. At the beginning of the nesting season in spring paired males did not display to their mates, but they did display to unpaired females when their mates had been removed. In many cases a female paired with a drake who had displayed to her. Social displays were also given by a male to a female in the absence of other drakes. These data suggest that social display is more likely to be based on courtship than on, say, hostility between males, except possibly in the case of the 'down-up' display.

Dominance hierarchies were formed during the autumnal courtship period, and in the spring the 'territorial' pattern of aggression between paired males changed to a dominance hierarchy when the resident females were replaced by strange females and display behaviour was resumed. The mating preference of a female for one of two males was closely associated with the dominance relationship between the males.

Social behaviour was studied in juvenile males injected with testosterone. The treatment facilitated the occurrence of many adult behaviour patterns, although the expression of the behaviour was dependent on the experimental conditions. Social display occurred only if the males were familiar with the females who were present. The displays of the young males were effective in attracting the sexual interest of adult females during the post-breeding period, thus supporting the conclusion that social display is functional in courtship.