Social especially agonistic behaviour in the pigeon

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SOCIAL ESPECIALLY AGONISTIC BEHAVIOUR IN THE PIGEON

by

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Finally, I would like to express my warm thanks and gratitude to my parents for their moral and financial support.

TO J.D.D.

ABSTRACT

This study describes the social behaviour of the pigeon, with particular reference to agonistic behaviour.

The ethogram, presented in Chapter 2, includes a description of the aggressive, courtship and maintenance behaviour patterns of pigeons. A selection of sonograms of pigeon vocalisations, which shows the diversity of the calls, and their association with the accompanying behaviour, is presented. The function and causation of some of the behaviour patterns are discussed.

In an attempt to investigate the mechanisms involved in the regulation of aggression between conspecific neighbours, the agonistic behaviour shown by a dominant male pigeon, when allowed to interact with a subordinate male, was recorded over 10 days (Experiment 1). It was found that aggressive behaviour showed a large decrement over the first two days. Threatening behaviour became more evident thereafter. The causal and functional significance of these and other agonistic behaviours are discussed in this context. It was shown that diurnal rhythms did not affect agonistic behaviour.

The effects of total social isolation on agonistic behaviour was investigated in three male pigeons (Experiment 2). The results obtained do not suggest a build-up of an "aggressive drive", during the periods in isolation, which is expressed through the performance of aggressive behaviour after isolation. The possible effects of isolation on other agonistic behaviours are discussed.

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CHAPTER ONE

INTRODUCTION

This thesis describes the social behaviour of the pigeon (Columba livia). One class of behaviour is investigated in particular, namely agonistic behaviour.

The pigeon is unusually well suited for behavioural research. It adapts very quickly to a laboratory environment, breeds well in captivity, and exhibits discrete functional units of behaviour which are readily and clearly recognisable by an observer. Moreover, it has been the subject of investigation by workers such as Levi (1941) and Whitman (1919), who have provided a good informative background about its behaviour. Although the reproductive behaviour of this species has been systematically studied by workers such as Fabricius and Jansson (1963), investigation of the pigeon's agonistic behaviour has been neglected. This thesis presents two experiments which, it is hoped, will act as a foundation for further investigation into this class of behaviour.

In Chapter 2, I present: first, as comprehensive a coverage as possible of the aggressive, maintenance and courtship (including reproductive) behaviour patterns of pigeons, which includes a selection of sonograms of pigeon vocalisations showing the diversity of and between the calls. Second, a concise description of the courtship and agonistic encounters in this species; and third, analyses of the possible causation and functions of some of the behaviour patterns described.

Previous experimental work using fish and mice demonstrated that intraspecific fighting "can vary as a function of the degree of exposure to aggressive experiences in an otherwise constant testing environment" (Connor, 1974). With this in mind, these experiments followed two main trends: (a) Habituation experiments and (b) Isolation experiments. Chapters 3 and 4 present an investigation into the effects of (a) constant exposure of a male pigeon to a neighbouring male conspecific and (b) social isolation, on the agonistic behaviour of pigeons.

Peeke and Veno (1973) suggest that in fish and birds similar mechanisms may be responsible for the maintenance of lowered levels of aggression between territorial neighbours. In Chapter 3, the experiment tests whether male pigeons can maintain lowered levels of aggression over a period of days as well as investigating other agonistic behaviours. The experimental design ensured that the expected waning and any recovery of aggressive behaviour cannot be attributed to either changes in environmental factors (such as changes in photoperiod or territorial neighbours) or the frequency of encounters between pigeons. All of these factors are kept constant throughout the experiment.

Chapter 4 describes a brief experiment investigating the effects of total social isolation on, mainly, the agonistic behaviour of male pigeons. In this experiment, dominant male pigeons previously placed in isolation for varying periods of time, are tested individually with a subordinate male, and their behaviour recorded. It is argued that the behaviours shown by the pigeons immediately after isolation may reflect possible changes in their motivatory or physiological states brought about by social isolation.

It is hoped that these experiments may throw some light on the manner in which "motivational" variables affect intra-specific aggression, as well as stimulating further research on the agonistic behaviour of pigeons.

CHAPTER 2

THE ETHOGRAM

2.1 Introduction

Even though the pigeon is one of standard laboratory bird species that are used in behavioural research, it is remarkable that a comprehensive descriptive catalogue of its behaviour is still lacking. Such a catalogue is fundamental for an accurate communication among investigators and also for advanced quantitative behavioural work, particularly for those workers who need to assess behavioural change even though their interests be primarily elsewhere (e.g. physiologists, pharmacologists, endocrinologists etc..). The first part of this thesis is intended as a foundation for such a catalogue.

Whitman (1919), Carpenter (1933), Heinroth and Heinroth (1949) and more recently Fabricius and Jansson (1963), have all described the courtship and reproductive behaviour of the pigeon. However, there has been very little description of the agonistic behaviour encounters and maintenance behaviour in this species, with the exception of Goodwin (1955, 1967) and Levi (1941). Some of the agonistic, as well as courtship and maintenance behaviour patterns of ring doves are very similar to those of pigeons. Miller and Miller (1958) give a synopsis of the behaviour patterns of ring doves (Streptopelia risoria), and more recently Harwood and Vowles (1967) have described the defensive behaviour of this species; but both accounts are far from complete.

In the following section, the behaviour patterns which are associated with courtship, maintenance and aggression in the feral pigeon, are described. Eibl-Eibesfeldt (1970) describes such an inventory of behaviour patterns as an ethogram. As part of the ethogram, a selection of pigeon vocalisations are presented, chosen to show diversity within and between pigeons.

Both Craig (1908) and Beer (1970) indicate the important role of pigeon and dove vocalisations in influencing social behaviour, as a means of communication and recognition between individuals, and also of species recognition. Craig states: "the voice (of pigeons) is a means of social control..... a means of influencing the behaviour of individuals so as to bring them into co-operation, one with another", and "the young doves have impressed upon their minds..... the fact of differences (in their voices) between individuals". Several authors (e.g. Heinroth and Heinroth, 1949, Fabricius and Jansson, 1963, Akerman, 1966a, b) have used onomatopoeic renderings of the calls loosely and sometimes, when these are described in conjunction with the accompanying behaviour, incorrectly.

Some of the terminology used in the following ethogram is similar to that used by Delius (1969), and Feekes (1971), but this does not necessarily imply that I consider the relevant behaviour patterns of pigeons to be homologous with those of skylarks and Burmese red junglefowl.

2.2 Subjects and Methods

The pigeons used were of homing stock obtained through a local dealer, and were housed for at least four months before they were used for observation and experimentation. The pigeons were kept in galvanised metal cages measuring 40 x 40 x 45 cm., at a constant room temperature of +21°C, and a lighting schedule of 12 hrs. light : 12 hrs. dark, the lights coming on at 08.00 hours and switching off at 20.00 hours. Food and water were given ad libitum. During this acclimatisation period the birds became accustomed to handling and observation, so that subsequently the observation of behavioural data were easily accomplished. All the pigeons used were over one year of age.

For the recording and observation of behaviour, a variety of techniques was employed: notation, tape recording, video recording, cinematography and still photography. In order to observe and record pigeon behaviour in various contexts, all the possible pairings between the pigeon sexes were used, i.e. male - male, male - female, and female - female pairs. When using male - female encounters for behavioural observations, both breeding pairs and 'strange' pairs of birds were used. The observations were made over a period of nine months.

2.3 Sound recording

The sound recordings presented in this study were made with the aid of a Marconiphone model 4218 tape recorder (British Radio Corporation Ltd.) at a tape speed of 18 cm. per second (the frequency response of the tape recorder at this speed is 40 - 18000 Hz.). For the purposes of call analysis, contoured sound spectrograms were made from the tape recordings by means of a Sono-graph (Kay Electric Co., Sono-graph type B/65), at a 'narrow band' (45 Hz.) filter setting and a 'high shape' circuit. The frequency range covered was from 0 to 1 kHz., since the calls did not show main energies above 1 kHz.; the base-line for the spectrograms was a 45 Hz. band. In interpreting the contours, the darker contours indicate higher energies of a call at that particular frequency.

The sono-graph drum-speed was 12.7 cm. per second. The vocalisations of twelve pigeons are denoted by the prefix P followed by their ring number, e.g. P 35 etc.

Figure 2.1 is a diagrammatical representation of a driving call, which includes the Heinroths' onomatopoeic rendering. Referring back to the figure, one can see that each individual call is composed of elements, syllables and phrases. The elements are the smallest discernible vocal units in a syllable and one element or a group of elements having a fixed arrangment constitute one syllable. A phrase is made up of a group of syllables. Elements may be spaced over frequency or time or both and the temporal interval between elements should be less than 0.05 seconds. Inter-phrase spacing can

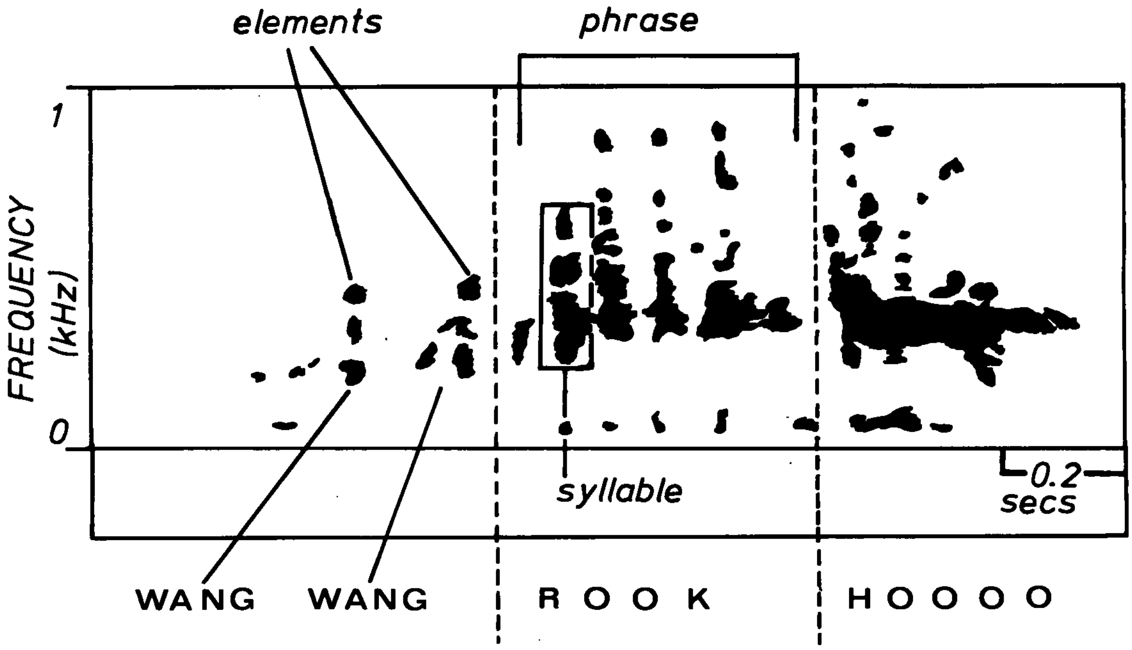


Figure 2.1 A diagrammatic representation of a driving call (P 17), illustrating the terminology used for sections of the call. Only the main energies at their respective frequencies within the call are shown, and consequently when determining the temporal intervals for the contoured spectrograms one must do so from main energy to main energy.

vary, but can be taken to be 0.075 seconds, and in certain circumstances single syllables can constitute a singular phrase.

2.4 Description of Behaviour

AGGRESSIVE PECKING: With its beak open, the pigeon pecks at the opponent, usually grasping areas of the head and neck firmly in its beak and giving vigorous head-shakes. Other areas, such as the wing and back feathers, may be grasped by the attacking bird. Sometimes the dominant pigeon will tread on the opponent's tail and back during intense aggression, while still grasping the neck in its bill. Aggressive pecking is seen most frequently during encounters between male pigeons, and can lead to further types of attack. This behaviour also occurs after a sequence of copulations during the pre-incubation phase of the breeding cycle, when the male pecks at the neck and crown area of the squatting female quite vigorously. This may be due to the male being both sexually and aggressively motivated (Fabricius and Jansson, 1963).

AGGRESSIVE INTENTION PECK: The bird is attentive, the neck is stretched upward and the head is brought sharply forward and downward; so that pecking actions are directed at the opponent's head, although contact seldom occurs. This behaviour was never seen during encounters between male and female pigeons.

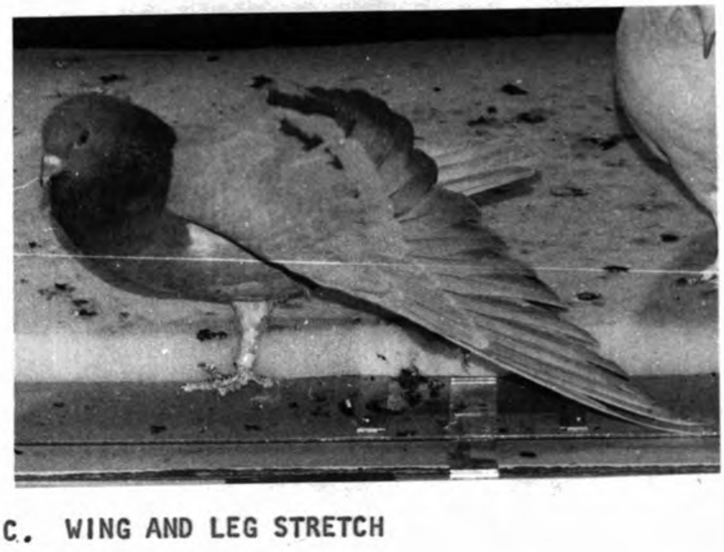
AGGRESSIVE BILLING: While body-pushing with their wings raised, the pigeons peck at each others' bills and one bird may grasp the opponent's bill in his mandibles (Plate 1A). Both birds perform twisting movements, one bird obviously trying to escape the hold of the other.

BODY-PUSHING: During body-pushing the wings of both birds and the ones in close proximity are brought against each other (usually while the birds bill aggressively), and the tail is fanned

PLATE I

A. AGGRESSIVE BILLING

B. FEMALE DRIVING



C. WING AND LEG STRETCH

out if not already so. The pigeons then move around a common centre with their wings still in a raised position (Fig. 2.2.3). The lower breast region also appears swollen, due to fluffing of the plumage and possibly to the enlargement of the crop. This region may serve as some kind of 'bumper', since this is the area used by the pigeons when pushing against each other.

WING FLICK: A sharp movement of the wing which consists of a powerful downward wing beat. The pigeon fans out its tail, raises the wing which is nearest to the opponent and brings it down sharply on to the other bird; the other wing is raised only slightly during wing flicks of low intensity (in this case, does not refer to the frequency but to the power of the wing beat) (Fig. 2.2.1). As the two pigeons encroach on each other, wing flick intensity (both the power and the frequency) increases, and the non-flicking wing is raised higher till it is held at a near vertical position during high aggression.

WING FEND: When a fleeing bird is being closely pursued by a dominant male, it may flick upward one of its wings, usually hitting and thereby warding off the pursuing bird. Wing fending can be seen when two birds take up a side-on orientation to each other: in this instance, it is also shown by the subordinate bird as a defensive behaviour, and the wing, rather than being flicked backwards, is brought sharply outwards (Fig. 2.2.2).

CHASING: The dominant pigeon runs in pursuit of a fleeing opponent. Sometimes intention-pecking or pecking actions are performed by the chasing bird. Chasing was not often seen, presumably because of the restriction in space; but it is quite common in the free ranging pigeon. During a chase, which incidentally is of some seconds' duration, the pursuing

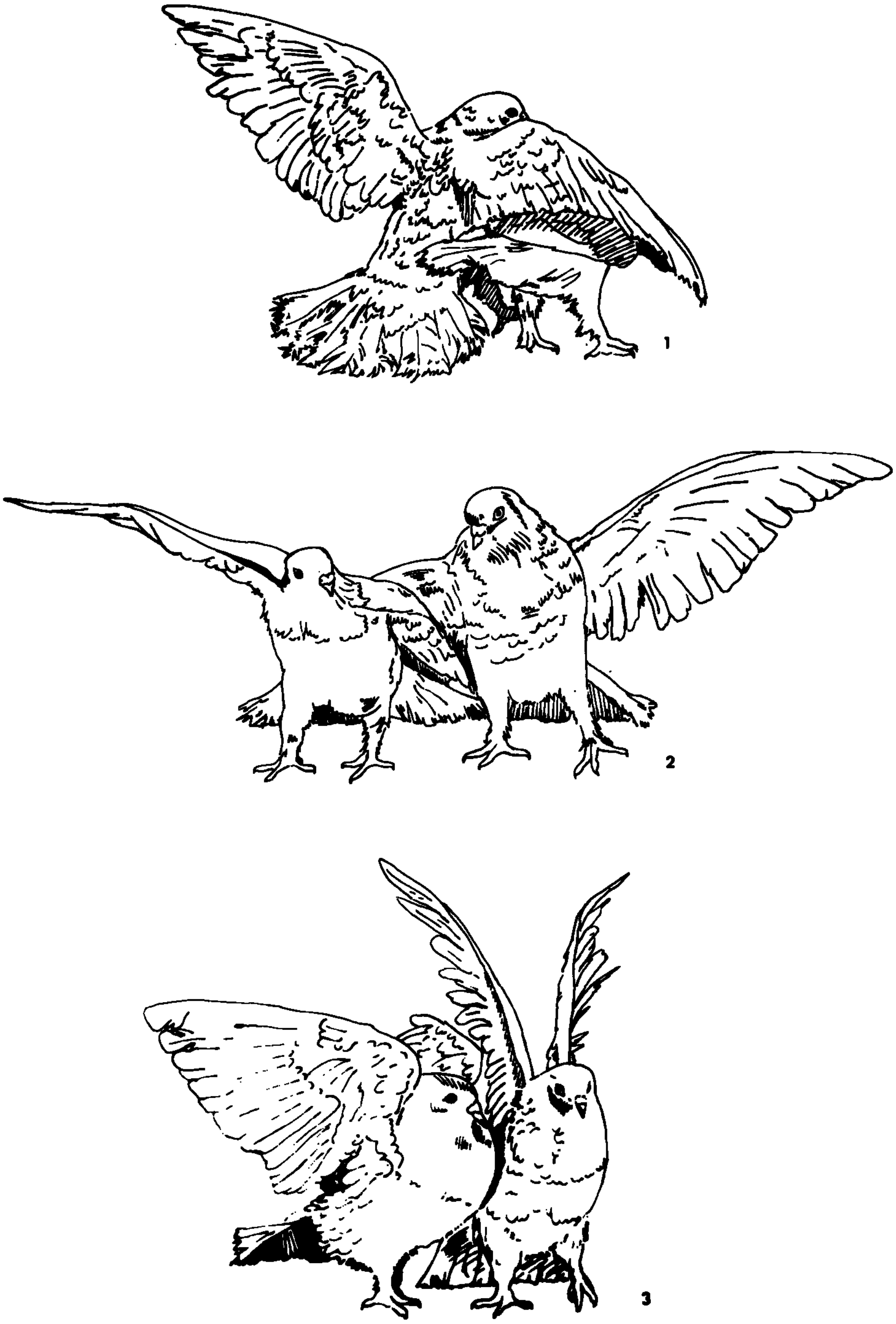


Fig. 2.2: (1) Wing flick. Notice the fanned-out tail and the raised wing on the side away from the opponent. (2) The pigeon on the left is showing wing-fending, while the one on the right is showing wing-flicking. Notice the fanned out tail in both birds. (3) Wing raising and body pushing. (Diagrams drawn from photographs).

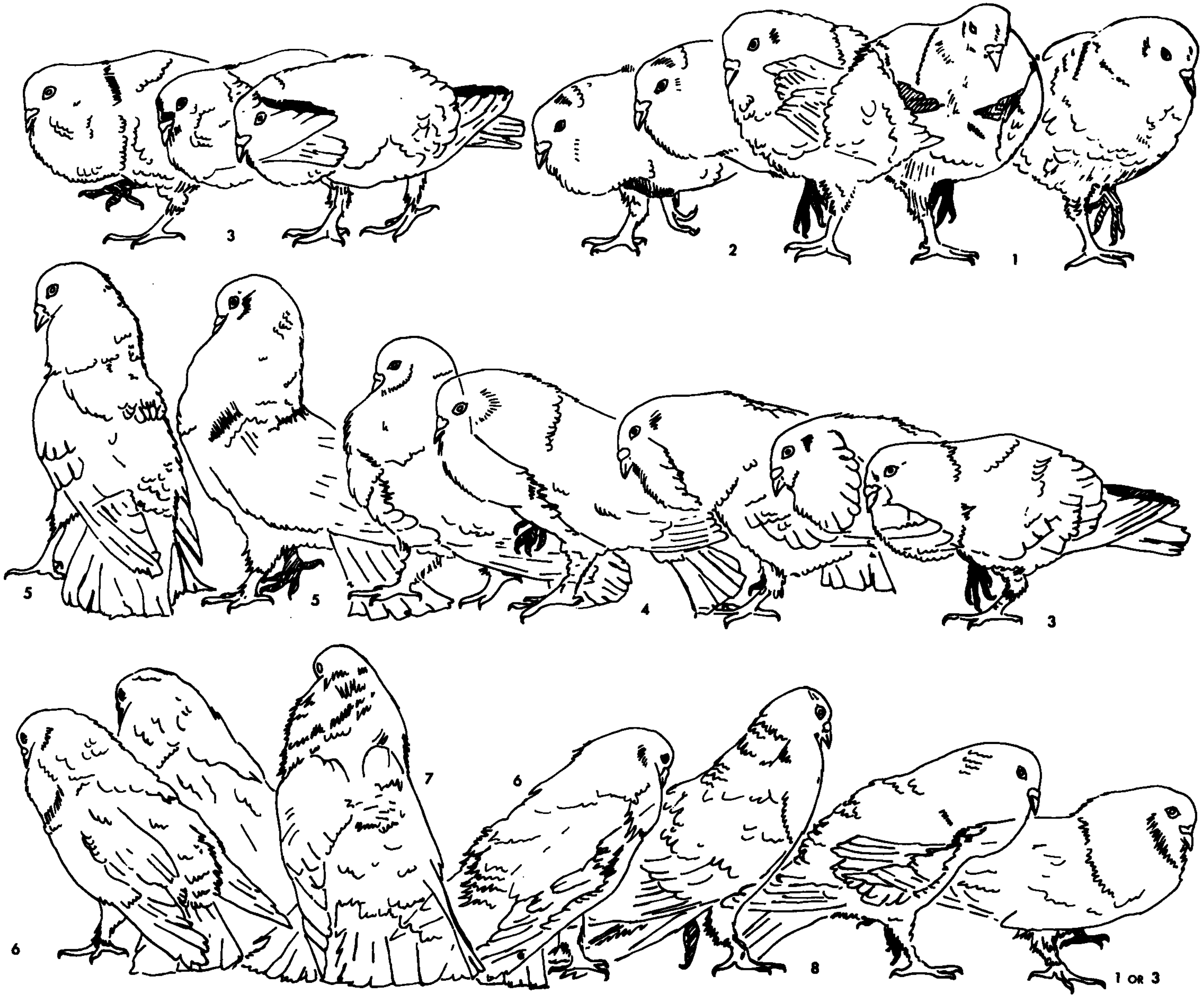
bird does not fan out its tail nor does it call.

FLEEING: Fast locomotion away from a pursuing opponent.

FREEZING: An alarm behaviour in which all movement ceases; so that the bird remains motionless in the same behavioural posture which immediately preceded freezing. In certain circumstances, freezing can be maintained for a relatively long period of time, and is usually released by auditory stimuli.

BOWING: Immediately preceding bowing behaviour, the male pigeon is erect, and vibration of the throat is noticeable (this vibration is probably caused by pre-vocalising movements of the trachea). The crown, neck and back feathers are raised; however, the most noticeable feature of the pre-bowing behaviour is the apparent swelling up of the upper part of the pigeon's body (the breast, neck and head regions), partly due to the feather fluffing of this region and partly to the swelling up of the crop. As the bird lowers its head, it utters the first two syllables of the bowing call. The head is raised slightly again (completing the bowing action), and the remainder of the bowing call is uttered as the head is raised, although this is very difficult to determine since some birds do not have a very pronounced bowing action. Normally bowing is performed while the bird is walking in a circular direction, alternating clockwise and anti-clockwise (Fig. 2.3, sequence 1-3).

When two male birds come in close proximity to each other, they may bow in a sideways-on position, while remaining in the same place. I have termed this as 'SIDE-ON' Bowing. 'FULL-FRONTAL' Bowing can also be seen in this context, and in fact is identical to Side-on Bowing except for the orientation of the displaying bird, which is facing the opponent directly.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1 OR 3

THE BOWING CALL: The bowing call as a sound pattern perceived b the human ear is quite distinguishable from the driving call and consequently, as the names indicate, the two calls appear in different contexts. The bowing call in conjunction with bowing behaviour is normally directed at conspecifics whether these are male or female; but as Craig (1914) and others have noted, it can also be directed towards human observers. Depending on the context in which bowing behaviour is seen, so too the call may have different functions, depending on whether the situation requires agonism or courtship.

As one can see in Figures 2.4 to 2.6, which show the bowing calls of several pigeons, the calls themselves are highly variable in their frequency and energy structures and temporal patterning: they do not show the structured patterning of driving calls. Such individual variation in the bowing calls of pigeons would tend to support a hypothesis that these vocalisations may serve as identification calls for individual birds. It is interesting to note that mature female pigeons rarely produce this call and when they do, it is of a higher pitch and lower amplitude than a male call. The only time females bow-call with any sort of regularity is when they are three to five months of age, before the onset of sexual maturity.

DRIVING: At the onset of Driving, the bird is erect and has its neck, crown and back feathers ruffled. The tail is fanned out and is in contact with the substrate; so that a brushing noise is produced when the pigeon moves. The male bird is looking directly at the female pigeon keeping its beak at a negative angle to the horizontal. As the head is lowered, the bird utters a call which may be described onomatopoeically as 'wang-wang-kroooo', which is quite distinct from a bowing call (see Figures 2.10 to 2.14). Throughout the calling of the phrase, the bird raises its head again, so that it is fully erect at the end of the call as described above (see also Fig. 2.17). The male pigeon may jump or step on to the female's

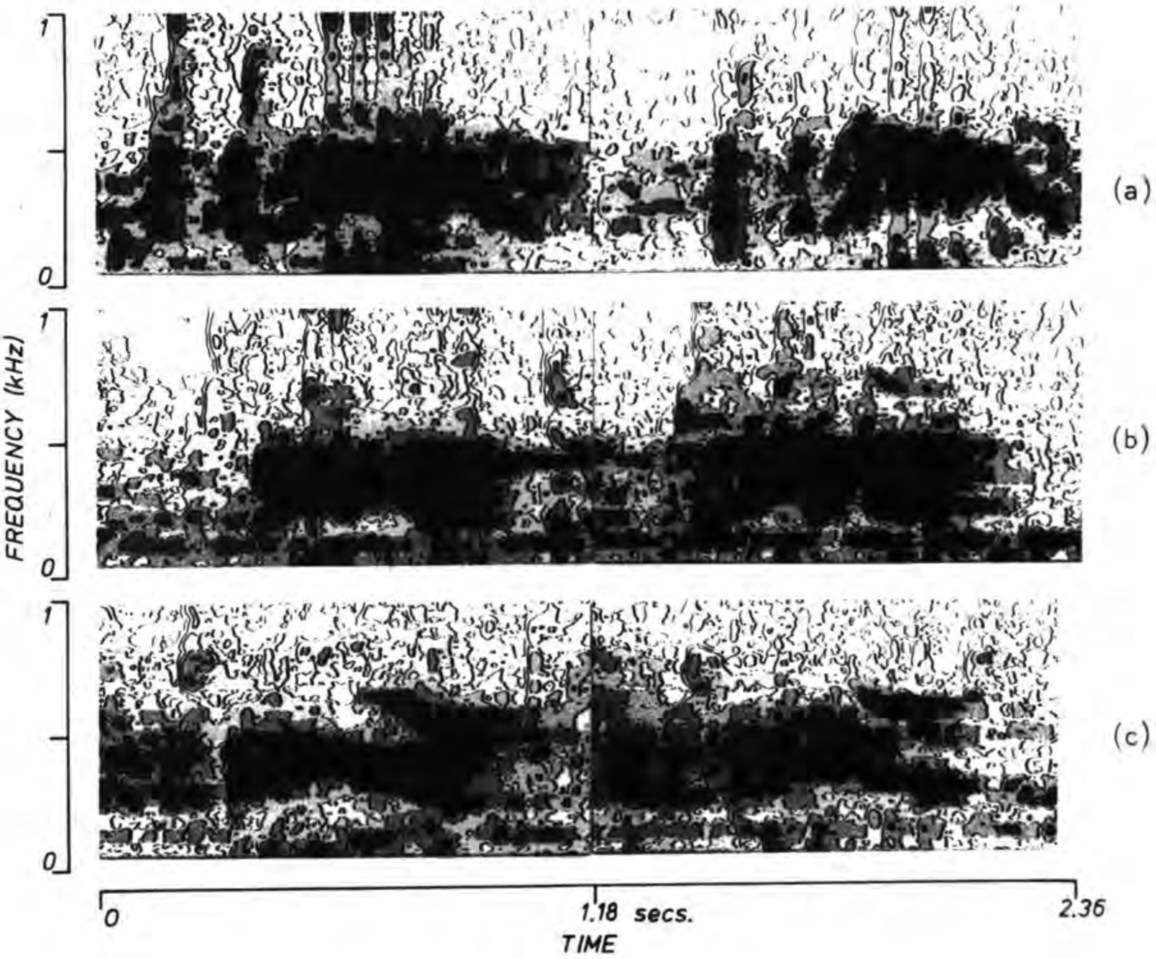


Fig. 2.4 (a) P 15. Bowing call. (b) P 34. Bowing call. (c) P 28 Bowing call. (A small editing error in C).

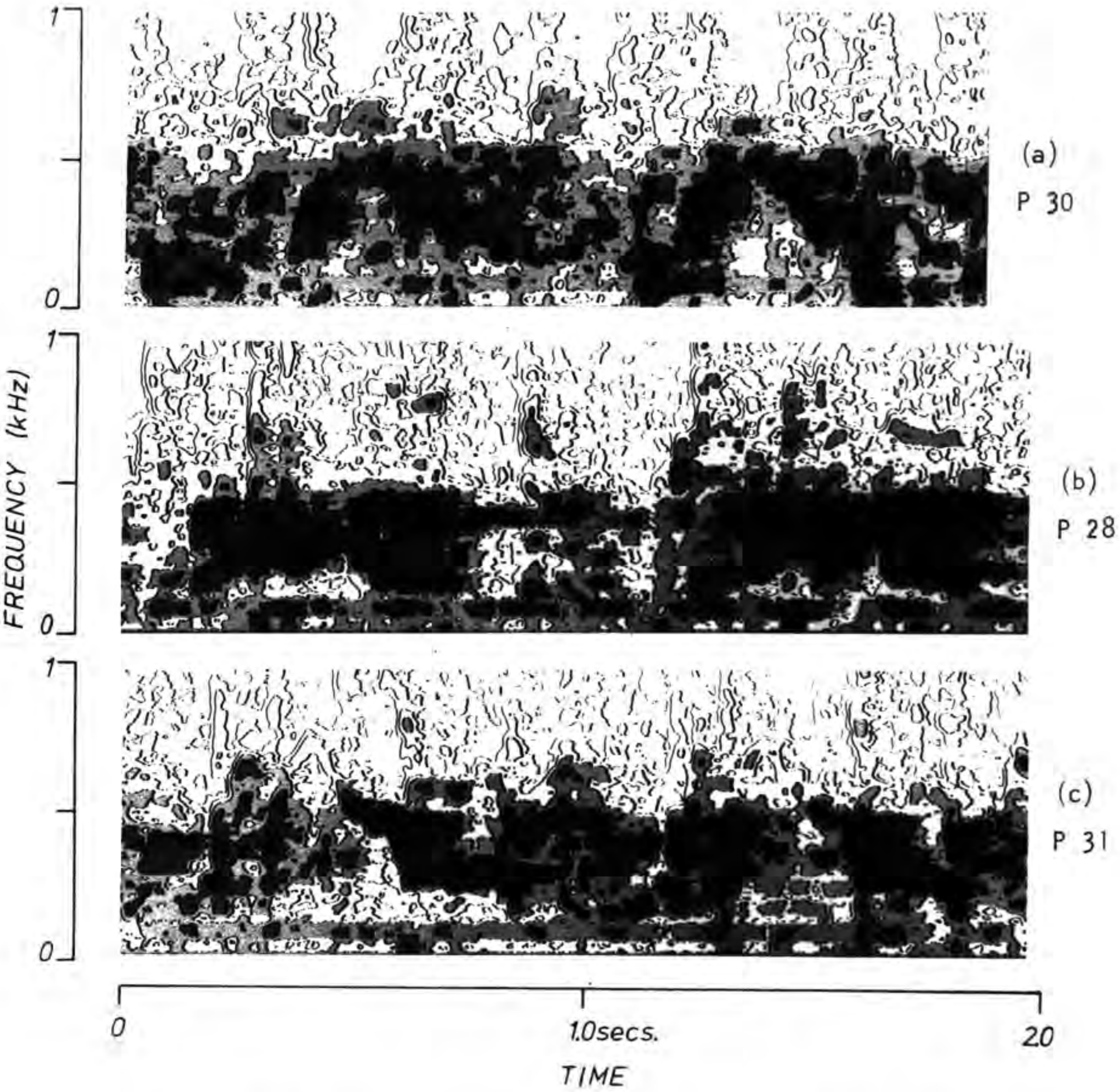


Fig. 2.5 (a) P 30. Bowing call. (b) P 28. Bowing call. (c) P 31. Bowing call. Notice the different frequency/energy structures for the three pigeons.

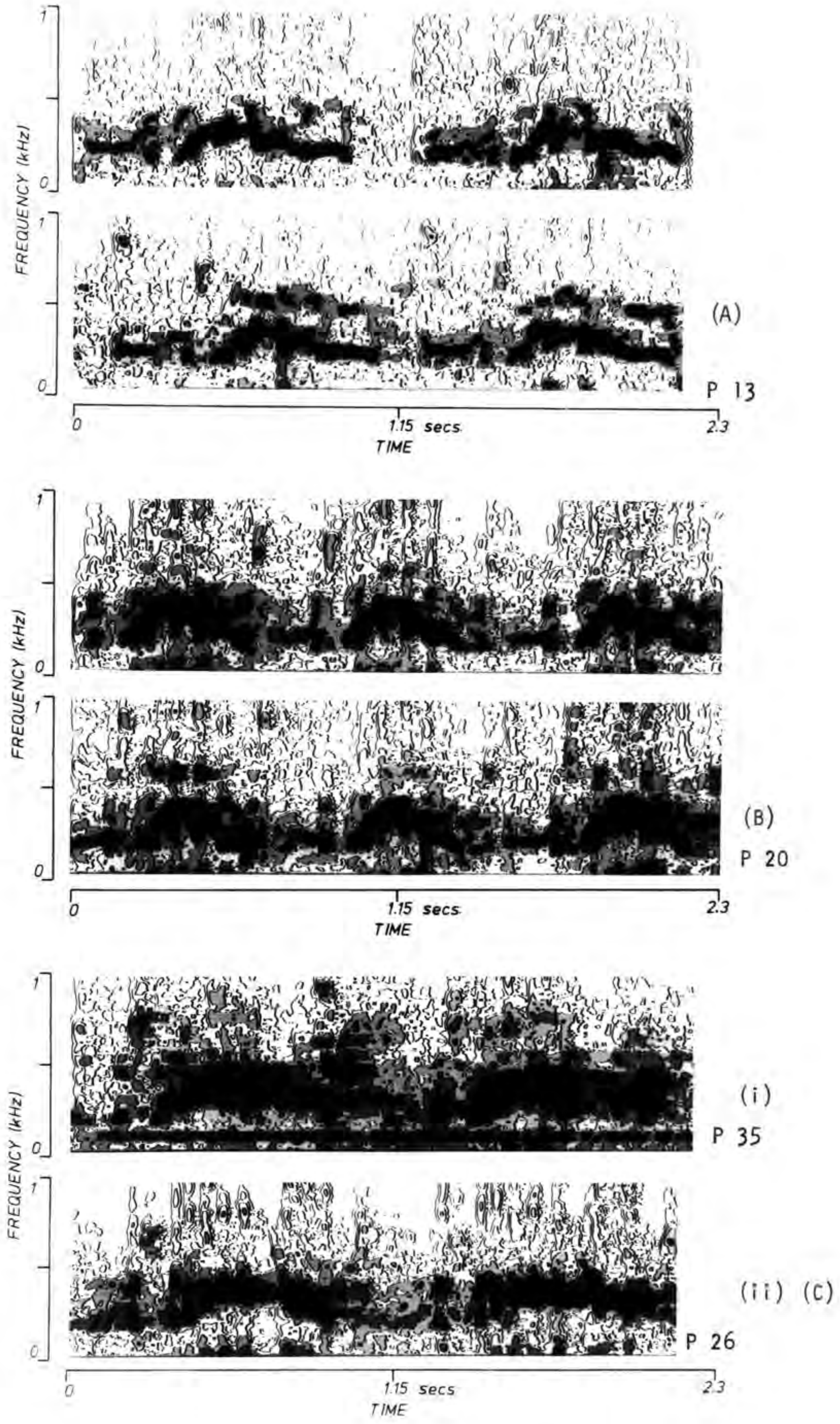


Fig. 2.6 Bowing calls. (A) P 13. (B) P 20. (C) i: P 35. ii: P 26.

tail, and the behavioural sequence is repeated (see Fig. 2.3, sequence 6-8).

Driving can result as a direct transition from the Bowing behaviour and one is again referred to Fig. 2.3, sequence 3-7. During a Driving sequence in male-female encoutners, the male bird may remain quite stationary, although performing all the actions which are characteristic of the Driving behaviour. This is termed 'FULL-FRONTAL' Driving (cf. Full-Frontal Bowing). Treading on the other bird's tail by the dominant pigeon, whether it takes place during male-male or male-female encounters during Driving sequences, is quite common.

A form of driving is shown by some females after copulation: both wings are lowered so that the primaries are very near to the ground, and the tail is lowered and fanned out, as in the male driving display; but the body is kept in the horizontal plane (Plate 1B). While adopting this posture the female rushes about without any apparent orientation, sometimes bumping into the male bird.

DRIVING CALL: Driving calls show more temporal structuring than bowing calls, so that whereas the latter show some temporal patterning between calls (at least as perceived by the human auditory and, in spectrographic analysis, visual systems) as well as frequency patterning within calls, the former show temporal patterning mainly within calls, and sometimes also between calls. However, the temporal separation between the onset of successive vocalisations seems to be very irregular, and detailed temporal analysis is required before any further inferences can be made. Driving calls are accompanied by driving - a behaviour which is normally associated with courtship and the formation and maintenance of pair-bonds.

The onomatopoeic rendering of a driving call, as given in Fig. 2.1, is not quite correct. A driving call sounds more like 'wang-wang-krroooo'; but since driving calls themselves can vary an appreciable amount in their temporal

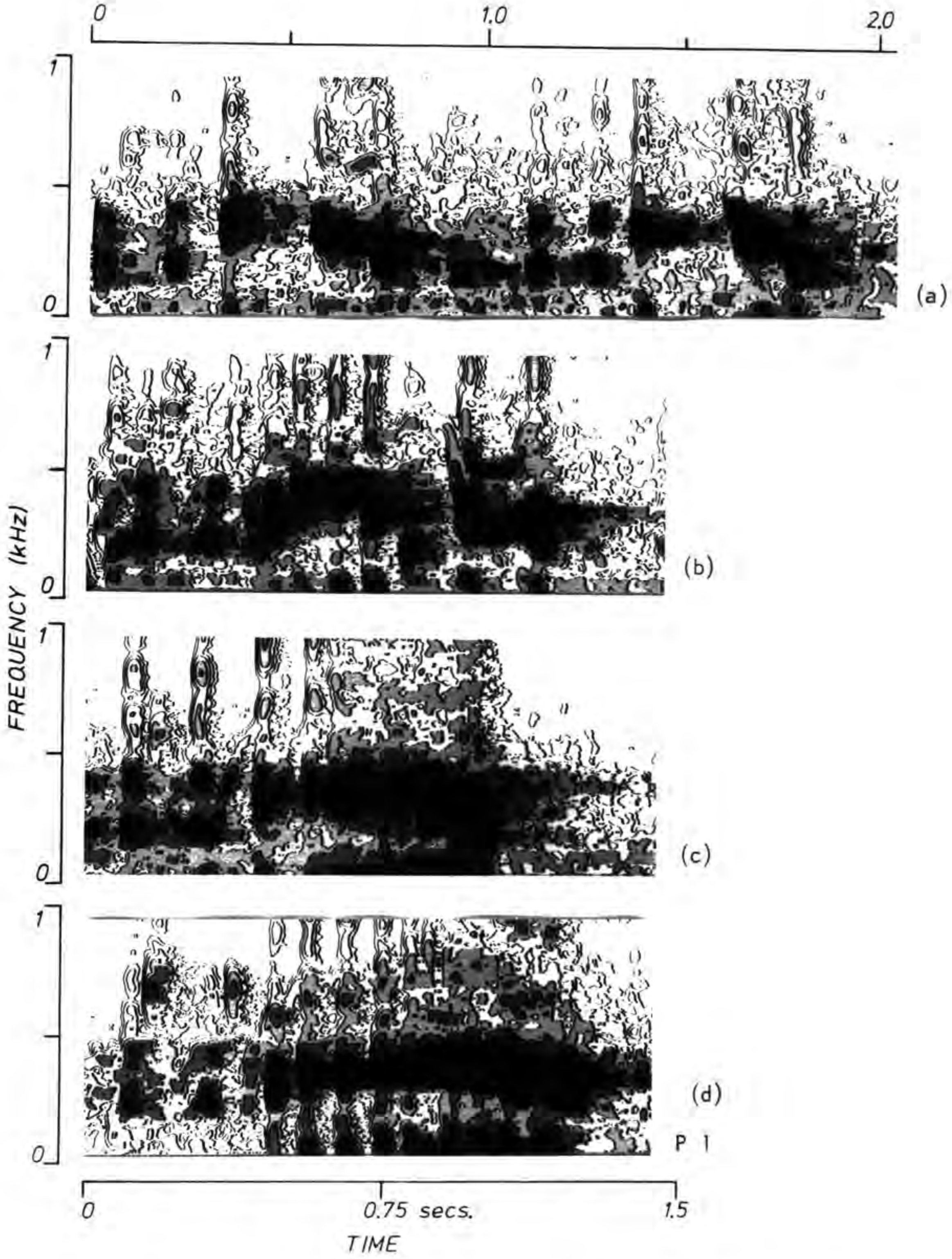


Fig. 2.7 P 1. Sequence of calls showing the transition from bowing calls to driving calls. (a) Bowing calls. (b) intermediate or extended bowing call. (c) and (d) Driving calls. Notice in (d) the increased temporal patterning of the call.

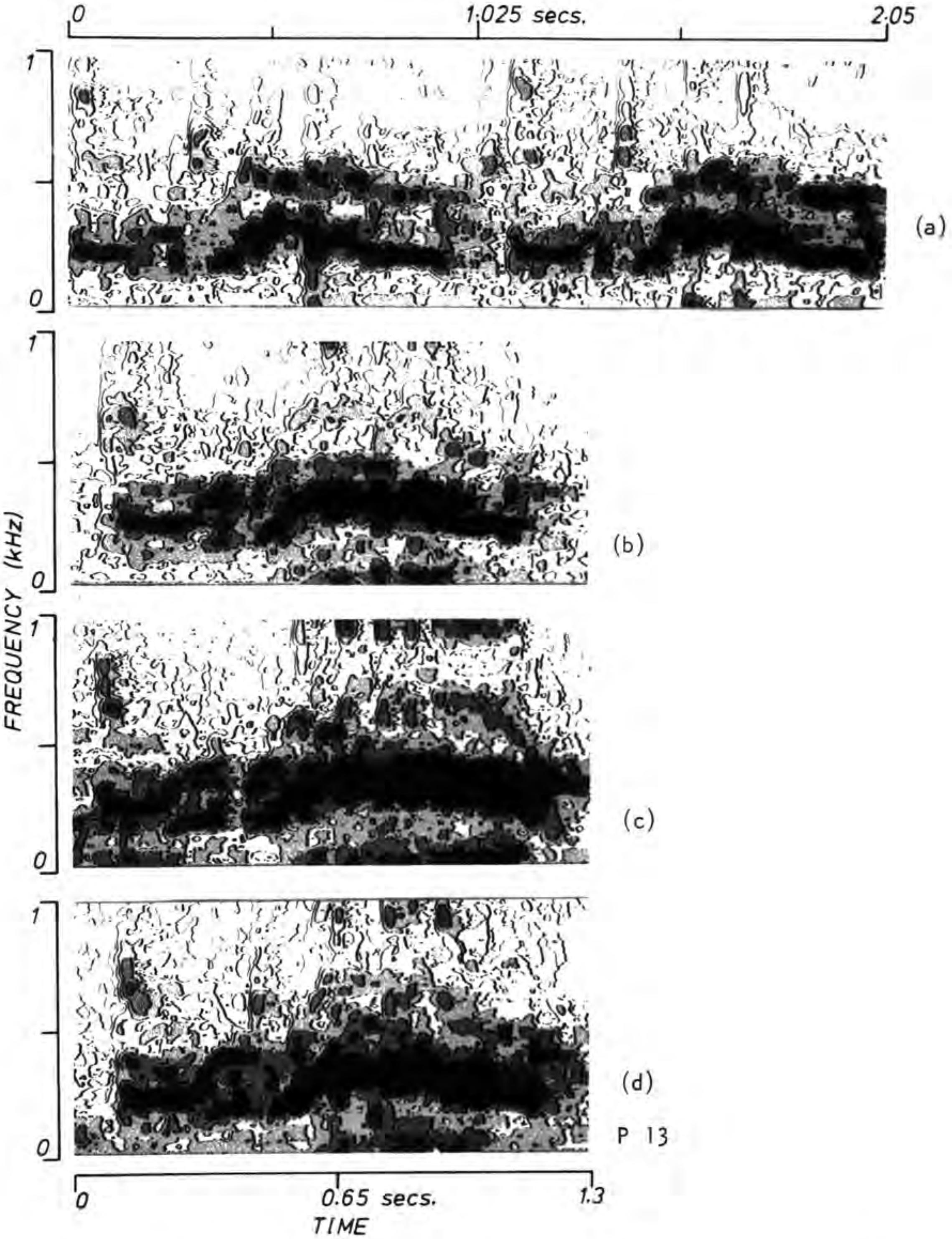


Fig. 2.8 P 13. Sequence of calls showing the transition from bowing calls to driving calls. (a) Bowing calls. (b) intermediate call. (c) and (d) Driving calls.

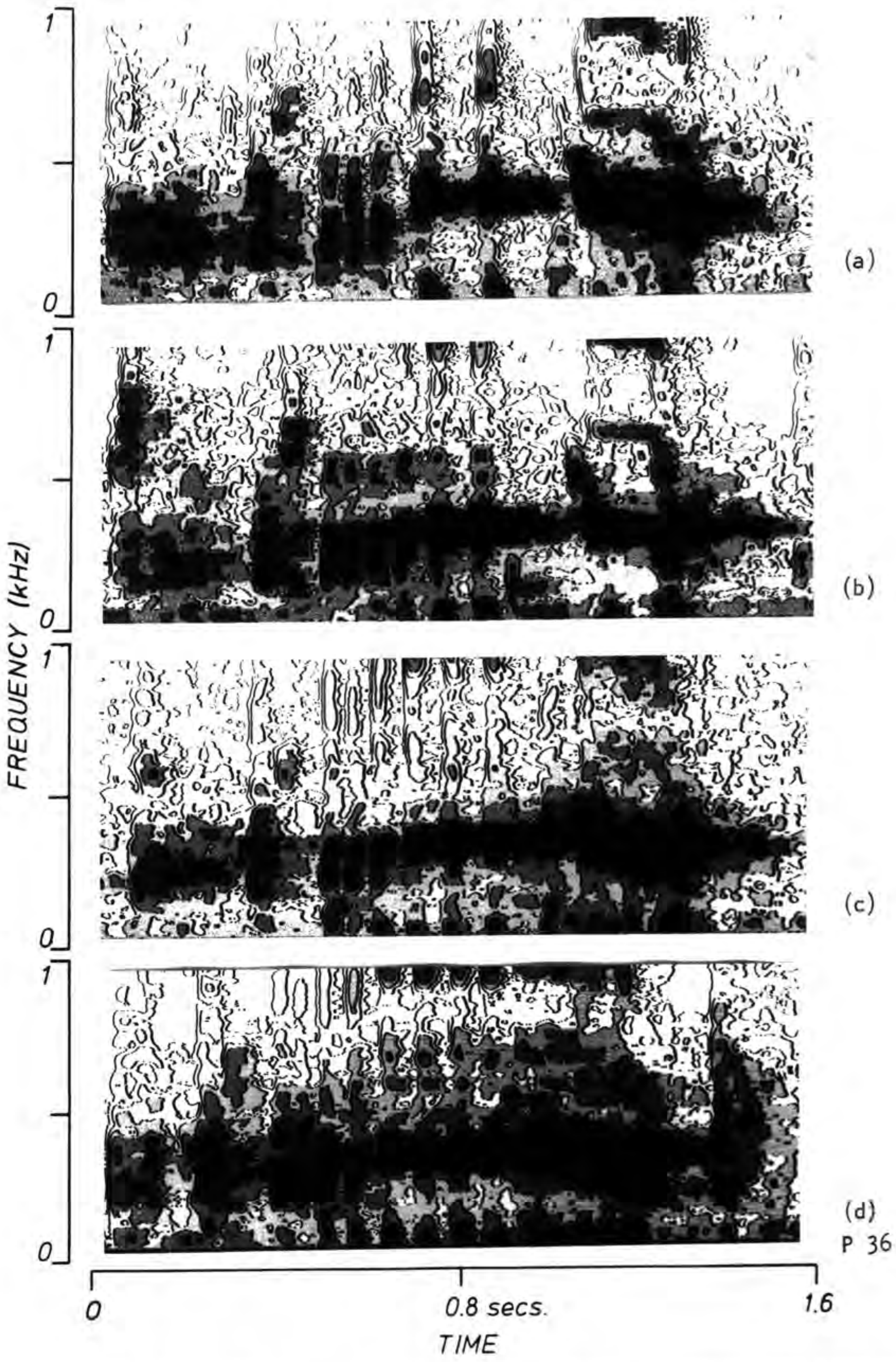


Fig. 2.9 P 36. Sequence of calls showing the transition from bowing calls to driving calls. (a) Bowing call. (b) intermediate call. (c) and (d) Driving calls. Notice the progressive change in the frequency and temporal patterning of the calls.

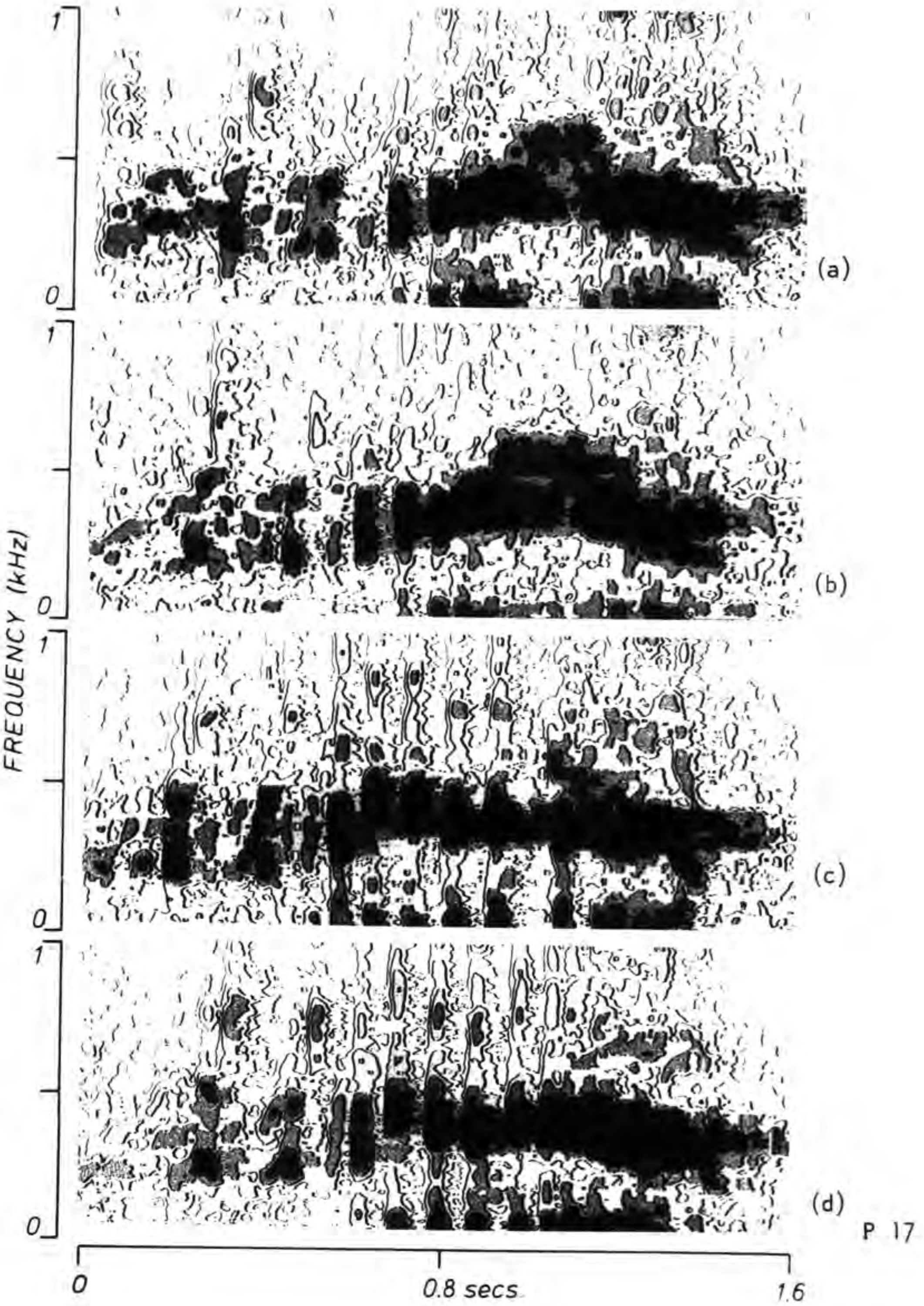


Fig. 2.10 P 17 Driving calls. Notice in (a) and (b) an increase in the frequency of the calls, half way through the end phrases, coupled with a decrease in the energy (or amplitude).

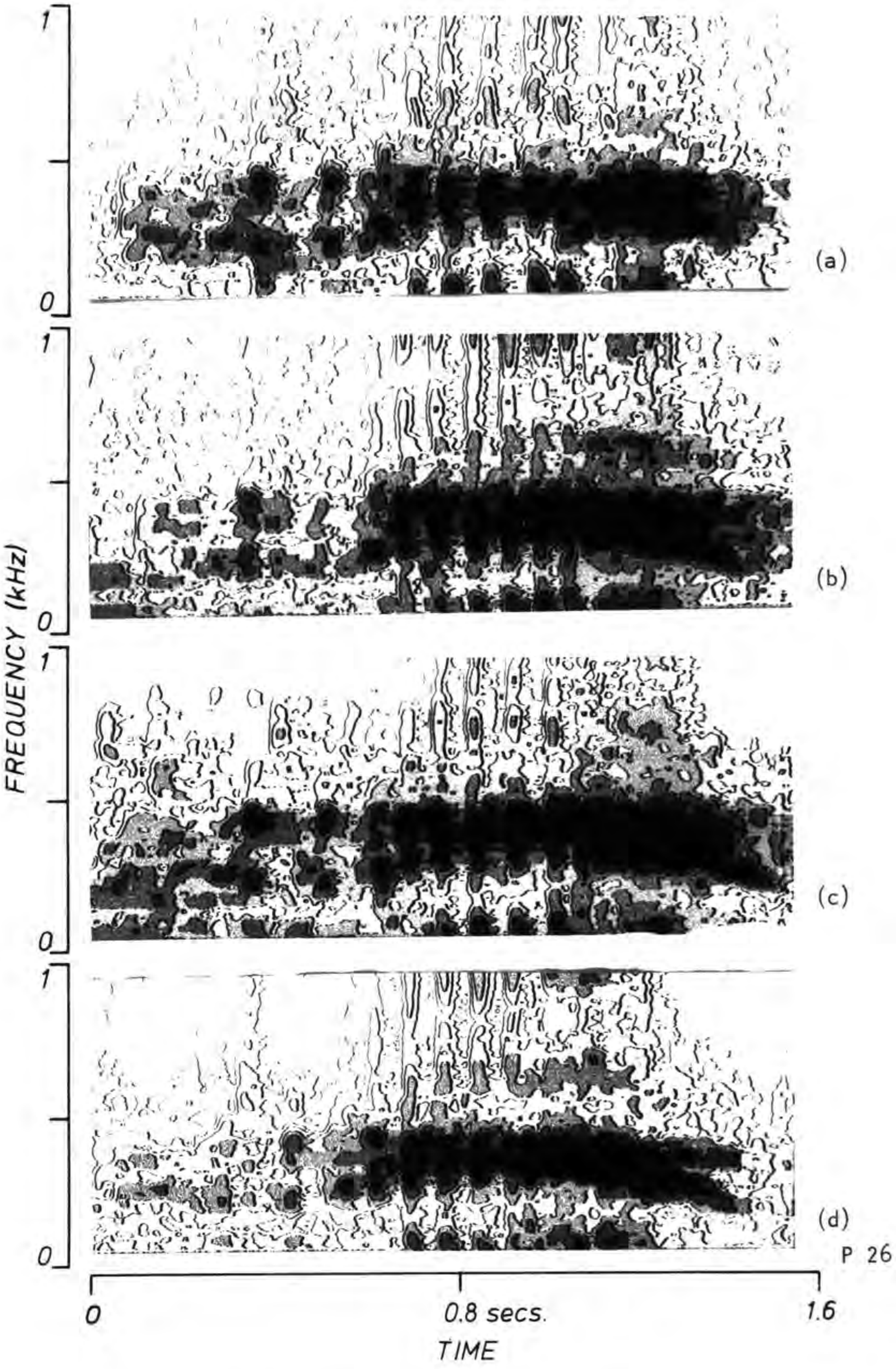


Fig. 2.11 P 26. (a) - (d) Driving calls.

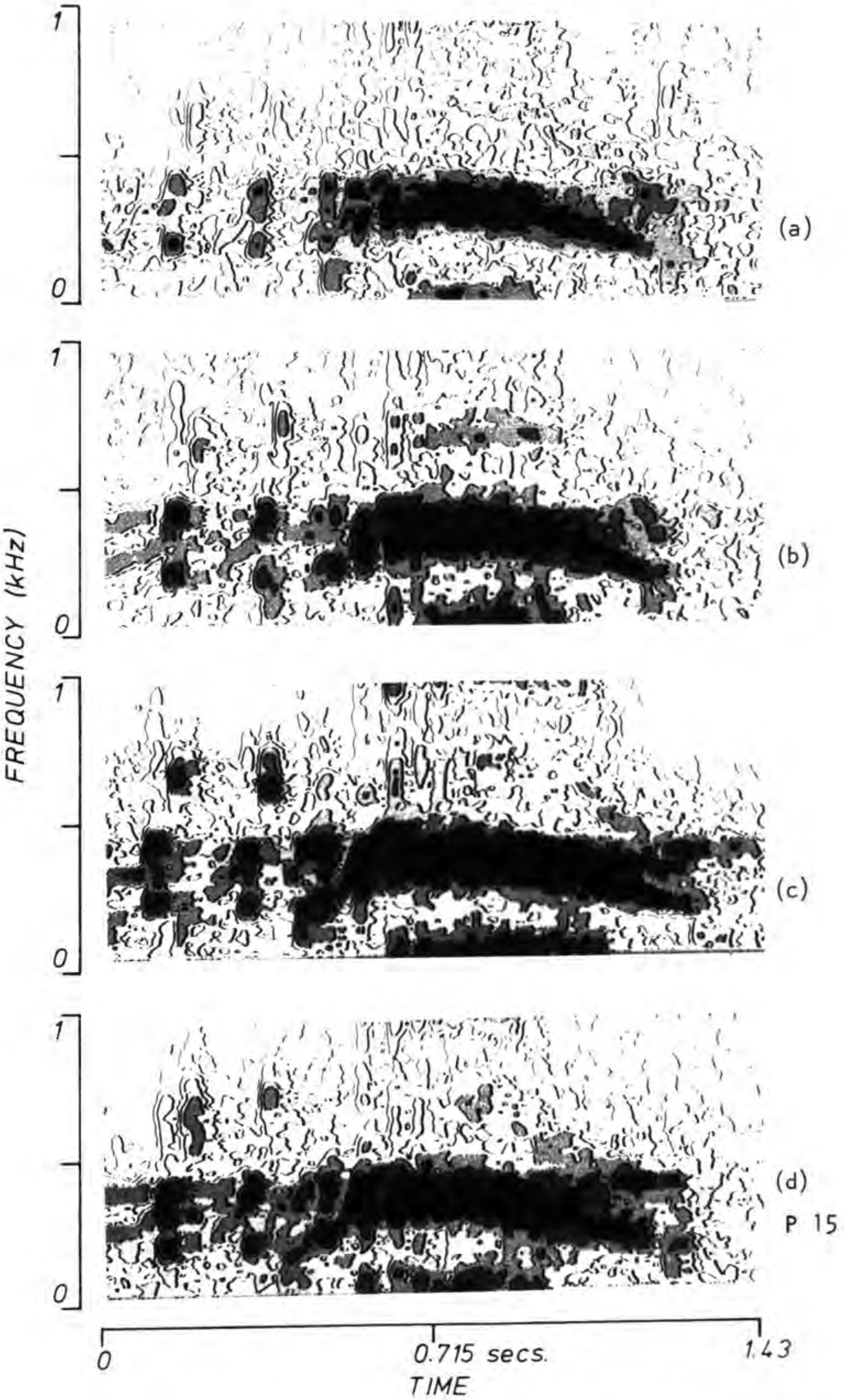


Fig. 2.12 P 15. (a) - (d) Driving calls.

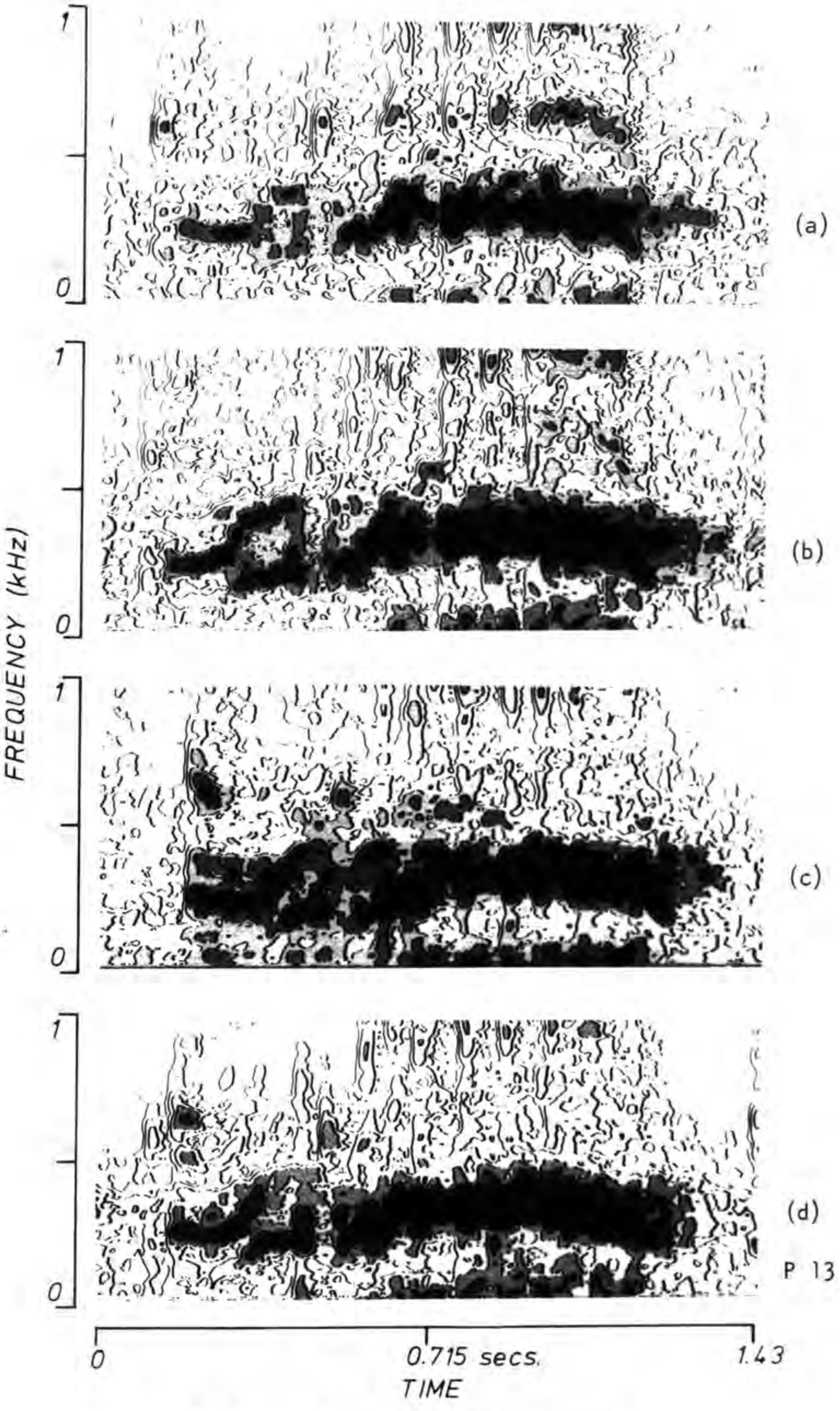


Fig. 2.13 P 13. (a) - (d) Driving calls.

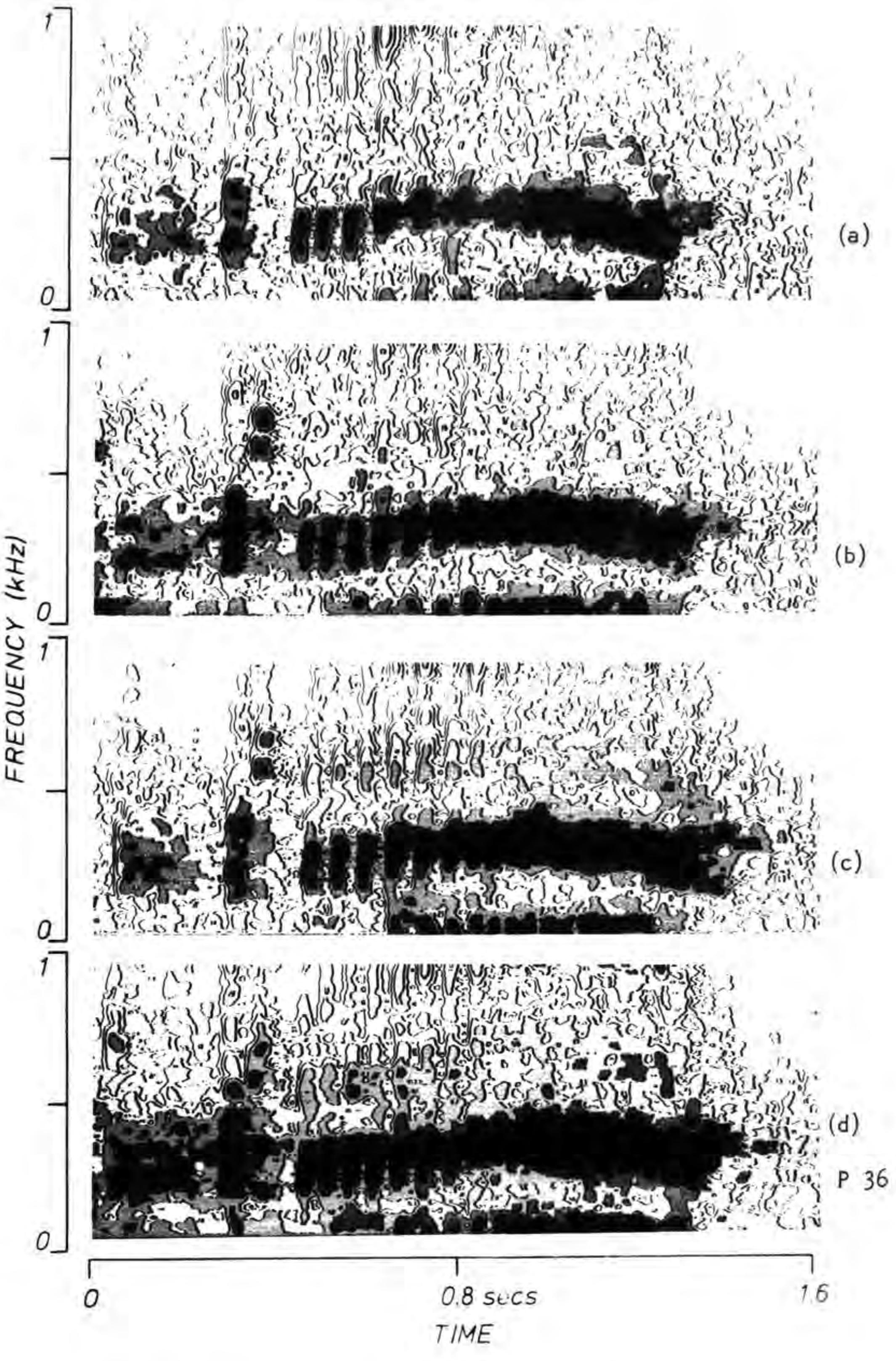


Fig. 2.14 P 36. (a) - (d) Driving calls.

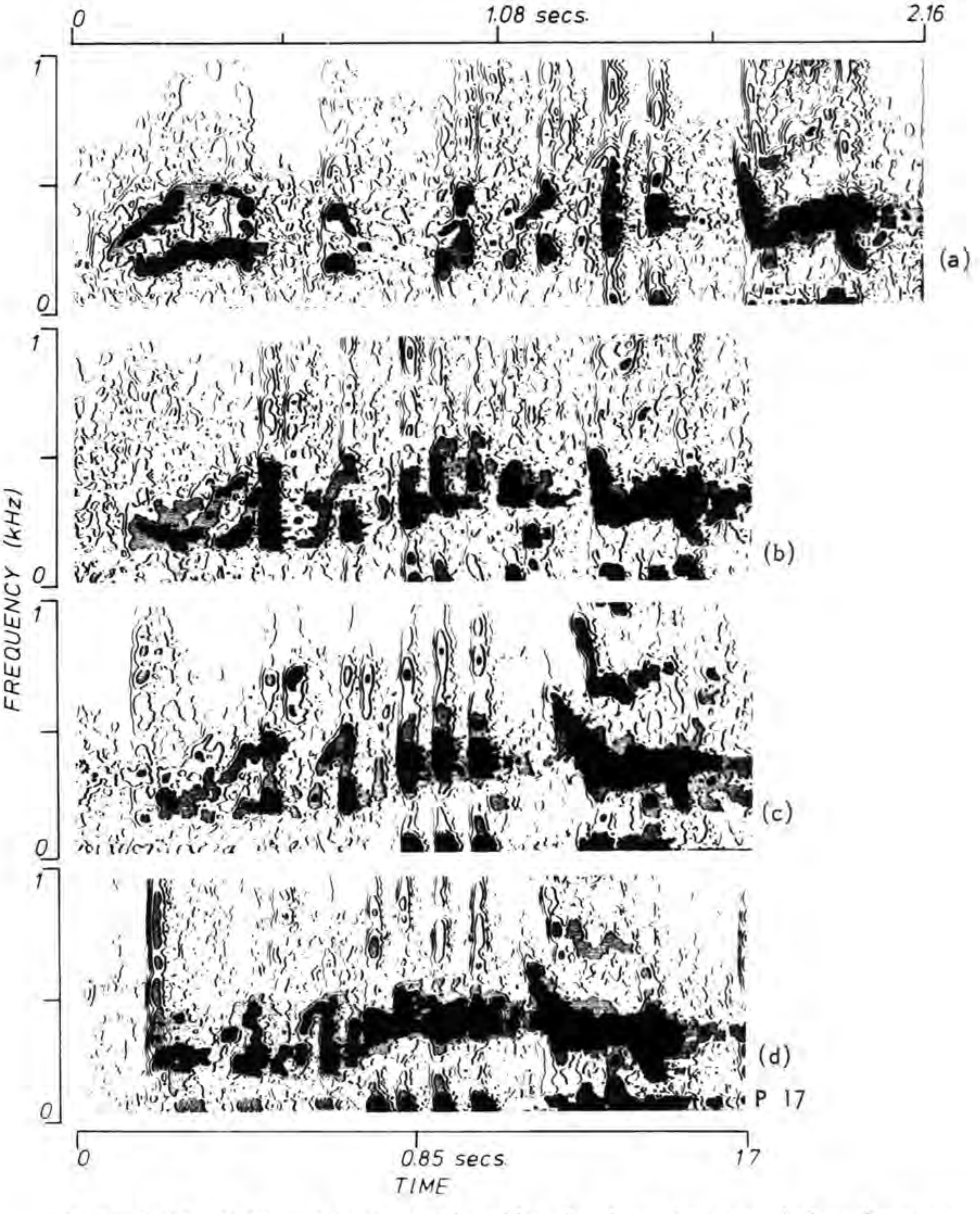


Fig. 2.15 P 17. Sequence of calls showing the transition from aoo call to driving call. (a) far left: aoo call followed by a bowing call. (b) and (c) intermediate calls. (d) Driving call. Again, notice the change in the frequency/energy structure and temporal patterning of the calls.

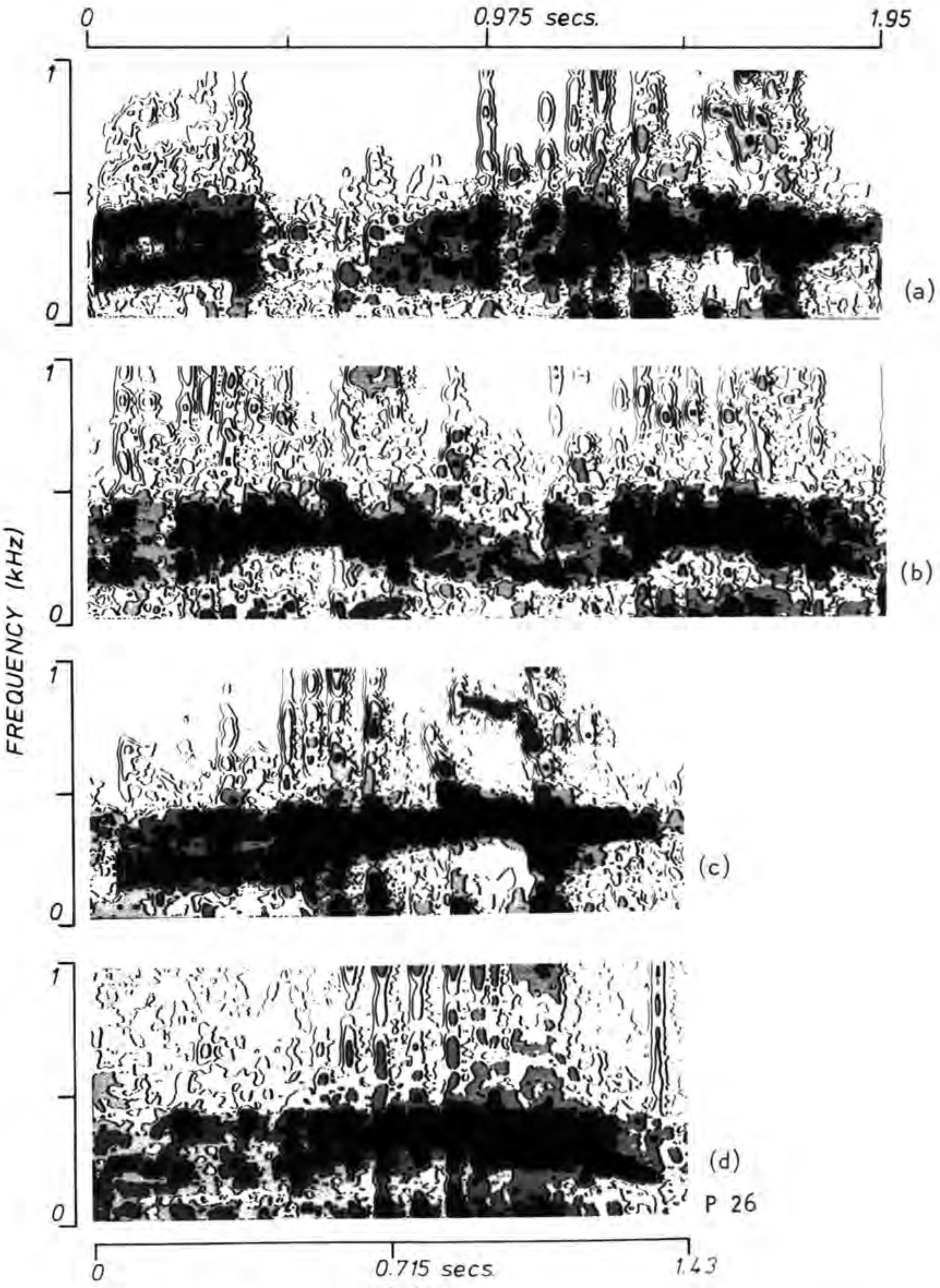


Fig. 2.16 P 26. Sequence of calls showing the transition from aoo call to driving call. (a) far left: aoo call followed by bowing call. (b) Bowing calls. (c) intermediate call. (d) Driving call.

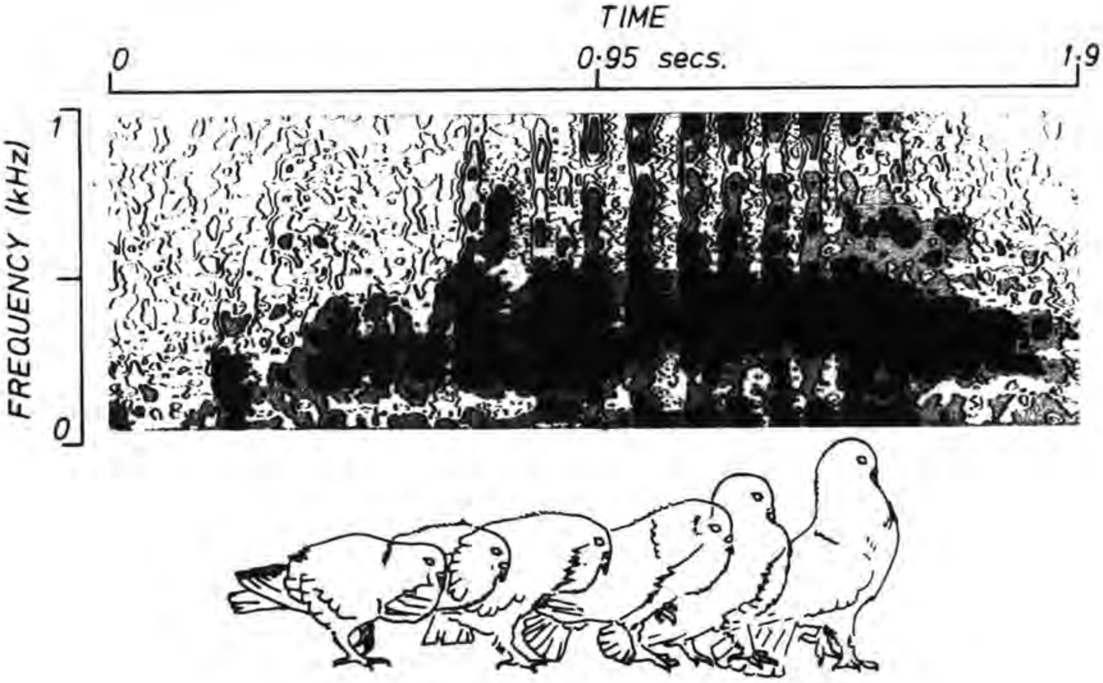


Fig. 2.17 Shows the relative co-ordination between a driving call and driving behaviour. The actual extension of the neck and the rapid opening and closing of the syrinx may be responsible for the stuttering effect in the structure of a driving call.

patterning, especially during transitions from bowing to driving, an 'ideal' call was chosen in order to illustrate the patterning of a driving call as opposed to a bowing call.

By using slow-motion video analysis, a relative co-ordination between the components of driving behaviour and the structure and temporal patterning within driving calls can be shown to exist (Fig. 2.17). The stuttering effect in the call is probably produced by the elongation of the neck in conjunction with a rapid opening and closing of the syrinx; while the amplification of the call depends on the extent to which the crop is inflated.

It has already been shown that a driving call is relatively more structured and contains more temporal patterning within it than a bowing call; but the two types of calls are not so dissimilar in the transitions from one type of call to the other (Figs. 2.7 to 2.9) occur with accompanying transitions from one behaviour to the other (Fig. 2.3). Since driving behaviour can be considered a courtship behaviour, the accompanying vocalisatio must have different functions to the bowing calls.

Differences are evident not only between the bowing and driving calls themselves but also between the calls of different pigeons. Individual differences in bowing and driving calls may be partly responsible for individual recognition between pigeons e.g. in recognising adjacently territorial neighbours etc.

NODDING: The bird lowers its head so that the beak is pointing verticall downwards and then raises its head again. This action is repeated several times in succession. One gets the impression that Nodding during male-male encounters is incomplete in its action; but this is not a clear-cut difference.

WING VIBRATION: This behaviour is seen during both male-male and male-female encounters. Generally shown by the subordinate male in male-male encounters, the wing nearer to the opponent is vibrated, while the bird is in an upright position with its neck feathers ruffled. Wing Vibration is also shown by the male at a prospective nest site; however, this behaviour may be performed at other sites in the cage and not necessarily by the male bird. During wing vibration at the nest site, the pigeon lies in an oblique position, head downwards and tail raised (although sometimes the tail is lowered and placed flat against the substrate), making quite a large angle with the horizontal. The wing nearest to the female bird is vibrated (but both wings are sometimes vibrated). Other behaviours appearing in conjunction with wing vibration are nodding and the "Aoo" call.

The former behaviour in conjunction with wing vibration is normally seen in agonistic situations while the latter in courtship situations ("nest demonstration"); but transition from one behaviour to another is common.

NIBBLING: This behaviour occurs throughout the preening bouts followin copulation and also during nest demonstration by the male (ref. Nibbling at the nest site). In the former instance, the female stands quite motionless while the male nibbles, rather than bill-combs, her neck and crown feathers (Plate IIA) concentrating at times in the region around the eyes, including the cere around the female's bill; and this almost always leads to begging by the male.

BEGGING: One bird pecks at the bill, cere or the feathers around the base of the bill (Plate IIB). Begging by the male bird was noticeable when the female crouched. On the other hand begging by the female was seen to occur during the preening bouts after copulation. This behaviour looks very similar to the begging shown by squabs.

BILLING: Following begging, the male opens its beak and swells up its crop. At the same time the female inserts her bill into the male's mouth (Plates IIC & D). As the male performs twisting actions, one can notice movement of the crop owing to the regurgitation of the food, which is immediately swallowed by the female. Although it seems that the female pigeon also performs these twisting actions, video analysis showed that the female only follows the actions of the male bird, the only actions she does being relatively unpronounced, and are brought about by her swallowing the regurgitated food.

CROUCHING: The female stands motionless in a huddled position, after being given a few pecks by the male (Plate IVD). The male may preen himself while the female is still crouching, and he may subsequently show begging in response to crouching by the female.

SQUATTING: The female lowers her head, usually directly to one side away from the male, while raising a slightly fanned out tail; at this stage the anal region moves in and out, and the wings are kept close to the sides (Plate IIIA). As the male approaches the wings are moved slightly away from the sides.

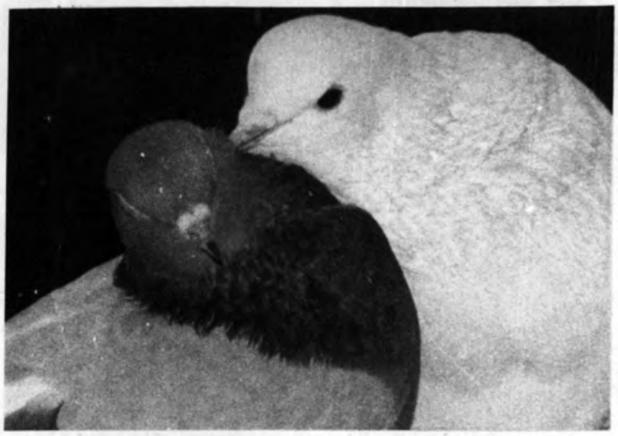
MOUNTING: is achieved when the male jumps on to the back of the female pigeon.

TREADING: The male bird folds its wings and treads with its feet, while resting his tail on the female's tail. The male generally positions his feet partly on the arc of the wing and partly on the female's back (Plate IIIB). During treading the female brings her wings into a horizontal plane.

COPULATION: The male fans out his tail and bends it while pushing the female's tail to one side; the male then bends the lower part of his abdomen inwards under the female, so that cloacal contact can be achieved, and performs very fast, thrusting movements ensuring cloacal contact (Plate IIIC). These very fast thrusting actions unbalance the male, which then dismounts. The female lowers her tail, raises her head and sometimes pseudo-drives.

The male showed squatting if the female preened his back although the female showed no intention of mounting the male (Plates IIE & F). Copulations were interspersed with long bouts of preening and other maintenance activities.

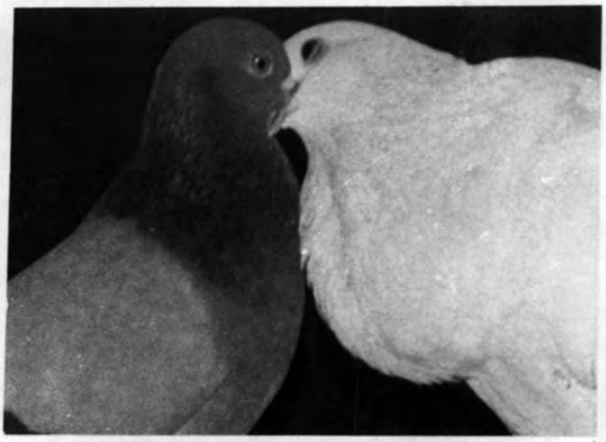
PLATE II



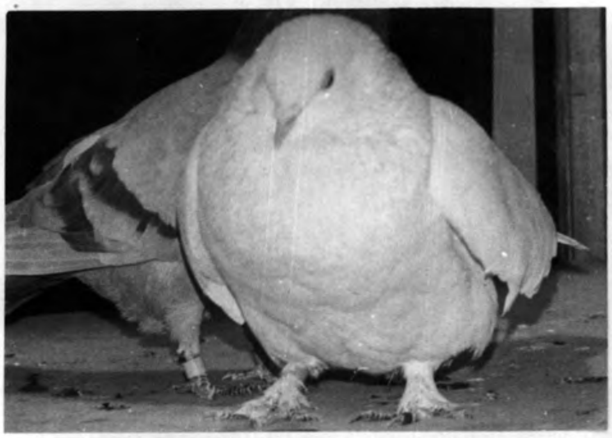
A. NIBBLING

B. BEGGING

C. BILLING (i)



D. BILLING (ii)

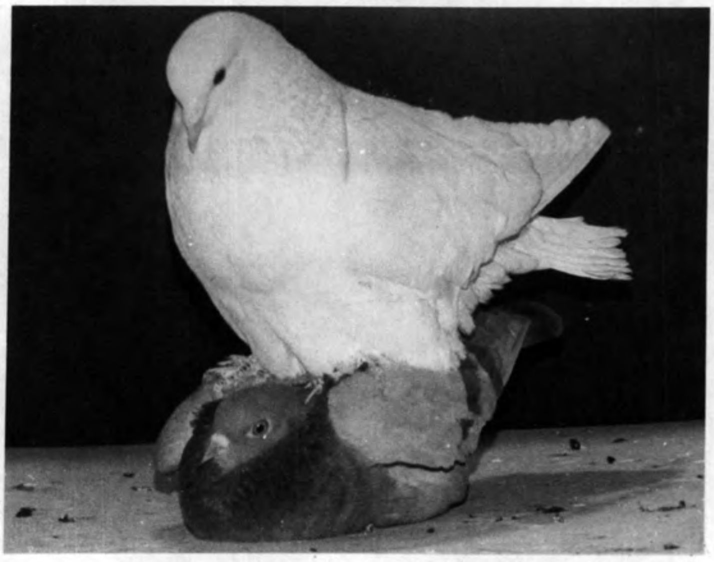


E. MALE SQUATTING

F. PREENING BY FEMALE DURING MALE SQUAT

PLATE III

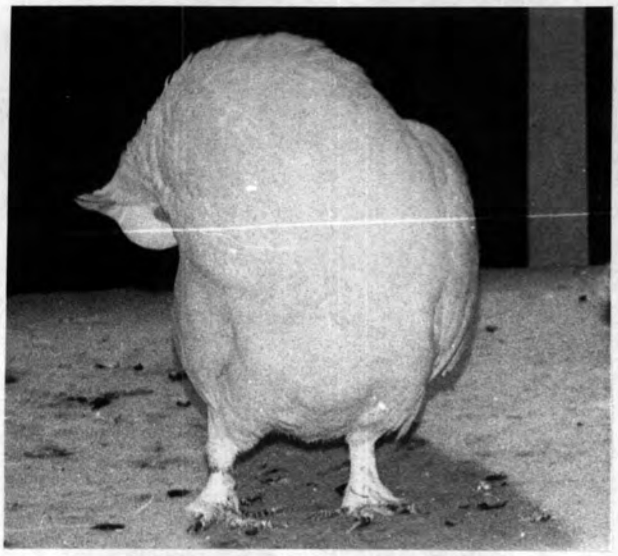
A. SQUATTING



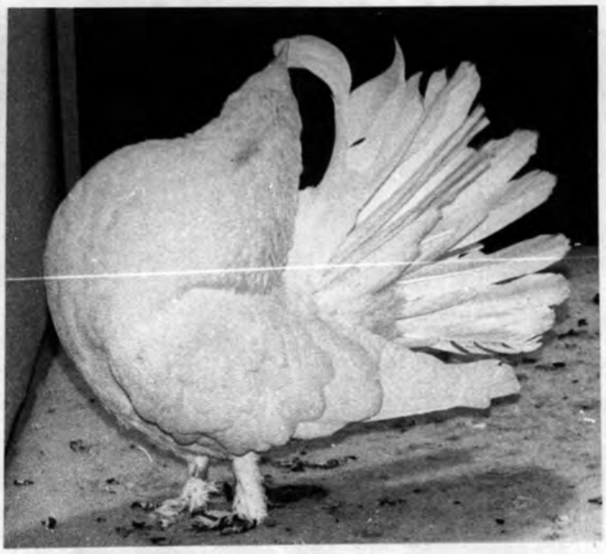
B. MOUNTING

C. COPULATION

PLATE IV



A. HEAD RUBBING



B. PREENING

C. BOTH WING STRETCH

D. CROUCHING

E. FLUFFING

F. FOOT PECKING

DISPLACEMENT PREENING: The pigeon turns its head backwards and sometimes touches or bill-combs the scapulars very rapidly. Goodwin (1956) suggests that the pigeon places its bill between its body and the scapulars while Fabricius and Jansson (1963) say that the scapulars are touched. In fact, the pigeon may or may not touch the scapulars and sometimes the bill is not even lowered that far, resulting in an incomplete action, unlike preening where the pigeon bill-combs the scapulars. I have also seen displacement preening down the side of the breast in several birds and in some instances this type of preening resembled head rubbing against the side of the breast.

HEAD RUBBING: The head is turned backwards as in displacement preening, but instead the head is lowered sideways and the side nearest to the body is rubbed quickly forward. This rubbing action is repeated two or three times (Plate IVA). The possible functional significance of head rubbing will be discussed later.

FOOT STOMPING: A very rapid, alternating stepping action of the feet during which the bird remains more or less in the same place, but may at times move slightly backwards. Foot stomping was seen in both agonistic and courtship situations, between intervals of fighting, and between successive sequences of copulations, respectively.

FOOT PECKING: The pigeon pecks at its foot or feet, thereby removing any loose particles of matter. Occasionally the foot is raised to meet the bill (Plate IVF). Foot pecking is most frequent during the time the bird is moulting, since the skin around the feet also sloughs off and the pigeon usually pecks at the loose skin, removing it from its feet.

PREENING: was probably the most common activity observed. The feathers are drawn through the bill with very fast, unidirectional movements (bill-combing). Several body areas are preened throughout a preening bout: neck, breast, abdominal and back preening require no description. For wingbow preening, the wing is brought slightly outward and forward giving a skewed appearance - the primaries are preened by drawing each feather separately through the bill, starting at the base of the feather and drawing it outward.

For wingface preening the wing is moved outward only very slightly and approached from above. For tailcovers and tail preening the bird turns its head backwards and stretches its neck: the tail is fanned out and brought forwards towards the head. The bird begins by preening the tailcovers but then progresses to the tail feathers themselves. These are preened in a similar fashion to the wing primaries: the bird preens the base and then bill-combs each feather separately, bringing it forward in an arc (Plate IVB).

Preening of each separate area is stereotyped; however, no detailed sequential analysis was carried out in order to determine whether there was any specific pattern in preening behaviour. Each preening bout was of varying duration.

A similar procedure is followed for oiling the feathers. During sequences of oiling, the pigeon reaches for the oil gland with the beak, at the base of the upper tail covers. The feathers are drawn more rapidly through the beak, and head rubbing seems to be more frequent during sequences of oiling.

WING and LEG STRETCH: The bird stretches one of its wings upward and backward then downward and outward, at the same time bringing the leg upward and outward spanning the wing and following it backwards (Plate IC). The tail is also fanned out and tilted towards the outstretched wing and leg. Pigeons tend to stretch the wing on one side first, and soon afterwards the other.

BOTH WINGS STRETCH: The bird moves its wings slightly outward and upward, so that the bows of the wings are very close to each other; the wings are not fully stretched and the whole sequence does not last for longer than two to three seconds (Plate IVC). When this behaviour precedes leg and wing stretch the tail is also fanned out in an arc, and the wings are not moved outward so much.

BODYSHAKE: The bird fluffs up its feathers, especially the ruff, back and wings, spreads out its wings slightly and ruffles its whole body while shuffling its wings very rapidlyin an alternating sequence (Plate IVE). This body shake is transmitted to the head, resulting in head-shaking, and to the tail which is wagged very rapidly from side to side almost simultaneously with the body shake. TAIL WAGGING also occurs on its own especially in between preening bouts.

FLUFFING: In its less transient form, fluffing is a thermoregulatory behaviour (McFarland and Baher, 1968). Fluffing can also be seen during preening and prior to bodyshake, and also during sexual and agonistic postures. During preening and bodyshake, ruffling of the feathers is most noticeable around the breast and back region; although when it is seen in conjunction with sexual and agonistic postures, fluffing is seen mainly around the head, neck and also the lower back areas.

HEADSHAKE: A very rapid side to side movement of the head which also undergoes some rotation and ends abruptly. Headshaking generally occurs by itself, although it can be seen during bodyshake and preening. It is performed probably to remove foreign matter from the bill.

HEAD-SCRATCHING: The head is lowered and bent towards the foot, on the side to be scratched. The foot is raised to the head, which is scratched with rapid, downward strokes of the leg.

PECKING: The pigeon pecks at the floor (GROUND-PECK), or sides of the cage, sometimes picking up an object in its beak and then dropping it again. The bird might repeat the same behaviour with the same object several times in succession, pecking at the ground rapidly.

Apart from pecking at food particles prior to (and sometimes during) feeding, without actually ingesting any, the pigeon pecks at grit or other particles on the floor, especially if it is placed in a new environment. Usually it isdifficult to determine whether the pigeon is looking for food particles or whether it is investigating the edibility of a novel object.

INTENTION GROUND PECK: With relatively slow, downward movement of the head, the bird performs a pecking motion towards the ground or food particle although contact does not occur. This behaviour occurs throughout ground-pecking. Sometimes the motion of the head gives the impression of zig-zagging.

ATTENTION: While standing in a normal, upright position the pigeon looks around with jerky head movements made in a horizontal plane, but some are also performed in the vertical plane. The neck feathers are sleeked and the neck is stretched slightly.

LOCOMOTION: Walking or running by the pigeon from one place in the cage (or environment) to any other place; ie. movement with no apparent direction. Locomotion can be slow or fast (as in chasing or fleeing).

PANTING: After an aggressive encounter between two male birds, or when a pigeon has done a certain amount of strenuous activity (eg.

fleeing in a confined space), one or both birds may show panting which is visually recognizable by the open bill and vibration of the throat. The neck feathers are slightly fluffed.

FEEDING: While pecking at food particles, some are picked up in the bill and swallowed, although undesirable food particles are dropped. When eating from a feeding tray, the pigeon may give a few sharp flicks with the beak, scattering grains of food and/or other material. This behaviour may be useful during food selection. Unlike most other birds, during DRINKING pigeons suck the water up rather than gulp it.

DEFECATION: The bird crouches slightly, lifts the tail and protrudes the cloaca. This is followed by a lower abdominal contraction resulting in the expulsion of the faeces. Defecation is particularly noticeable when a pigeon is subjected to stress situations, such as being placed in a new environment.

YAWNING: This behaviour was most common during preening bouts or after courtship 'sequences'. The neck is stretched upward and backward while the beak is opened wide, and is closed again as the head is brought forward to its normal position.

DOZING: The bird becomes inactive, and assumes a withdrawn or huddled posture with its feathers slightly ruffled. The nictitating membrance may be drawn over both eyes or over one eye at a time. Sometimes one leg is withdrawn so that the bird stands on only one leg.

2.5 Behaviour at the nest site

MUTUAL PREENING: While the male shows nest demonstration the female approaches and passes her bill through the head feathers of the male very rapidly - a behaviour which looks like preening (Plate IIF). It is very difficult to determine whether this behaviour is in fact preening or whether it is displacement preening or nibbling by the female, at the nest site (Goodwin, 1956, refers to this behaviour as caressing; Miller & Miller, 1958, as hetero-preening).

NEST DEMONSTRATION: This term has been used very loosely by several authors, when describing a 'behaviour' which appears not only in courtship situations, but also in agonistic situations. This 'behaviour' in fact is composed of several behaviours namely, nodding, wing vibration and the 'aoo' call which (excluding the call), have already been described in the previous section.

THE AOO CALL: Aoo calls are given by both males and females but predominantly by the former. In the field, male pigeons aoo-call regularly at the beginning of the breeding season. Pigeons of both sexes aoo-call at the nest site, usually in conjunction with nodding and wing vibration; but sometimes the birds aoo-call while performing wing vibration only. This call is most noticeable during the early stages of the preincubatory phase of the breeding cycle; however, it is also given by single male birds and sometimes seems to be directed towards pigeons in neighbouring cages whether these are male or female. Male pigeons which are placed in total social isolation (see Chapter 4) also give this call.

Apart from the alarm call, the aoo call is very simple in structure (see Fig. 2.18 to 2.21) and can be rich in harmonics. The call frequency rises from about 200 Hz. at the beginning of a call, peaking at about 450 Hz. and then falling off again to the starting frequency. It is not uncommon for sequences of aoo calls to last for over a minute. The temporal intervals in between the calls are more or less constant, although the amplitude increases

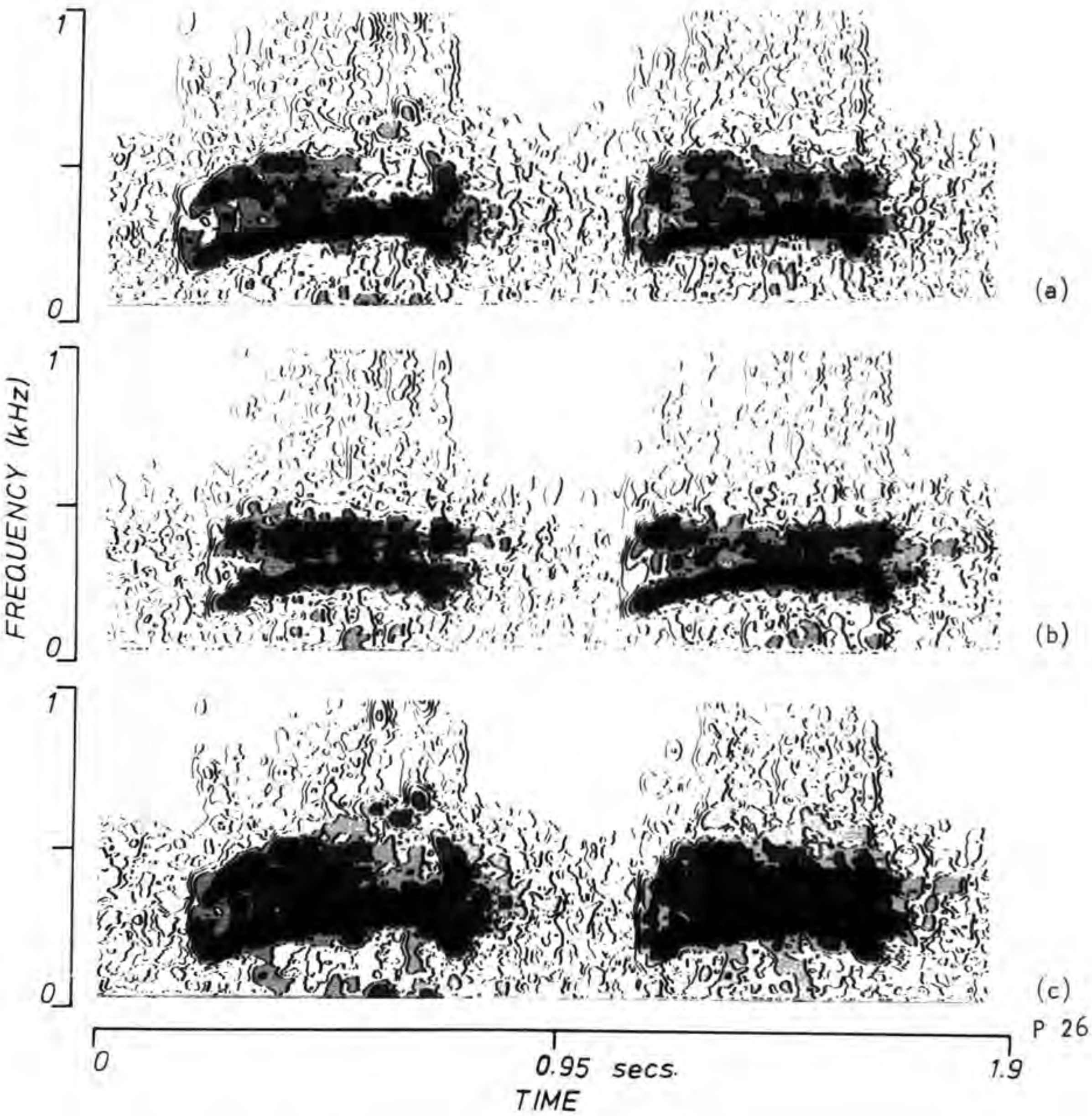


Fig. 2.18 P 26. (a) - (c) Aoo calls. Notice the non-harmonics in (b).

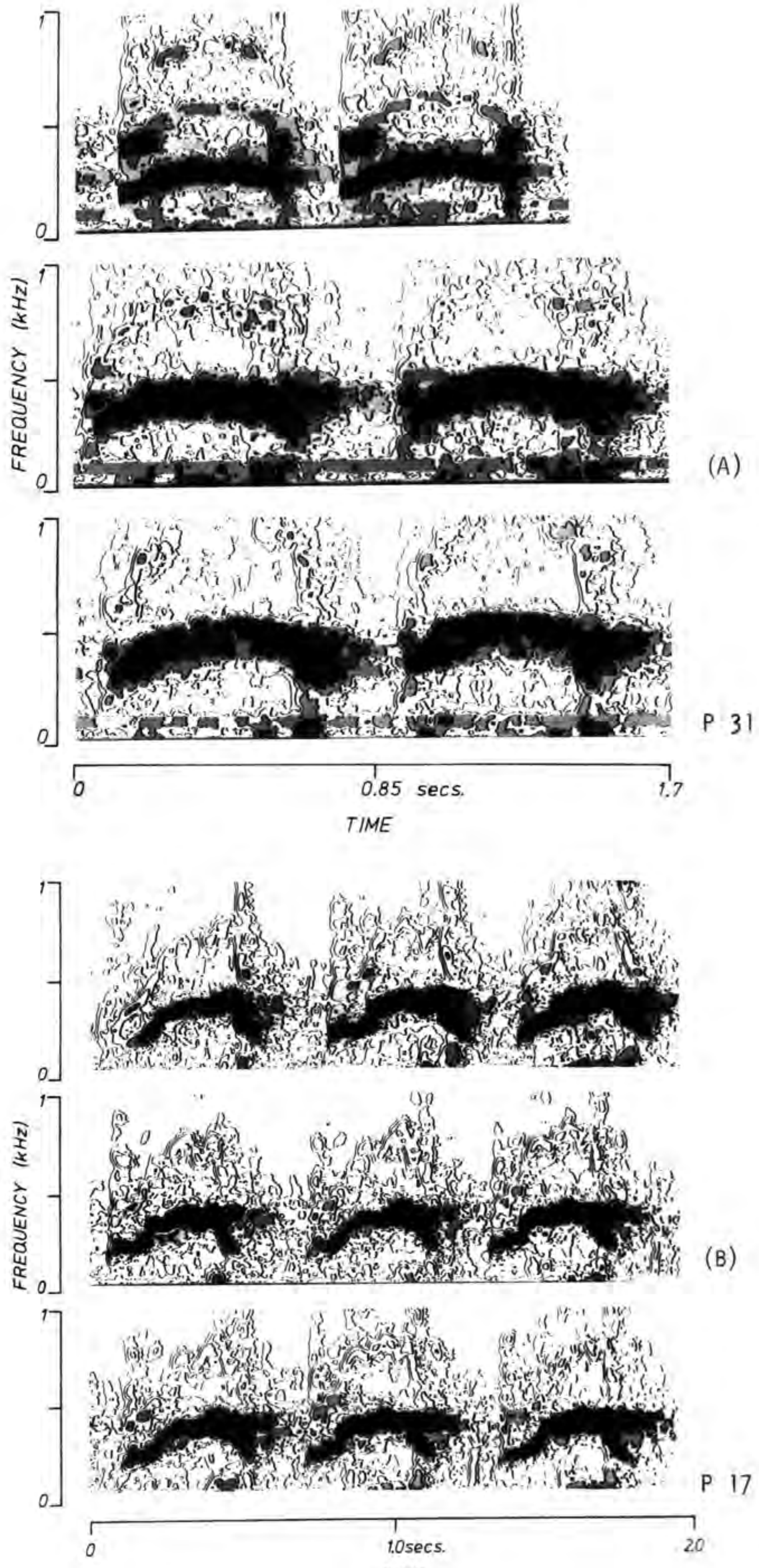


Fig. 2.19 Sequence of Aoo calls. (A) P 31. (B) P 17. It is interesting to compare (A) of this figure with (A) of Fig. 2.20. Notice that as the energy and duration of the call increases, the energy at the higher frequencies decreases.

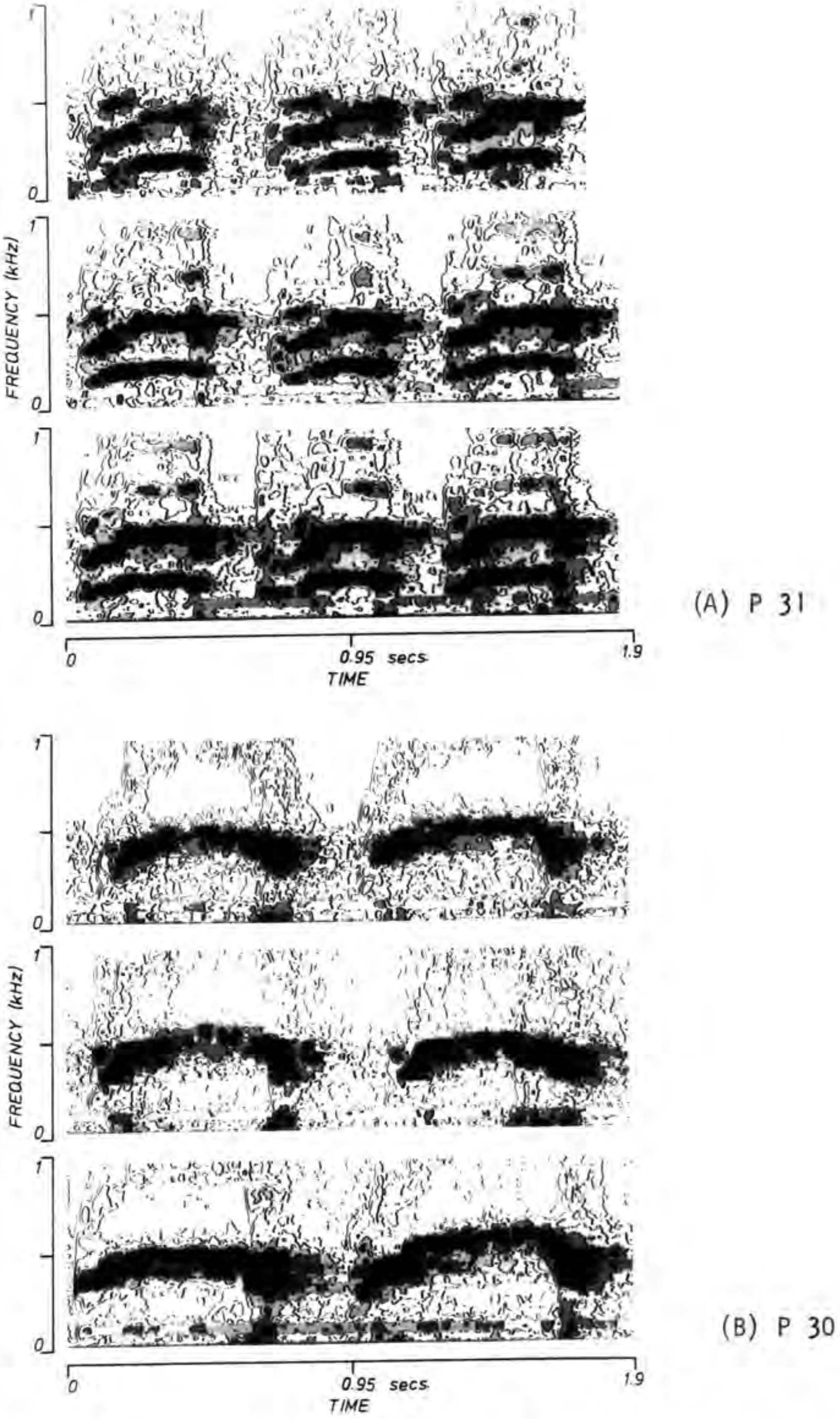


Fig. 2.20 Sequence of Aoo calls. (A) P 31. (B) P 30. The two tones visible in (A) are harmonically unrelated, suggesting that pigeons may be capable of using 'two voices'.

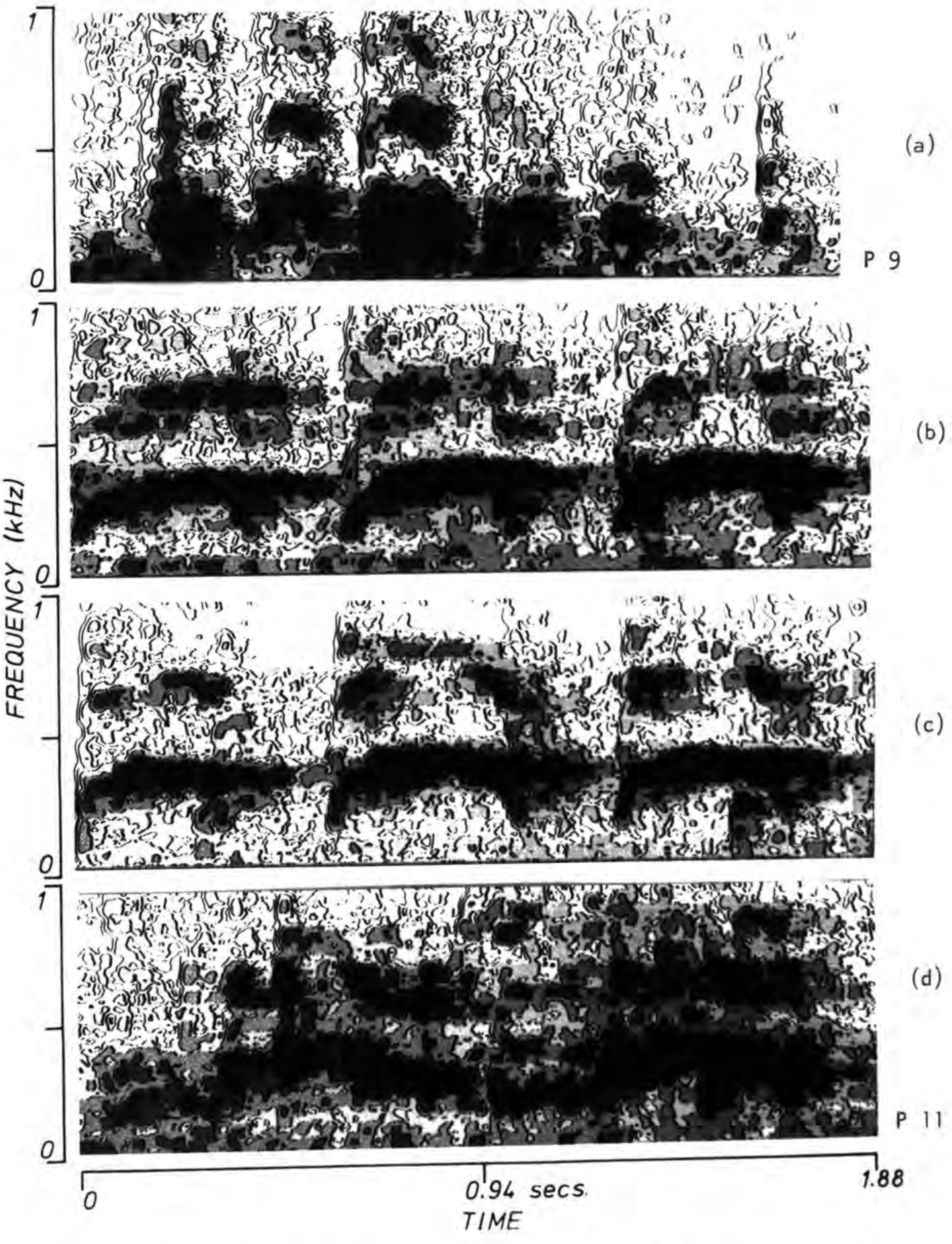


Fig. 2.21 Calls given by female pigeons. (a) P 9. Alarm calls. (b) to (d) P 11: (b) and (c) aoo calls; (d) Bowing calls. Notice the similarity in structure between some aoo calls and the bowing calls.

with time throughout a sequence of calls. The duration of each call also increases.

THE ALARM CALL: The alarm call is probably the simplest vocalisation pigeons produce (Fig. 2.21). It is very similar to the alarm note produced by ring doves (Miller and Miller, 1958) but harsher in tone, sounding like a harsh 'hinnnh'. Moreover, the pigeon that gives the call, usually a female at the nest site, is in a slightly squat posture with feathers ruffled. Pigeons give the alarm call when a stranger or a strange object (such as the observer's hand) approaches too close.

NEST-BOWING: When this behaviour is performed at the nest site by the male, the orientation of his body is quite different from that adopted for the 'normal' bowing behaviour. The body is held obliquely, head downwards. The bird bow-calls and rotates although remaining in the same place. Sometimes the abdomen brushes against the nesting material, and this has the effect of moulding the nest into a circular shape.

BODY REST: During the early stages of the pre-incubatory phase of the breeding cycle, when the female approaches the male in response to his 'nest demonstration', she will rest her abdominal region on to the head and neck of the male. Consequently, the intensity of the male call increases and he may also push his head further underneath the female's body (PUSHING by the male at the nest site).

PUSHING: Unlike Fabricius and Jansson (1963), I have regularly observed pushing by males at the nest site. When the female approaches the nest site and shows body resting, the male will push himself underneath the female's body while performing intense wing vibration and calling at the nest site. Pushing by the female was seen at a later stage in the pre-incubation phase, usually when the male is standing at the nest site. 'Nest Demonstration' by the female is also very intense at this stage, and the pushing pigeon, whether male or female, is 'preened' (mutual preening) by the other mate.

NEST MATERIAL COLLECTION: Because of the nature of the nesting material provided (wood, wool or shredded paper), the pigeons showed elements of this behaviour very clearly. The bird picks a single strand of nesting material in its bill and gives several head shakes in order to loosen it from the bunch. When the strand is loose, the bird tucks it underneath its abdomen and positions it by its legs. The pigeon may do this with several strands of material, until it picks up one strand of adequate length (or seemingly so), carries it to the nest site and deposits it in front of its mate.

NEST BUILDING: The pigeon standing at the nest site immediately picks up the strand and tucks it among the others sometimes rearranging other strands in the process. If it so happens that the other pigeon is not at the nest-site, then the bird collecting the nesting material will arrange the strand in a similar manner to its partner. If the female pigeon is at the nest site, the male will pick up a strand of material and carry it to the nest site where the female is showing 'nest demonstration'. Although it is more common for the male to collect nest material during the early stages of nest building, and for the female to arrange it at the nest site, the female will collect material if the male is at the nest site, thereby reversing nest-building roles. This behaviour is very similar to the nest building shown by doves (Streptopelia risoria; see Lehrman, 1958a).

2.6 The Courtship encounters

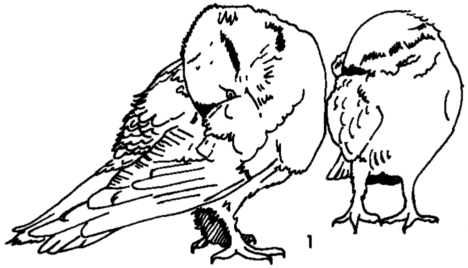
The encounter begins by the male pigeon approaching, bowing and bow-cooing in front of the female. This bowing may change to driving if the female moves away from the male, with an accompanying change in the call to the driving call. Following driving the male stops and nods, and the female responds by nodding.

Another behaviour which both pigeons perform and which follows nodding is displacement preening. This is a characteristic behaviour seen during courtship encounters in pigeons and is listed by many authors (eg. Fabricius and Jansson, 1963; Levi, 1941; Heinroth and Heinroth, 1949; Goodwin, 1955, 1956). The female will then stop displacement preening and moves away slowly from the male, to which the male responds by driving the female very closely (Fig. 2.22: 2 & 3), at times bumping into her. It is not as yet very clear what elicits squatting in the female, but she will stop moving suddenly, lower her head and squat. The male pigeon mounts, treads and copulates, the latter action unbalancing the male, which dismounts (see Fig. 2.22). The female stands up and often performs a form of driving behaviour, which is dissimilar to the driving behaviour performed by the male.

Bowing behaviour is frequently seen during first encounters between male and female pigeons and also during the early stages of the pre-incubatory phase of the breeding cycle (Fabricius and Jansson, 1963) possibly suggesting that the courtship behaviour in pigeons, as indeed in many other bird species, is an outcome of a conflict between sexual motivation and agonistic tendencies (eg. see Tinbergen, 1952, 1954).

2.7 The Agonistic encounters

The following behaviours can be seen during agonistic encounters: Aggressive pecking, aggressive billing, body pushing, wing flicking, aggressive intention peck, bowing, bow-cooing and sometimes nodding, wing vibration and the aoo call. Fleeing and chasing are not often seen in the confined spaces of the observation cage, however they can be seen during agonistic encounters in the free-ranging pigeon.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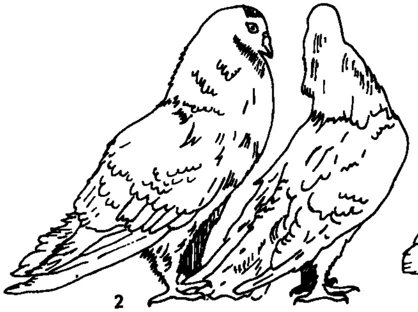
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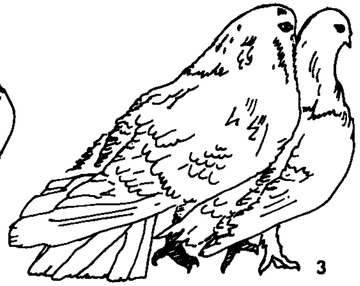
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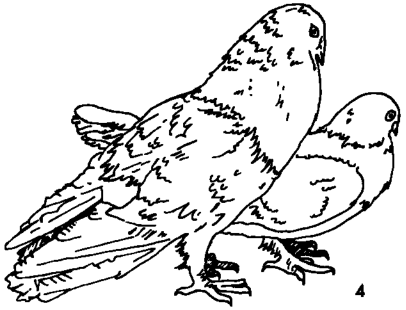
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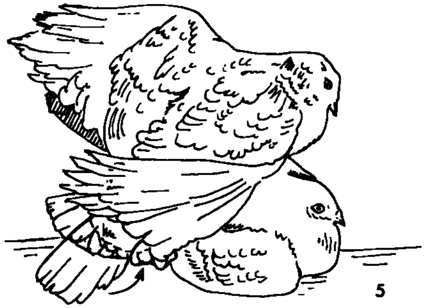
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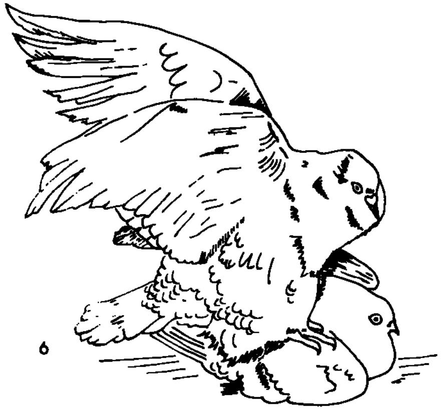
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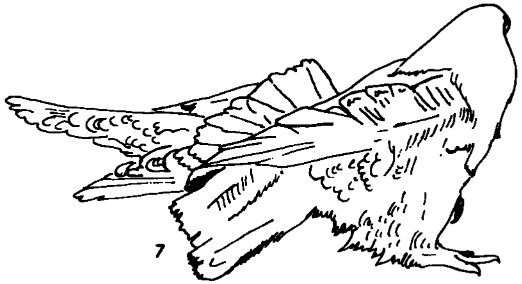
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When a strange male approaches another male pigeon, both birds perform bowing. In this situation this behaviour is probably the outcome between attack and escape tendencies. If neither of the birds moves away, one of the pigeons wing flicks the other and approaches closer. However, I consider wing flicking to be a threat behaviour (see Tinbergen, 1959), since although it is an aggressive behaviour, there is no close bodily contact between the two birds; and at times it may also serve as a deterrent to the strange bird to approach any closer. This behaviour leads to aggressive billing and body pushing which last for several seconds. When one of the birds moves away or flees, the other, dominant bird chases and often aggressively pecks the fleeing male. After a few seconds the dominant pigeon gives up the chase. Aggressive intention peck and nodding are usually performed by both dominant and subordinate males, if these encounter again shortly after a fight. Nodding may be an appeasement behaviour performed in order to suppress aggression. Although wing vibration is seen during encounters between male pigeons in the laboratory situation after prolonged encounters, I have never observed this behaviour between free-ranging male pigeons.

2.8 Some comments on the function and causation of some of the behaviour patterns

In contrast to other more "straightforward" behaviour patterns such as feeding, escape behaviour and copulation, the function and causation of the following behaviour patterns is difficult to understand: Bowing, Driving, Nodding, Wing vibration, Displacement preening, Head-rubbing, Foot-stomping, and mutual preening. In the following section I propose to discuss some of the general features of these behaviours and displays which, to my mind, have been misinterpreted. The behaviours and displays listed are used in agonistic as well as courtship or pair formation "ceremonies", with the possible exception of mutual preening.

Bowing and Driving

Beach (1951), and Fabricius and Jansson (1962) call the driving behaviour shown by a male pigeon before mounting, strutting; likewise, there exists some confusion as to which behaviour should be termed as "bowing". I have tried to describe this behaviour and driving behaviour visually, in the ethograph (Fig. 2.3). The confusion may have arisen in the first place because several authors have watched these behaviours (rather they give the impression that they have) in only one context - that of courtship. I agree with Goodwin (1955) when he suggests that the posture adopted by the driving male is similar to its behaviour prior to copulation. In their discussion, however, Fabricius and Jansson do mention that "driving is even more similar to the behaviour of a dominant male chasing a submissive male intruder in the territory, and further, actual attacks occur during driving showing that the aggressive instinct is activated". Consequently, I believe it to be unnecessary to call a behaviour, which appears in different contexts, by different names.

Bowing is normally seen during first encounters between birds, whether these are both male or male and female. This behaviour is also seen sometimes at the nest site and, as suggested earlier, one of its functions may be to mould the nest into a suitable shape. In male-female pairs, bowing occurs during the early stage of the pre-incubatory phase of the breeding cycle; but its occurrence decreases during the later stages. During male-male encounters, however, the occurrence of bowing alternates with aggressive behaviour.

In this context, bowing by a dominant male may have an intimidating effect on the subordinate bird or on other intruding pigeons or near-intruders. So the tendency here is one of aggression. However, on unfamiliar ground, a pigeon performing bowing behaviour may promote an attack by the opposing pigeon. In this case the tendency is one of withdrawal or escape. Both tendencies are evoked by the opponent's agonistic behaviour. It may be suggested, therefore, that bowing behaviour is a conflict behaviour showing both a tendency to attack and escape in the pigeon performing the behaviour.

Abs (1970a) has shown that the voice of immature and hypophysectomised pigeons is 'broken' by testosterone injections: the calls of a 9 month hypophysectomised pigeon had a mean frequency of 2532 ± 19 Hz; but after injection with 17.5 mg of testosterone, the mean call frequency was reduced to 208 ± 3 Hz. From my own casual observations on the development of the bowing behaviour in pigeons, it seems to me that the voice breaks before the fully developed bowing display is seen. However, the calls are of lower amplitude than the ones accompanied by the full bowing display.

From these observations I tentatively suggest that (1) the development of bowing behaviour is testosterone-dependent (Abs does not describe whether the hypophysectomised pigeons developed or lacked bowing behaviour) and (2) the bowing behaviour (ie. the movements of the display components) is responsible for the amplification of a bowing call.

Bowing behaviour is probably more closely associated with territoriality and agonism than with courtship although Fabricius and Jansson (1963) suggest that "both the aggressive and sexual instinct are activated in the male when he bows in front of the female". I have shown that bowing can be clearly differentiated into two behaviours - bowing and driving. It is this latter behaviour which I closely associate with courtship, and would certainly explain why Fabricius and Jansson suggest the functional ambivalence of the behaviour they term as bowing.

Whitman (1919), Heinroth and Heinroth (1949) and Levi (1941) all suggest that the function of driving is to impress the whereabouts of the nest on the female; and Whitman goes on to say that the driving male "is impelled by feelings of jealousy or possessiveness towards the female". This has been denied by Goodwin (1955, 1956) and Fabricius and Jansson (1963) and by my own observations, since driving can occur during the first encounters between birds (also between male birds), before any nest site has been chosen. Unlike Goodwin and Fabricius and Jansson, I have observed driving between male birds and male-female pairs which were completely isolated from the rest of the colony and from human observers (closed-circuit T.V. was used for observation), since Goodwin (1956) states that "a male pigeon that is reacting socially to man will often begin to drive his mate when a human being approaches them closely".

Andrew (1961) suggests that movements accompanying testosterone dependent calls in courtship displays, for example bill-lowering in gulls, are probably components of nest-building in origin. Head- or bill-lowering is a display component of driving behaviour, and the action is similar to both nodding and tucking of nesting material under the abdomen, in pigeons. The functional significance of driving, however, remains unclear. In conjunction with the driving call, driving may initially serve in the formation of pair-bonds between pigeons; it may also help to maintain the bonds once these are formed. Apart from this, driving may be responsible in some instances, for eliciting squatting in the female. On the other hand, driving away from the nest may be purely extrovert behaviour, in the form of an intimidating display towards other pigeons, or as an indication to other pigeons of the existence of a bond between the displaying bird and its mate.

Sometimes a female pigeon will show a form of driving, after copulation. It is possible that this is some form of escape behaviour in a confined space, since free ranging female pigeons fly away from the male after copulation.

Nodding and Wing Vibration

Fabricius and Jansson list these two behaviours as one, termed as 'nest demonstration'. However, because these behaviours are seen in several contexts, I believe that this term is incorrect. I shall discuss the two behaviours independently of one another, but examine their function when the two occur concurrently.

Goodwin (1956) has observed nodding in the following circumstances: "(1) by both members of a pair when at the nest-site or when coming together after a short parting, (2) by a female, in response to sexual, self-assertive or aggressive behaviour from a male with whom she is eager to pair, (3) by a bird alone (normally with its mate nearby) on the nest-site, (4) by a bird threatening (usually defensively) another."

My observations support this; however, I would like to make the following comments: with regards to point (2), the male will nod in response to a female bowing (one of the few instances in which bowing by a female takes place) in an adjacent cage; or could also begin nodding, in response to which the female would either bow or nod. I have also observed nodding between two males in separate cages. It would seem that nodding, in this instance, need not necessarily act as a threat (point (4)) nor as a defensive behaviour, since there is no danger of either bird approaching or attacking the other. Moreover, Goodwin confuses the context by suggesting that a bird threatens defensively. Surely this depends on the relative 'status' of one bird in relation to the other; in other words, a dominant bird will threaten another subordinate bird. But the latter only shows behaviour which tends to reduce or suppress the aggression of the dominant bird (it is doubtful whether such behaviour should be called defensive behaviour). Therefore noddin may have the function of indicating to other pigeons possession of an area.

Wing vibration is seen in the following situations:
(1) By a male pigeon at the nest site during the early stages of the pre-incubatory phase of the breeding cycle, or by the female later on in the cycle, (2) by a male in response to sexual behaviour (eg. nodding) from a female, (3) by a male alone, usually to other birds (not necessarily female) in adjacent cages, possibly in response to bowing or driving by other males, (4) during an encounter between two male birds.

In discussing the apparent functions of wing vibration, one must look at this behaviour in conjunction with nodding, since wing vibration is always seen together with nodding (but not vice-versa). Sometimes the pigeon aoo calls during wing vibration.

At the beginning of the reproductive cycle, when the two behaviours are shown by the male, their main function seems to be to attract the female to the prospective nest-site, and to indicate to the female that the site is in fact owned by the male. Later on in the cycle, when the behaviours are mainly shown by the female, they may serve to suppress the aggressiveness in the male and to strengthen the bond between the pigeons. Moreover, it may indicate to the male that the female intends to nest at the site chosen by the male. During agonistic encounters, the subordinate male may shown wing vibration and nodding in order to suppress the aggressiveness in the dominant bird, and to maintain a low level of aggression. In this situation these behaviours may be considered as appeasement behaviours. Since there is no way of sex recognition between pigeons except by the performance of certain behaviours, a single male pigeon may show these two behaviours towards males in adjacent cages, probably to determine whether the birds are male or female by observing the resulting behaviours in the other birds.

Since nodding is very similar to the abdominal tucking of nesting material, it is possible that this behaviour has been derived from nesting behaviour. This possibility has been suggested by Goodwin (1956), who also states that the nodding movement in the bar-shouldered dove (Geopelia lumeralis) culminates into the typical movement of a bird arranging a twig in the nest.

Hence these two behaviours may primarily function as courtship behaviours. However, they certainly have other functions depending on what the situation or the circumstance calls for. As we shall see in Chapter 3, nodding and wing vibration also occur in agonistic contexts.

Displacement Preening

This behaviour seems to be common to most dove and pigeon species.

Goodwin (1956) suggests that the male pigeon displacement preens because, although sexually aroused, "he is unable to copulate or to commence the pre-copulatory billing either because the female is not yet giving the appropriate responses or because of his own incapacity." Contrary to Goodwin (1956) and in accordance with Fabricius and Jansson (1963), I have observed displacement preening probably as frequently in female pigeons.

Therefore a female may also show displacement preening either because the male refuses to show the appropriate pre-copulatory behaviour, or once this has been performed, the male does not mount the female. In both instances, there may be a thwarting of expectations which is shown by the performance of an 'irrelevant activity'. I have also observed displacement preening down the side of the breast frequently in males (cf. Goodwin, 1956).

Head Rubbing

This behaviour was seen in both courtship and maintenance situations, and may be shown by pigeons in response to stimuli which are either physically or psychologically displeasing or both.

Its function is probably to remove particles or foreign matter which have become lodged around the eye, since head scratching might prove painful and possibly dangerous to the bird. Psychologically displeasing or irritating stimuli are those stimuli which confuse the bird visually; for example, a male pigeon performed head-rubbing after courting his mate and attempting to get through a glass partition. Bright lights causing shallow reflections also seem to elicit head-rubbing; but the brightness of the lights themselves may have caused optic irritation. However, the function of head-rubbing in this situation remains unclear.

Foot-stomping

This behaviour is seen in both maintenance and agonistic contexts. The behaviour itself may be performed irrespective of the situation and only when the pigeon is standing on a solid substrate (not on wire mesh). Rarely it is shown by a pigeon fleeing from an opponent.

Foot-stomping in pigeons is probably elicited by mechanical irritation of the feet, caused by foreign matter (such as feces) lodging itself in between the toes and probably also sticking to the underside of the feet; but since this behaviour was also performed on clean substrates, its function in certain instances, still remains unclear.

Mutual Preening

This behaviour is generally performed by the female while the male is showing intense 'nest demonstration' at the nest-site, during the early stages of the pre-incubatory phase.

Unlike Goodwin (1956) I have only observed mutual preening (or caressing, as he calls it) of the back, head and neck regions. Usually the preening bird concentrates on the head and neck, these being areas which the bird being preened cannot reach with its own bill. So that the physical function of mutual preening is the removal of foreign material or ectoparasites from the mate's head and neck.

However, on other occasions the female passes her bill over the male's feathers very rapidly, although there is physical contact between bill and feathers. In this case, mutual preening may serve to (a) stimulate sexual behaviour, (b) as appeasement behaviour, inhibiting aggressive behaviour, (c) stimulate the male and (d) strengthen the bond between the two birds. These probable functions of mutual preening also apply if the male performs this behaviour.

CHAPTER 3

EXPERIMENT 1: REGULATION OF AGGRESSION BETWEEN MALE PIGEONS

3.1 Introduction

One of the main problems in the study of animal behaviour is the regulation of intra-specific aggression. The general consensus of opinion on the subject of aggression is that fighting can have the following functions: (1) defence against predators; and (2) territorial maintenance or gain.

An animal will engage in "ritualised" aggressive behaviour, the function of which would be to achieve dominance over an antagonist, thereby increasing the size of the territory, gain access to additional food, sexual partners etc. Eibl-Eibesfeldt (1961) suggests that these "ceremonial struggles" may serve as a measure of strength in bodily contact between the two contestants, without harming each other seriously. At the end of these ritualised aggressive encounters, the winner may often continue displaying; and indeed, in some species of animals, stereotyped displays are necessary for one animal to maintain dominance over a conspecific (Simpson, 1973).

We ought to consider aggressive behaviour, therefore, in terms of what J. P. Scott (1970) calls agonistic behaviour. He defines this type of behaviour as "a system of related behaviour patterns having the common function of adaptation to situations of conflict between members of the same species". These behaviour patterns could be classified loosely into defensive threat, defensive attack, overt attack and non-contact display behaviours. But active defence (i.e. fighting) is not a necessary condition for the maintenance of some degree of exclusive occupation of an area, which is the most important ecological consequence of territoriality.

Mutual avoidance between individuals, achieved by certain non-contact stereotyped displays, can result in a similar type of spatial distribution. Moreover habituation of one individual to another may be one more mechanism involved in the maintenance of lowered levels of aggression during constant exposure to a conspecific neighbour (Peeke and Veno, 1973).

Individual characteristics are immensely important in eliciting or inhibiting aggression. In animal societies composed of individuals which recognise one another, a stranger elicits aggression more readily than a familiar individual (Marler and Hamilton, 1966). Consequently it can be argued that, as for social fighting, individuals must be able to recognise each other as individuals if habituation of one individual to another is to take place.

Several recent papers have clearly demonstrated that responses of aggressive territorial fish habituate on repeated exposure to conspecifics, whether these conspecifics are confined to glass tubes (Peeke, 1969; Peeke and Peeke, 1970), free-swimming, adjacently territorial neighbours (van den Assem and van der Molen, 1969; Peeke, Herz and Gallagher, 1971; Gallagher, Herz and Peeke, 1972), or conspecifics represented by crude models (Peeke, 1969; Peeke, Wyers and Herz, 1969). Other papers demonstrating habituation to live conspecifics and to mirror images are the ones by Baenninger (1966, 1968, 1970), Brown and Noakes (1974), Clayton and Hinde (1968), Figler (1972), Simpson (1968) and Thompson (1963, 1969). On the other hand, Heiligenberg has shown that the cichlid fish Haplochromis burtoni becomes more and more aggressive on repeated presentation of a life-like dummy (Heiligenberg and Kramer, 1972).

Peeke and Veno (1973) have shown that territorial fish (Gasterosteus aculeatus) can discriminate individual morphological as well as positional cues. Although individual recognition of territorial neighbours, resulting in an increase in the response thresholds to the neighbour's song, has been clearly shown in birds (for example, see Falls, 1969), there have been no studies reported, as yet, on the modulation of agonistic behaviour and the maintenance of lowered levels of aggression between neighbouring, conspecific birds.

The present experiment is a preliminary investigation into whether or not male pigeons are capable of maintaining lowered levels of aggression between territorial neighbours. Secondly, to look at the possible causal and functional relationships between the agonistic behaviours; and thirdly, to investigate whether or not male pigeons show diurnal rhythmicity in agonistic behaviour.

Hinde (1970, pp. 333-336) has discussed the difficulties involved in defining and classifying aggressive behaviour. In the following chapters, fighting behaviour, during which actual bodily contact between individuals takes place, will be referred to as aggressive behaviour; whereas agonistic behaviour includes aggressive behaviour, avoidance behaviour such as escape and fleeing, as well as non-contact stereotyped displays.

3.2 Materials and Methods

The pigeons used in this experiment were individuals ranging from 350 grams to 580 grams body weight which were obtained from a dealer, and were housed in the animal wing for four months before they were used for experimentation.

The experiments were conducted in two adjoining, galvanised metal cages, each measuring 40 x 40 x 45 cm., which were separated from each other by a wire mesh partition. The room temperature was kept at +21°C, and the illuminatior was by fluorescent lighting set on a daily light schedule from 08.00 hours to 20.00 hours. Food and water were given ad libitum. The experimental set-up is shown in Fig. 3.1. Each encounter was monitored with an EMI T.V. camera in an adjoining room, to avoid disturbing the subjects.

Only the behaviour of the dominant bird was recorded, for the following reasons: In a small pilot study, prior to this experiment, an attempt was made to record the behaviour of both birds, using video recording equipment. However, it was found that the equipment was liable to technical failure during the experiment. So this method proved unreliable. Secondly, by using just the T.V. monitor, it was impossible to record the behaviour of both birds simultaneously.

Ten male pigeons were used for the experiment. The pigeons were paired on a random basis and each pigeon was, initially, a complete stranger to the

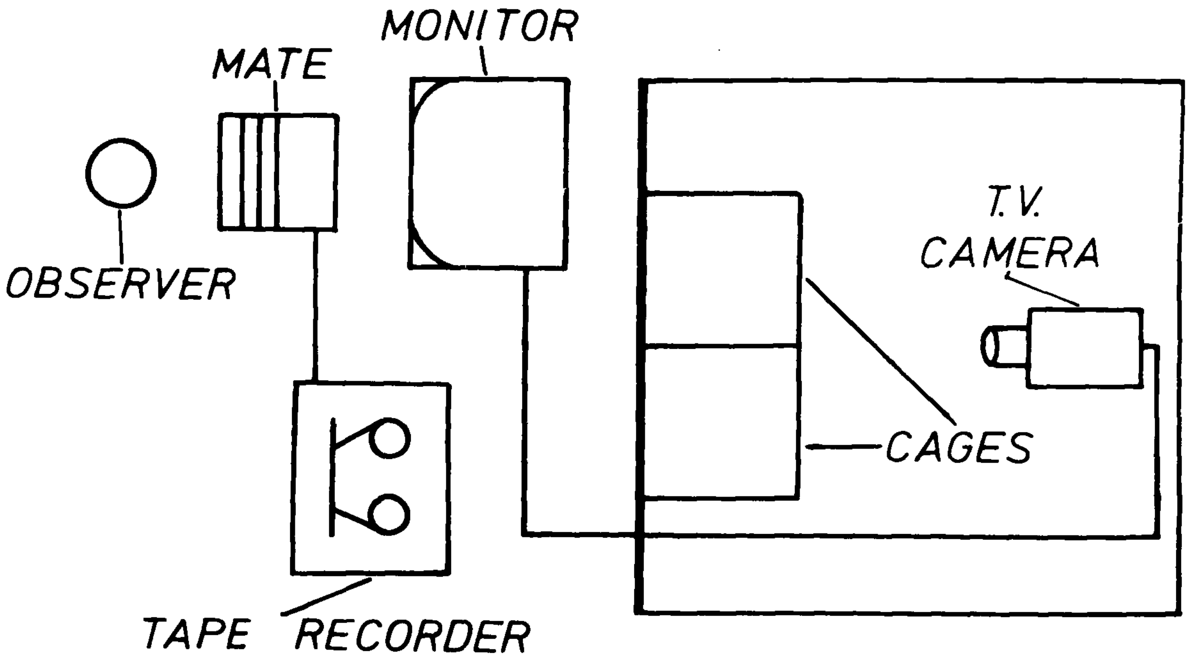

Fig. 3.1 Diagram of the experimental set-up. The cages and T.V. camera were placed in a separate room.

other. At the beginning of the first encounter, the pigeons were allowed to interact for two minutes before any recording of the behaviours was made. This allowed for behaviours such as fleeing and escape to appear in one of the birds, so that only the behaviour of the eventual dominant bird was observed and recorded. In the event were no such behaviours appeared after two minutes, no recordings were made until the observer could clearly identify one of the pigeons as the dominant bird.

Each recording session lasted for 32 minutes, beginning when the partition between the adjoining cages was removed thereby allowing the pigeons free access to each other. There were three recording sessions per day, at 10.00 hours, 14.00 hours and 18.00 hours over a period of ten days. These times were selected in order to investigate the possible effects of diurnal rhythmicity on agonistic behaviour. The first day of the experiment was designated as day 1, and each ten day experiment between two pigeons will be referred to as a 'Series'.

Recordings of the observed behaviours were made with the MATE (see Appendix B), using a Marconiphone tape recorder at a tape speed of 18 cm. per second. The duration of each behaviour pattern was recorded automatically onto the tape recorder and data decoding was processed with the use of a WDV interface and an IBM 1130 computer. The program for data decoding was written by J. D. Delius.

3.3 Statistical Analysis

The following non-parametric tests have been employed: (1) Spearman rank correlation coefficient; (2) Friedman two way analysis of variance. These tests were applied and computed as described in Siegel (1956). The chosen level of significance was $\alpha = 0.01$. Most of the data analyses and statistical tests were made using an IBM 1130 computer.

3.4 Description of behaviour observed and recorded during encounters

The behaviour patterns described in the following section are all performed by a dominant male pigeon in the experimental situation, and recorded.

In the recognition and recording of behaviour patterns, the observer must make certain subjective decisions; and in behaviour analysis this is an issue one cannot afford to neglect. Furthermore, if certain behaviours are not qualitatively discrete, the observer may fail to record these events due to inattention. The behaviour patterns observed and recorded in the following experiment were considered to be qualitiatively discrete, clearly differentiable and which were obvious enough as not to pass easily unnoticed by the observer.

Although some of the behaviour patterns to be described are not usually associated with agonistic behaviour under normal field conditions, their frequent occurrence in the experiment, which may be considered abnormal relative to field conditions, warranted their recording. A short description of the behaviour patterns on which subjective decisions were made, now follows. For a more complete description of the movements involved in their performance, one is referred to Chapter 2.

Aggressive Pecking This behaviour was recorded when one pigeon pecked at and made contact with the antagonist's head, neck or any other part of its body. Only the dominant pigeons showed aggressive pecking, and this behaviour was used as a criterion in beginning to record the behaviour of one or the other pigeon.

In Aggressive Billing, the pigeon pecks the opponent's bill, sometimes grasping it in its own bill. This behaviour usually occurred during body pushing.

Body Pushing This behaviour was easily recognisable, and consisted of one pigeon pushing against another with its upper thorax. The pigeons may or may not have their wings raised.

Bowing This behaviour is explained extensively in Chapter 2. Frontal and side, or lateral, bowing were also recorded as 'Bowing', since transitions from frontal to lateral bowing were very frequent and fast. The observer could not clearly differentiate the point at which body-orientation frontal bowing became lateral bowing and vice-versa.

Nodding was recorded every time the pigeon lowered and raised its head, as described in Chapter 2.

Wing Vibration This behaviour was observed when the pigeon was in either an erect or in a sitting position. No differentiation was made between the two postures, wing vibration being recorded in either case.

Aggressive Intention peck The head is brought sharply forward and downward, and contact is never made with the opponent.

3.5 Experimental results

The results obtained for all the experimental series are presented diagrammatically in Figs. 3.2 to 3.6. Because of the nature of the data obtained, reflecting the individual variability between the interactions, each series will be considered separately.

By analysing each interaction individually, one obtains a better picture concerning the relationships between these behaviours, and between the pigeons themselves. The grouping of highly variable data can lead to a significant loss of 'information'; and in ethological studies of this nature, such a loss could lead to erroneous interpretation of the data.

The session totals (total number of seconds spent performing a particular behaviour per session) and the daily means (mean performance of a particular behaviour in seconds per 32 minutes per day) for each series, as well as for the series overall (daily means only), are presented in Appendix D. Both the session totals and the daily means for each behaviour were intercorrelated using Spearman's correlation coefficient, and the correlation matrices for each individual series and the series overall are presented in Appendix E.

Experimental series 1

Interaction between P13 (dominant) and P35: The results for the interaction are presented in Fig. 3.2. Aggressive behaviour (Aggressive pecking, Aggressive billing, Body pushing and Wing flicking) and Bowing were predominant on Day 1. Aggressive behaviour declined thereafter remaining low through to Day 10.

Significant intercorrelations over sessions were found between Aggressive pecking, Aggressive billing and Body pushing ($p < 0.001$), between Bowing and these aggressive behaviours ($p < 0.01$) and between Wing flicking and these aggressive behaviours ($p < 0.001$). Wing flicking and Bowing were unrelated. The general picture presented by these data is that the measured aggressive behaviours were related. However, a further interesting finding was that Nodding (generally considered a courtship behaviour, Fabricius and Jansson, 1963), was correlated with Aggressive intention pecking ($p < 0.001$).

Experimental Series 2

Interaction between P30 (dominant) and P3: the results of this interaction are presented in Fig. 3.3. As in the previous interaction, all the aggressive behaviours and bowing were predominant on Day 1. This was followed by a subsequent decrement in the performance of the aggressive behaviours. After

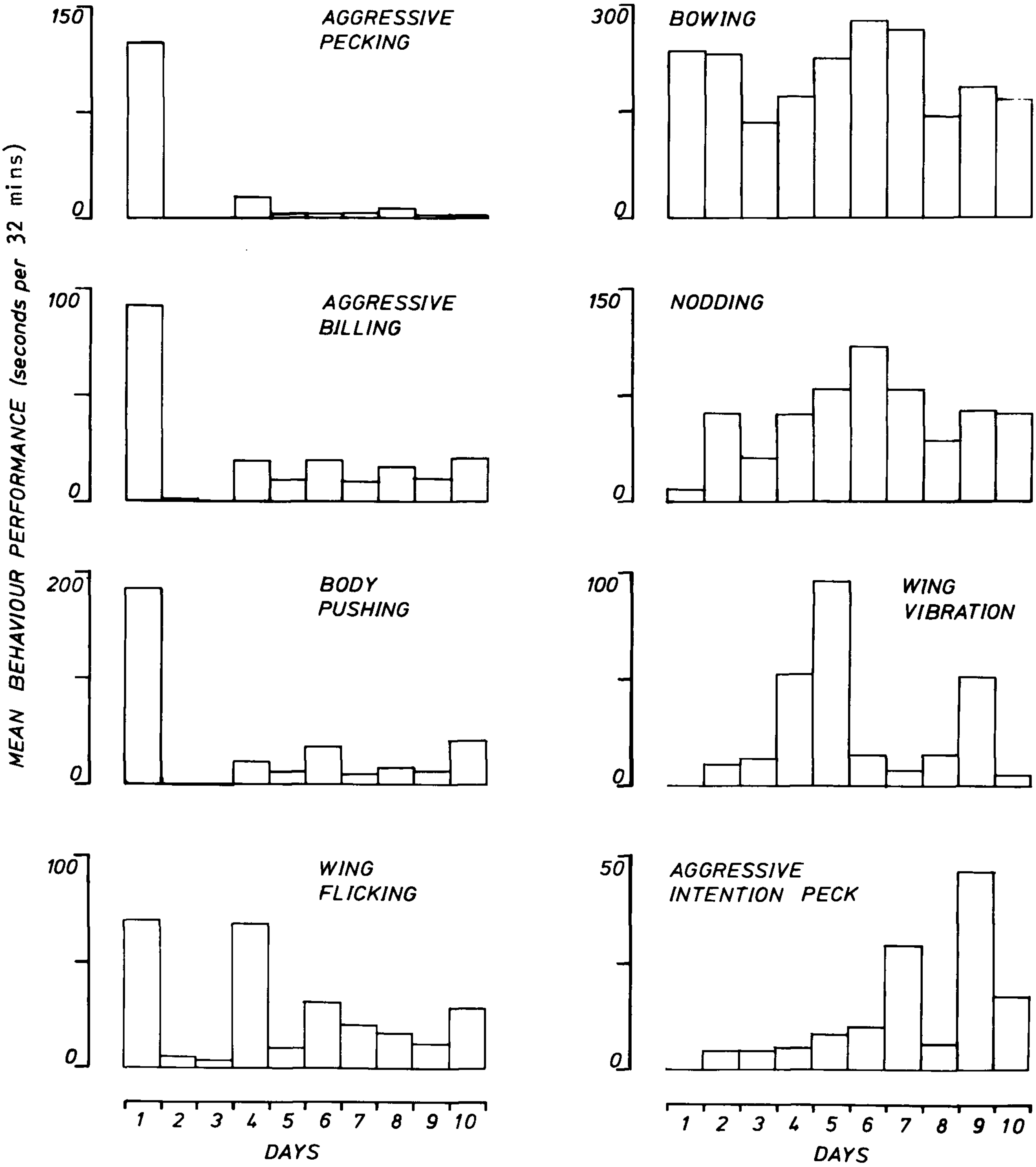

Fig. 3.2 Experimental series 1. Histograms for the behaviours recorded during the experiment, with the ordinate showing the mean duration of each behaviour per 32 minutes for each day; and the abscissa, the number of days in the experiment. All of the aggressive behaviours showed a decrement over the first three days, whereas aggressive intention peck showed an increment thereafter.

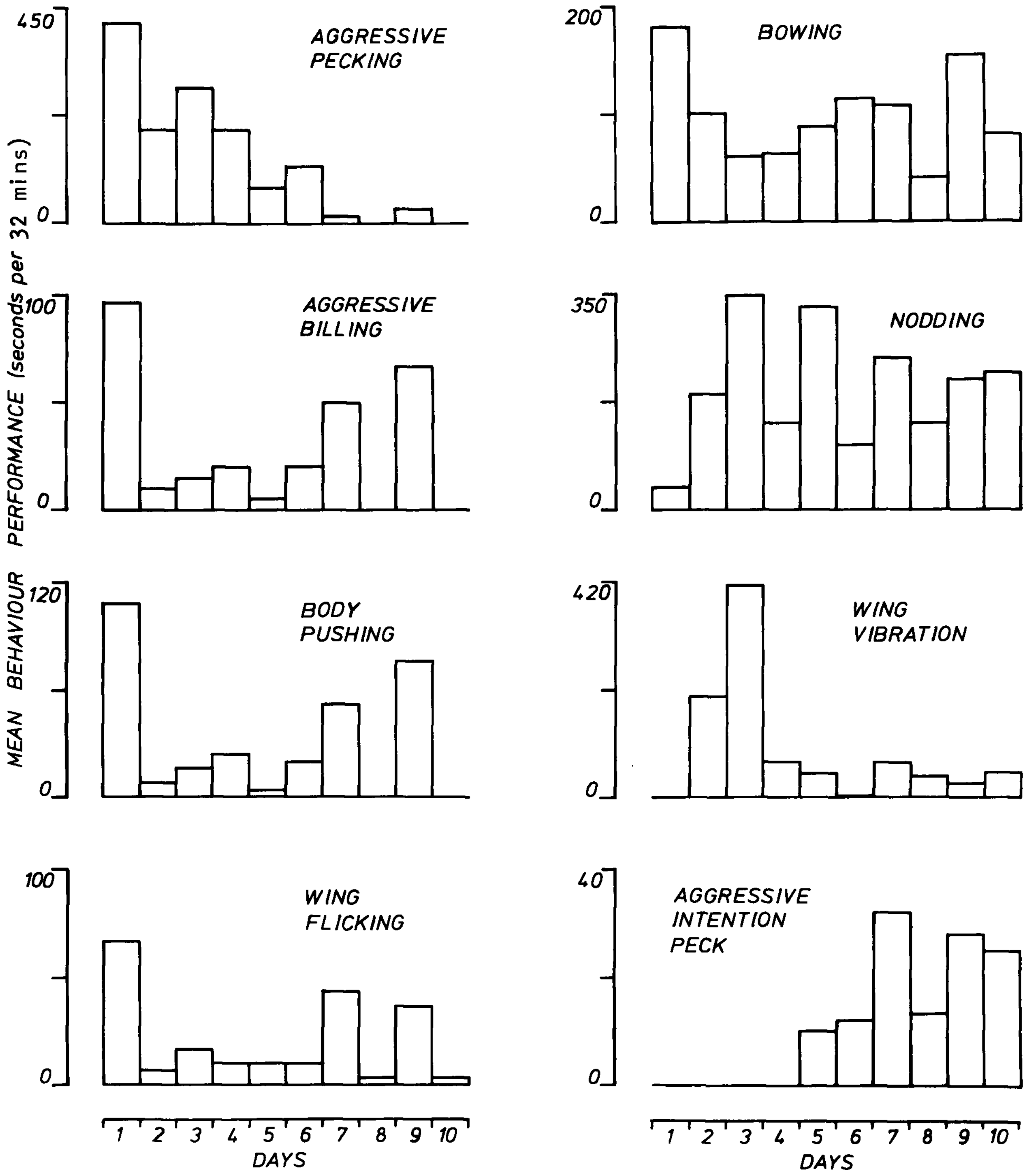

Fig. 3.3 Experimental series 2. Histograms for the behaviours recorded during the experiment, with the ordinate showing the mean duration of each behaviour per 32 minutes for each day; and the abscissa, the number of days in the experiment. Again a decrement in aggressive behaviour is noticeable over the first two days, aggressive intention peck showing an increase after day 4.

Day 5 there is some recovery of these behaviours, excluding aggressive pecking, but this fluctuates over the remaining days. Aggressive intention peck showed an increment in the level of performance after Day 4.

A significant negative correlation over sessions as well as over days was found between aggressive intention peck and aggressive pecking ($p < 0.01$), but not with the other aggressive behaviours. Significant intercorrelations were found between bowing and the aggressive behaviours (excluding aggressive pecking; $p < 0.01$), between the aggressive behaviours themselves ($p < 0.001$) and between Nodding and Wing vibration ($p < 0.001$).

Experimental series 3

Interaction between P28 (dominant) and P36: The results for the interaction are presented in Fig. 3.4. It is immediately evident that although the aggressive behaviours decline over the first two days, their performance becomes rather irregular, or so it seems, subsequently. Bowing shows a steady decline in performance after Day 1. The significance of these results will be discussed at a later stage.

Significant positive intercorrelations were found between the aggressive behaviours over sessions and days ($p < 0.005$), between bowing and aggressive pecking ($p < 0.01$) and between nodding and wing vibration ($p < 0.001$) over sessions. Bowing and the other aggressive behaviours were not related. As in the previous two experimental series, it is interesting to note that the measured aggressive behaviours are related, although in this case bowing is only related to aggressive pecking.

Experimental series 4

Interaction between P10 (dominant) and P26: The results for this experimental series are given in Fig. 3.5. A decline in aggressive behaviour is evident, again taking place over the first two days. Bowing also declined during these days. On the other hand, nodding, wing vibration and aggressive intention peck showed an increment in performance over the same time.

Significant intercorrelations over sessions and days were found between

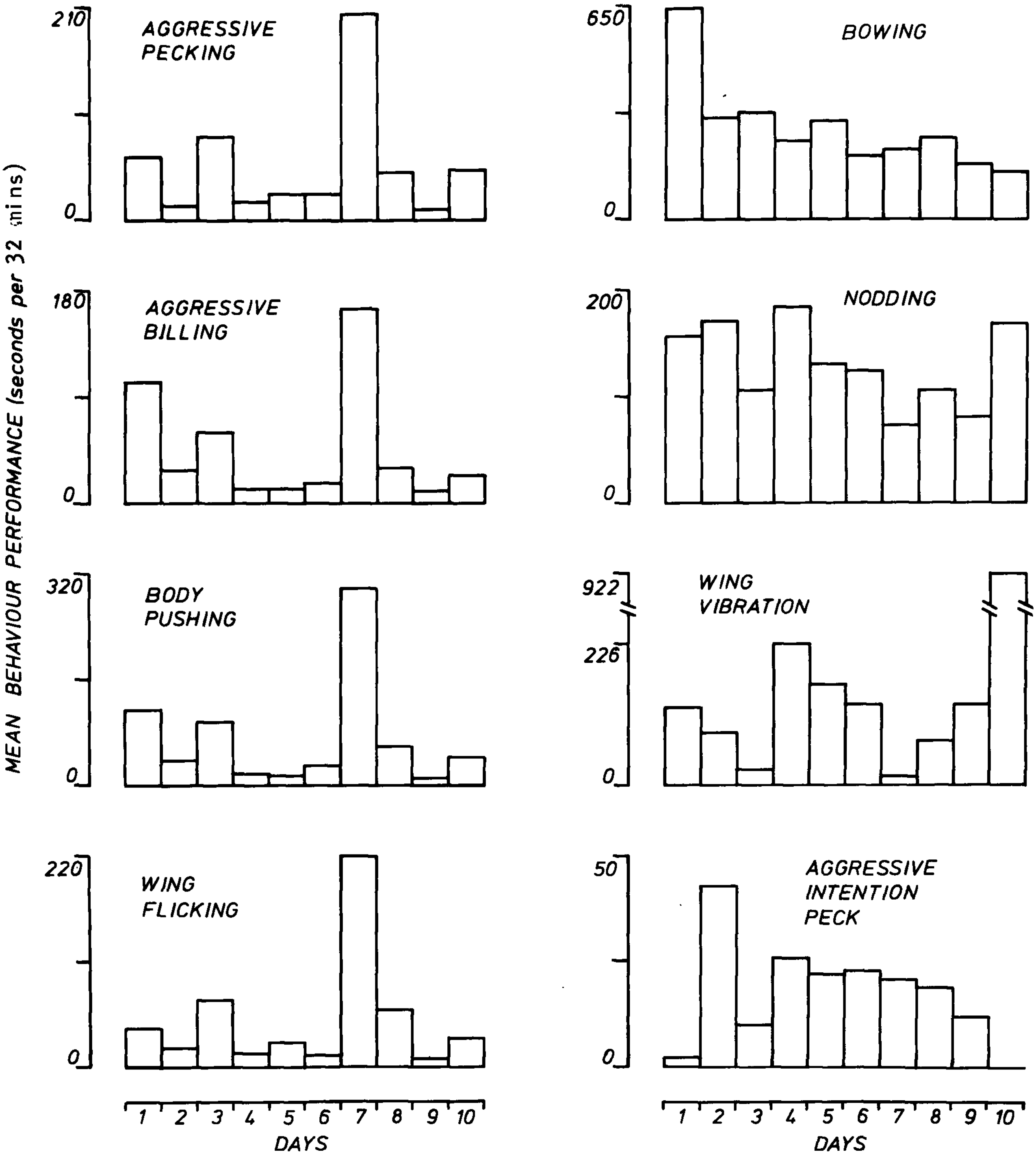

Fig. 3.4 Experimental series 3. Histograms for the behaviours recorded during the experiment, with the ordinate showing the mean duration of each behaviour per 32 minutes for each day; and the abscissa, the number of days in the experiment. A similar decrease in aggressive behaviour to the one in experimental series 1 and 2 can be seen. A possible explanation for the "spontaneous" surge in aggressive behaviour on day 7 and wing vibration on day 10 is given in the text.

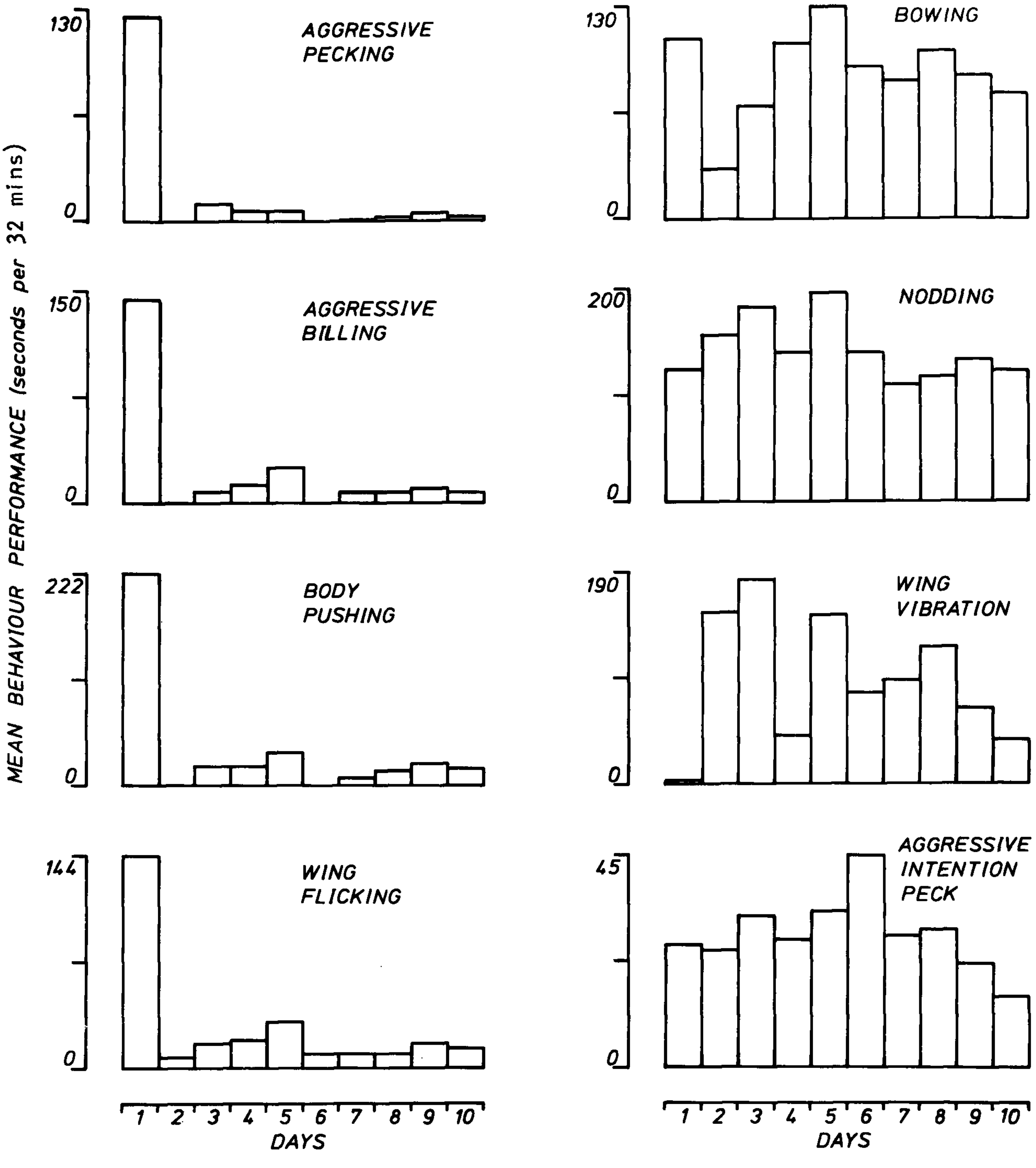

Fig. 3.5 Experimental series 4. Histograms for the behaviours recorded during the experiment, with the ordinate showing the mean duration of each behaviour per 32 minutes for each day; and the abscissa the number of days in the experiment. A decrease in the aggressive behaviours from day 1 to day 2 is again noticeable.

the aggressive behaviours ($p < 0.005$), between bowing and wing flicking over the 32 minute sessions ($p < 0.001$), and between bowing and aggressive billing ($p < 0.01$) over days. Bowing, wing flicking and the other aggressive behaviours were unrelated over days.

An interesting and significant relationship was found between the aggressive behaviours and nodding ($p < 0.001$), between bowing and this behaviour ($p < 0.001$), and between wing vibration and this behaviour ($p < 0.001$) over the sessions, but no relationship was found between these behaviours over days.

Experimental series 5

Interaction between P77 (dominant) and P15: The results for this series are presented in Fig. 3.6. As in all the previous experimental series, aggressive behaviour was predominant on day 1. Thereafter aggressive behaviour showed a decrement through to day 3, which was followed by a fluctuation in the performance of this behaviour through to day 10, although the overall level remained low.

A recurrence of the significant intercorrelations between the aggressive behaviours, and between bowing and these behaviours ($p < 0.01$) is evident in this experimental series. Other correlations between bowing and nodding, and between wing vibration and this behaviour were significant over sessions ($p < 0.01$).

The trend which was established in the previous series between Bowing and the aggressive behaviours recurs in this series, as well as the relationship between Nodding and Bowing.

Fig. 3.7 shows the mean duration per 32 minutes, per day, of all the behaviours over 10 days, for the series overall. One can immediately see that by grouping all the series together, there is a considerable loss of information on the individual interactions.

During a decrement in the performance of Aggressive pecking, Aggressive

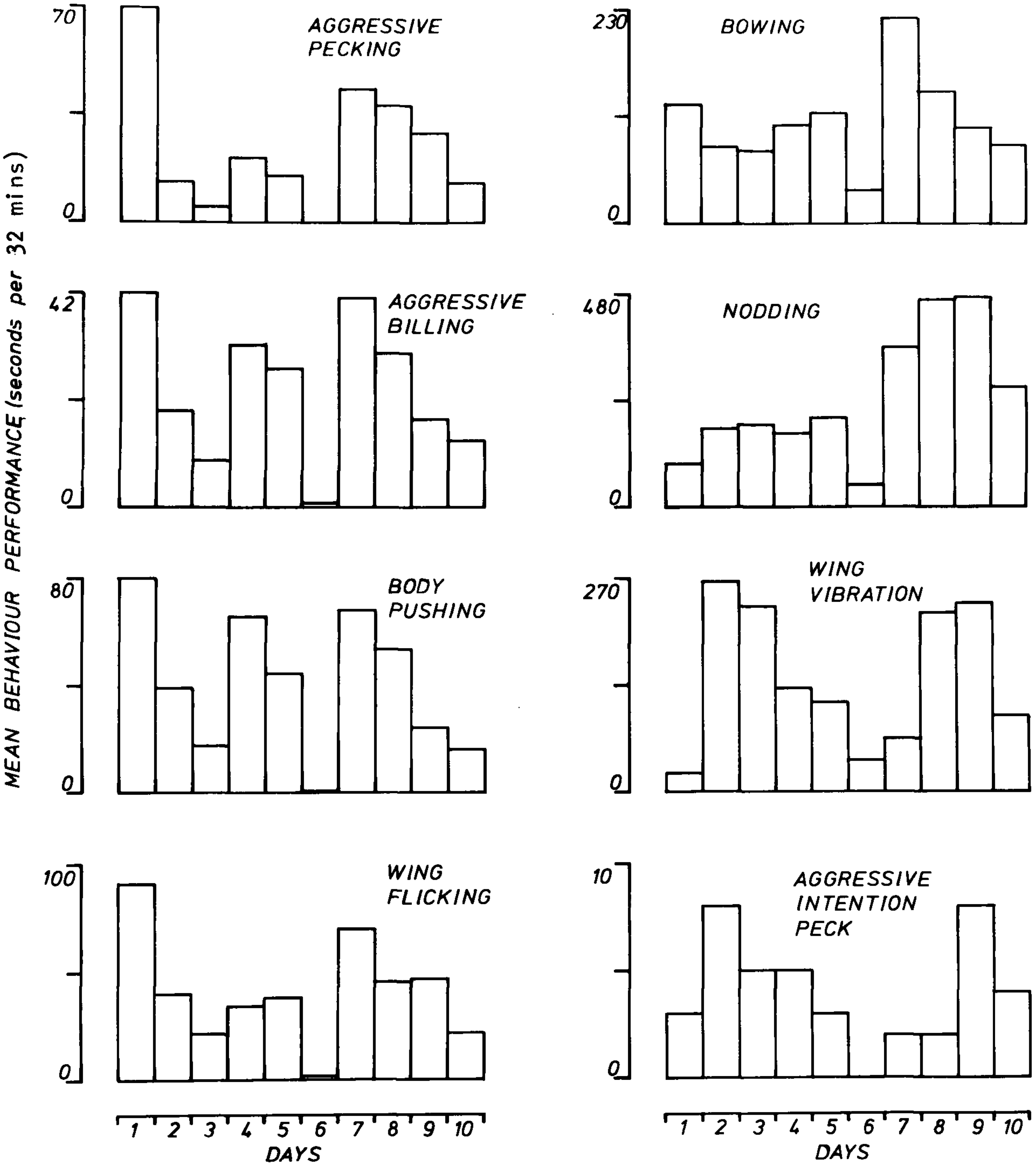

Fig. 3.6 Experimental series 5. Histograms for the behaviours recorded during the experiment, with the ordinate showing the mean duration of each behaviour per 32 minutes for each day; and the abscissa, the number of days in the experiment. Aggressive behaviour shows a decrease from day 1 to day 2, but overall there is a low mean level of aggression relative to the previous series, over days. No explanation is immediately evident for the low level of behaviour on day 6.

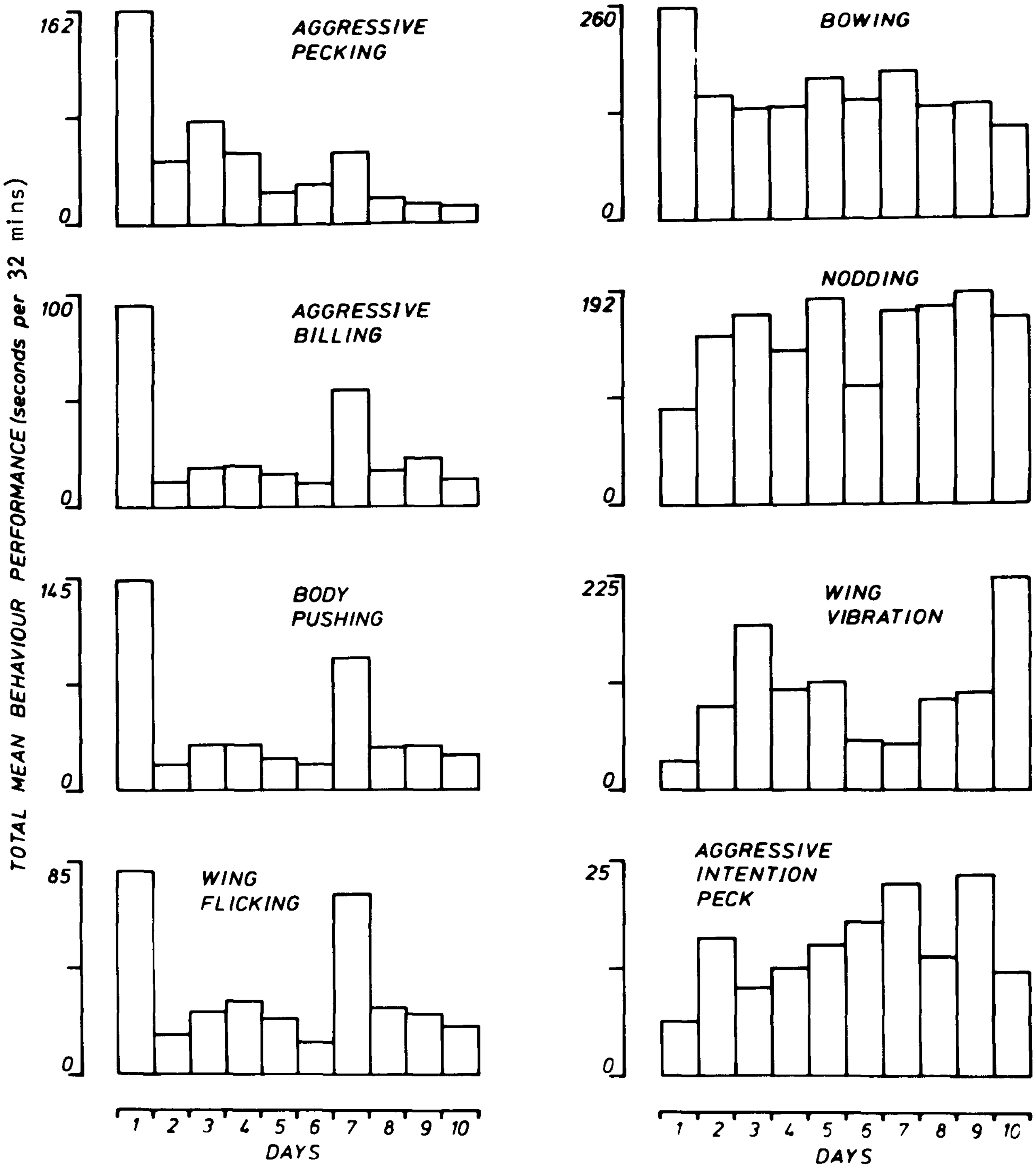

Fig. 3.7 Histograms showing the mean duration of the behaviours (seconds per 32 mins, for each day) for all the experimental series (ordinate), during days (abscissa). The aggressive behaviours all show a decline after day 1, while aggressive intention peck shows an increase. The surge on day 7 is probably caused by the relatively high level of aggression on that day, in experimental series 3.

intention peck showed an increment over days. This is a situation where an aggressive behaviour is being "displaced" by a threatening or possibly a conflict behaviour. Overall, the other aggressive behaviours, namely Aggressive billing, Body pushing and Wing flicking, all showed a decrement after day 1. The sudden and unexpected increase in the performance of aggressive behaviour on Day 7 is probably due to one of the pigeons (P28, Experimental series 3) showing a high level of performance of these behaviours, relative to the other pigeons.

Looking now at the correlation coefficients, one might obtain an indication of the relationships or causal systems operating between these agonistic behaviours.

The correlation measures for the overall number of sessions ($n = 150$) show that bowing is significantly correlated to the aggressive behaviours ($p < 0.001$). These correlations, excepting the one with aggressive pecking which is not significant, are maintained over days during the experiment. Aggressive intention peck shows a significant negative correlation with aggressive pecking ($p < 0.001$), aggressive billing ($p < 0.01$) and body pushing ($p < 0.02$) over 30 sessions, but with only aggressive pecking over days ($p < 0.005$). Nodding and wing vibration are significantly correlated both over sessions and days ($p < 0.001$). Moreover, nodding is also correlated with aggressive pecking and wing flicking ($p < 0.001$) and with body pushing ($p < 0.01$) over sessions.

3.6 Diurnal rhythm effects on agonistic behaviour

3.6.1 Experimental Results

From a preliminary statistical analysis on all the behaviours for each experimental series using Friedman's two way analysis of variance (sessions x days), it was concluded that diurnal rhythm effects did not affect agonistic behaviour performance in any way throughout the series.

BEHAVIOUR	1	2	3	4	5	6	7	8
EXPERIMENTAL SERIES 1	1.399	2.599	0.649	2.399	3.949	3.149	0.649	2.449
2	0.349	0.349	0.599	2.399	7.199^{*}	7.799^{*}	2.599	0.349
3	2.449	5.549	6.049^{*}	3.199	1.399	0.199	7.849^{+}	2.599
4	2.149	1.549	0.649	5.399	3.799	4.999	5.599	2.449
5	6.349^{*}	3.049	0.949	3.799	5.599	1.799	1.399	0.599

$^{*}p < 0.05$

$^{+}p < 0.02$

Table 3.a Table giving Friedman's statistic for the test on the three session times (10.00, 14.00 and 18.00 hrs.), for each behaviour in the experimental series. (Computed from the data presented in Appendix D). The behaviours are coded as follows: Behaviour 1 = Aggressive pecking; Behaviour 2 = Aggressive billing; Behaviour 3 = Body pushing; Behaviour 4 = Bowing; Behaviour 5 = Nodding; Behaviour 6 = Wing vibration; Behaviour 7 = Wing flicking; Behaviour 8 = Aggressive intention peck.

This quantitative evidence is presented in Table 3.a.

3.7 Discussion

The overall picture the experimental series present is that aggressive behaviour shows a decrement mainly over the first two days of the experiment. Bowing also shows this decrement in the series, but its mean level of performance fluctuates considerably after the second day. High performance levels of nodding and wing vibration were recorded on days which were preceded by relatively high levels of aggressive behaviour. Aggressive intention peck showed an increment in performance during a decline in aggressive pecking (see Figs. 3.3, 3.4 and 3.7). These impressions are supported by the significant negative correlations between aggressive pecking and aggressive intention peck.

Two interactions need mentioning in particular.

On day 7 of experimental series 3, a very high level of aggression was recorded. This was followed by a very high increase in wing vibration. Furthermore, P28 attempted copulation seven times with P36, on day 10. Nodding also showed an increment over these days. In behavioural terms, an analogous situation occurs between a male and female pigeon during the pre-laying phase of the breeding cycle: the male is very aggressive towards the female at first, but gradually shows more and more wing vibration and eventually the first copulations (Fabricius and Jansson, 1963). Of course, this takes place over a longer length of time. This analogy is suggestive, nevertheless, and may indicate that P28 was both aggressively and sexually motivated.

On day 6 of experimental series 5, there was a very low mean level of behaviour overall. This was followed by increments during the following days in most of the behaviours recorded, although some occurred much quicker than others. There seems to be no explanation available for this change in activity.

The behaviours observed during this experiment may have the following functional significance: (a) the maintenance of an established territory and (b) the maintenance of lowered levels of aggression between two neighbours. In pigeons, where competition for food does not occur within territories, aggression directed towards neighbours need not be maintained at a constantly high level; nor is it necessary for a bird to be overtly aggressive towards its neighbours for more territorial gain, once it has established a nest site.

Consequently, for the maintenance of lowered levels of aggression between territorially adjacent pigeons, some mechanism by which neighbouring birds might be recognised, and the territorial boundary maintained, would be required. Birds often use vocal displays to delineate territorial boundaries, and in pigeons, bowing could have such a function.

The results obtained here indicate that bowing behaviour is a conflict behaviour by which, possibly, the territorial boundary is maintained, as well as being a threat display, since the pigeon shows itself, feathers erect, from all sides to its antagonist. The bowing call, which is given in conjunction with bowing, has been observed during the pre-incubatory phase of the breeding cycle, as well as during territorial defence (Fabricius and Jansson, 1963).

Rashotte et al. (1975) have shown that pigeons show bowing during experiments on schedule-induced aggression. The behaviour (including the call) was performed during the first few minutes when a pigeon image was projected onto a screen and before treadle pressing began. In the present experiment, bowing was always the first behaviour to be performed by both birds as soon as the partition between the two cages was removed. It may be that the lack of a physical barrier caused each bird to assert its territorial area through this behaviour. It appears that this visual as well as vocal display must be reciprocated by the neighbouring pigeon, otherwise the dominant bird encroaches on the other pigeon and usually attacks it. Simpson (1973) suggests that "a situation where individuals frequently display ... is a situation where the prevailing social relations in the group are continuallybeing 'tested'." In this experiment, the high performance of bowing behaviour, suggests that this may be the case between the two pigeons.

The behaviour patterns nodding and wing vibration could be classed as displacement activities, because of the situations in which they were seen. Generally, however, the criteria for behaviours being relevant in a particular situation are introduced by the observer and could be erroneous. Displacement activities usually occur as a result of thwarting of a drive, and their manner of performance is typically nervous, often vigorous and incomplete. Nodding and wing vibration are not normally considered as agonistic behaviours (e.g. see Fabricius and Jansson, 1963; Goodwin, 1955, 1956), but the fact that these behaviour patterns were performed with such frequency and vigour in an agonistic situation, argues against their "irrelevance".

It is probable that these behaviours have a similar function in this context to when they are performed by the male during the pre-incubatory phase of the breeding cycle, i.e. one of appeasement. As well as functioning as appeasement behaviours, these two seemingly "irrelevant" behaviours are necessary in the maintenance of lowered levels of aggression between two male pigeons, as they are in the maintenance of a pair-bond between a male and female pigeon. Simpson (1968) found that most of the display actions performed by male siamese fighting fish when with a female, are also performed when he is with a strange male. A similar situation is found in pigeons and it is possible, therefore, that the behaviours mentioned have been merely overlooked, by observers studying them in only one situation.

Aggressive pecking, which is an aggressive behaviour performed only by dominant pigeons, always showed a decrement from day 1 to day 2. This suggests that once dominance has been established, there is no necessity for further aggression to maintain dominance. However, in a situation where dominance is being "tested", aggressive billing, body pushing and wing flicking are performed by both birds, probably "as a measure of strength in bodily contact" (Eibl-Eibesfeldt, 1961).

The relationships formed between these behaviours when using intercorrelations only give us a very partial picture. Meehl (1967) warns of the problems which arise from obtaining statistically significant results from biological data. Statistically significant correlations can be obtained between many measures of an animal's behaviour and any other measure one chooses, if the sample is large enough, because organisms are integrated systems. However, because the level of significance chosen is high and because significant correlations between the behavioural measures appear consistently throughout all the interactions (ref. to Appendix E), significant results probably should not be attributed to chance alone. Nevertheless, one must not forget that for a full understanding of these behavioural correlations, one _must_ understand the mechanisms that produce them.

An important difference between this experiment and conditions in the field is that in the experiment only one neighbouring pigeon was available. Hence habituation between the two birds may have occurred more quickly than when many pigeons are present. Furthermore, a pigeon in the field is likely to have a mate, and certain behaviours are undoubtedly directed towards her as well. These behaviours (such as nodding and wing vibration) were noticeable in the experiment, and it is possible that pigeons performed these towards other males in the absence of a mate.

In the field, therefore, each of the adjoining territorial boundaries would have to be maintained, and consequently the time spent displaying or showing aggression towards neighbouring pigeons would have to be divided between them, rather than being directed towards one pigeon in particular.

One factor that could affect the results is that the opportunity to behave aggressively can act as a reinforcer (Thompson, 1963, 1969). In this experiment, I had no way of assessing how much negative or positive reinforcement a pigeon normally receives when engaging in aggressive behaviour. Moreover, I had no measure of the usual daily amount of aggression in the pigeon.

More specifically, one must bear in mind that the analysis in this study had to be confined to only the behaviour-output of dominant pigeons, whilst keeping several of the input variables constant. The results indicate that while the agonistic behaviours showed strong causal connections between themselves and in certain instances, with other "irrelevant" behaviours, the relationships between these behaviour patterns is one of considerable complexity. The situation is, therefore, more than one of a "unitary causal entity" or unitary motivation of aggressive behaviour. Rather it is likely that these relationships are the outcome of multiple and complex interactions within the nervous system, which are subjected to varying stimuli or inputs and which involve the causal systems of other functional mechanisms than, but in conjunction with, those of agonistic behaviour.

Hinde (1970) presents the argument succinctly when he states: "... in any particular case, our initial assumption should not be that there is a single process underlying the change in responsiveness: rather we must expect processes with varied characteristics, presumably occurring at different points in the underlying nervous mechanisms... it would be safe to assume that exposure to a stimulus will be accompanied by processes (with varied, time characteristics) leading to an increase in subsequent responsiveness, and also to processes leading to a decrease". Similar points are made by Clayton and Hinde (1968) and Groves and Thompson (1970).

This experiment has been concerned with agonistic behaviour between pairs of male pigeons, whose members were initially strange to each other, in which the outcomes are relationships involving lowered levels of aggression between individuals. It is suggested that habituation may be taking place over a short period of time, and that this is one of the mechanisms involved in the regulation of aggression between territorial neighbours. Similar mechanisms are already known to operate in fish.

CHAPTER 4

EXPERIMENT 2: SOME EFFECTS OF SOCIAL ISOLATION ON AGONISTIC BEHAVIOUR

4.1 Introduction

In recent years there has been conflicting evidence as to the effect of isolation and various forms of deprivation on the readiness of animals to respond in the relevant context, and little agreement on the possible mechanisms involved.

Heiligenberg (1963) and more recently Heiligenberg and Kramer (1972) and Gallagher, Herz and Peeke (1972) found a waning of aggressivity with time, after periods of isolation in three species of cichlid fish. Moreover, there was a time-lag before the level of aggression reverted to normal again. This time-lag of several days before the readiness to attack builds up again suggests that the causal factors involved may be hormonally dependent.

On the other hand, Xiphophorus helleri males kept in social isolation for 14 to 56 days showed fights of increasing duration and intensity, with increasing isolation (Franck and Wilhelmi, 1973). Van den Assem and van der Molen (1969) and Jenni, van Iersel and Van den Assem (1969) demonstrated that male sticklebacks previously placed in isolation tended to be more aggressive towards conspecifics than males placed in visual contact with other males.

Experiments in dominance reversals with green sunfish (Lepomis cyanellus) have resulted in data showing a large increase in the number of attacks made by dominant fish on subordinate conspecifics, after the former had been held in isolation for several days (McDonald, Heimstra and Damkot, 1963). Rasa (1971a) has shown that in juveniles of the fish Microspathodon chrysurus, there exists an endogenous, appetitive behaviour for aggression for situations stimulating territorial borderline fights. Moreover these fish showed an increment in aggressive behaviour, when they were isolated from conspecifics for several days.

Other studies have demonstrated that mice placed in isolation for several weeks show a striking increase in their aggressive behaviour towards conspecifics (Charpentier, 1969; Banerjee, 1971; Valzelli, 1969). However, Krsiak and Janku (1969) could detect only a slight increase in the aggressive behaviour of mice isolated for similar lengths of time. Lagerspetz (1969) demonstrated that the presence or absence of this effect in mice is largely related to the genetic strain and the sex of the mice used in the experiments.

As yet, no investigations have been done on birds. The following experiment is a short study investigating the effects of social isolation on the agonistic behaviour of male pigeons.

The sample size, in this case three pigeons, is rather small. When small samples are used, the absence of statistical significance should not be interpreted as a confirmation of the null hypothesis. However, one may at least consider the results, particularly those of the individuals, as an indication of the possible effects of the experimental variable on the behaviour under test. The chosen level of significance in this experiment was $\alpha = 0.05$.

4.2 Materials and Methods

During the periods of isolation, the pigeons were kept singly in galvanised metal cages, each measuring 40 x 40 x 45 cm. The cages were housed in separate cubicles. White noise was maintained at a level of 70 ± 5 dB A, thereby minimising the possibility of auditory communication between the birds. The white noise generator switched on automatically at 08.00 hours and went off at 20.00 hours in synchrony with the photoperiod.

In a preliminary 'pilot' experiment, which was performed three months before this experiment, a pigeon which was subordinate to the three isolates was chosen as the test bird. This test bird provided a suitable test stimulus to record and measure agonistic behaviour in the isolates. Moreover, all the pigeons became accustomed to the test cage and did not show, at any time, any fright reactions when first placed in the test cage during the experiment proper.

Three individuals were placed for varying periods in isolation after which they were allowed to meet a subordinate antagonist. The encounters took place in a wooden cage measuring 120 x 60 x 60 cm., which was divided into two separate areas by an opaque partition. At the end of each isolation period, the isolate was placed in one area of the cage and its behaviour recorded (with the MATE) for eight minutes prior to the introduction of the test bird in the other area. The partition was removed, and the recording was continued for an additional 32 minutes. To compensate for possible diurnal rhythm effects, all the encounters took place at 14.00 hours.

The first encounter between experimental pigeon and test bird took place before the pigeons were placed in isolation, and this encounter will be referred to as Day 0. Subsequently, the pigeons were placed for 2, 4, 8, 16 and 32 days in isolation, allowing 15 days in a social situation (i.e. the pigeons were placed in their normal cages in the pigeon room, but did not have any visual communication with the test pigeon), between each isolation period. This may have allowed for any possible effect or change brought about by the preceding isolation period to disappear, thus minimising the cumulative effect due to several isolation periods.

Because of the small amount of aggressive behaviour shown and in order to obtain a satisfactory aggression score, the data for the aggressive behaviours, namely aggressive billing, aggressive pecking, body pushing and wing flicking, were added together.

Data are presented individually, and analysed statistically (Appendix F, tables F.4 to F.12) using non-parametric trend analysis (Still, 1967).

4.3 Experimental results

The results for the experiment are presented in Figs. 4.1 to 4.3. Owing to the variability in the behaviour of both the experimental pigeons and the test bird, results for the individuals in general and also for particular observations showed quite a large variation.

The effect of social isolation is reflected in the performance of aggressive bowing and driving behaviour. The level of performance of these behaviours may serve as an indication as to the possible changes in the internal stimulus state of the pigeons after differing periods in isolation. Statistical analysis, presented in Appendix F, supports the impressions conveyed in the figures.

Considering firstly the total results of the eight four-minute periods individually, for the three pigeons (see Appendix F, tables F.1 to F.3):

On day 0, P31 spent 334 seconds out of 32 minutes bowing and 717 secs/32 minutes driving (Fig. 4.1). After 32 days in isolation 1034 secs/32 mins were spent bowing and only 420 secs/32 mins were spent driving. Linear trend analysis on the data gave a positive linear trend for bowing ($p < 0.01$), whilst there was no significance in linear trend for driving. Aggressive behaviour performance decreased with increasing days in isolation. The data for P31 gave no significance in linear trend for aggressive behaviour.

P29 showed fluctuations in bowing behaviour performance with increasing days in isolation (Fig. 4.2). On day 0, P29 spent 385 secs/32 mins bowing and after 2 and 4 days in isolation it spent 502 secs and 129 secs out of 32 minutes bowing respectively. After 32 days in isolation, 225 secs/32 mins were spent bowing: trend analysis gave no significant results. Driving showed a definite decrement in performance over days, starting with 85 secs/32 mins on day 0 and showing no driving behaviour whatsoever after 16 and 32 days in isolation. Statistical analysis produced a significant negative linear trend with increasing days in isolation ($p < 0.05$). The increment in aggressive behaviour, particularly after 16 and 32 days in isolation, was not significant.

P34 spent 660 secs/32 mins bowing and 422 secs out of 32 mins driving (Fig. 4.3). Bowing performance showed an overall increase with increasing periods in isolation, so that after 32 days in isolation P34 spent 1115 secs/32 mins bowing. On the other hand, driving performance showed a decrease with increasing periods in isolation so that the bird spent only 189 secs/32 mins driving after 32 days in isolation. Bowing behaviour gave a significant

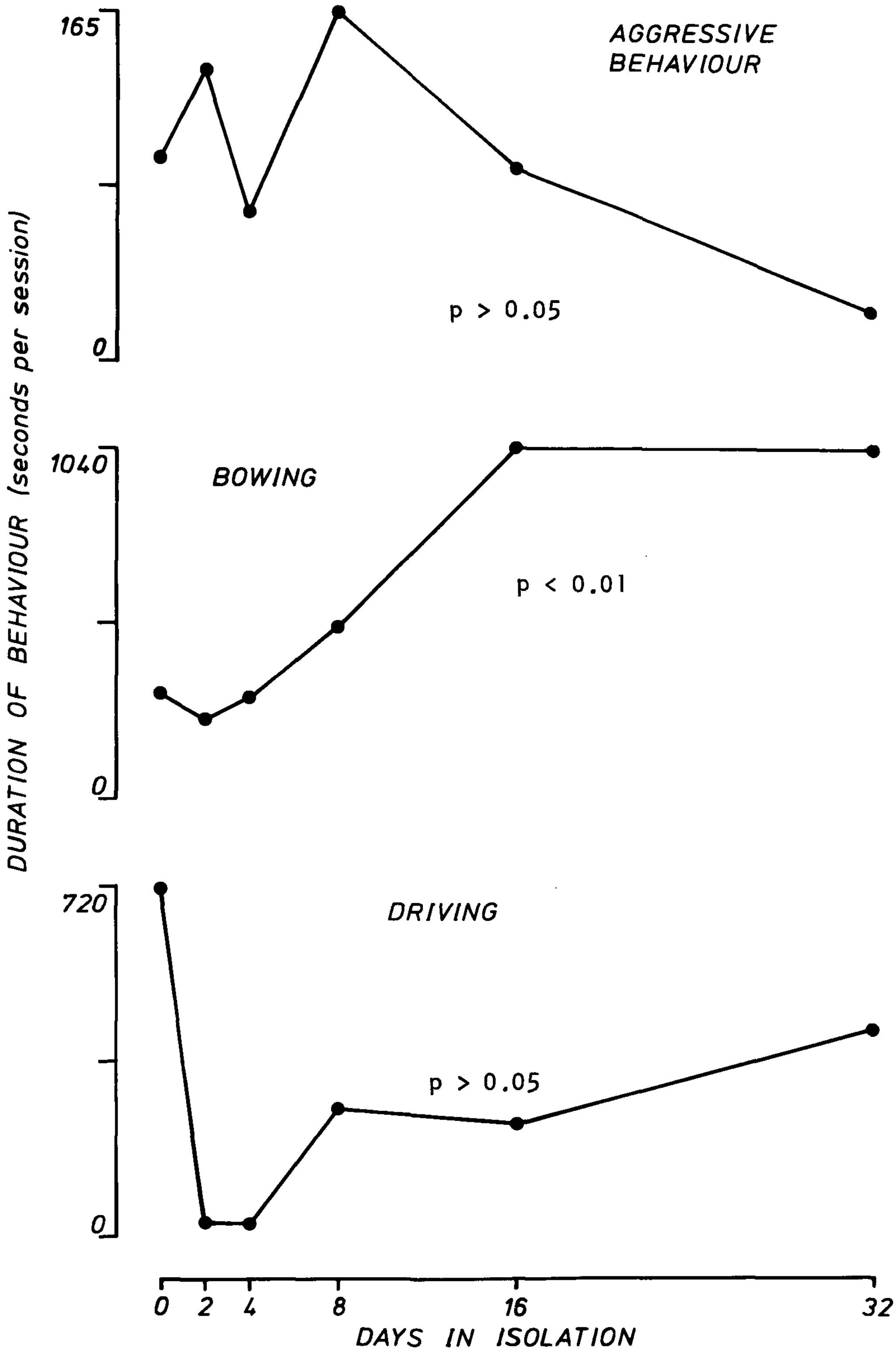

Fig. 4.1 P31. Graphs showing the duration of bowing, driving and aggressive behaviour, in seconds per session (ordinate), with increasing days in isolation. Bowing shows a significant trend with increasing days in isolation ($p < 0.01$), while driving and aggressive behaviour showed no significance.

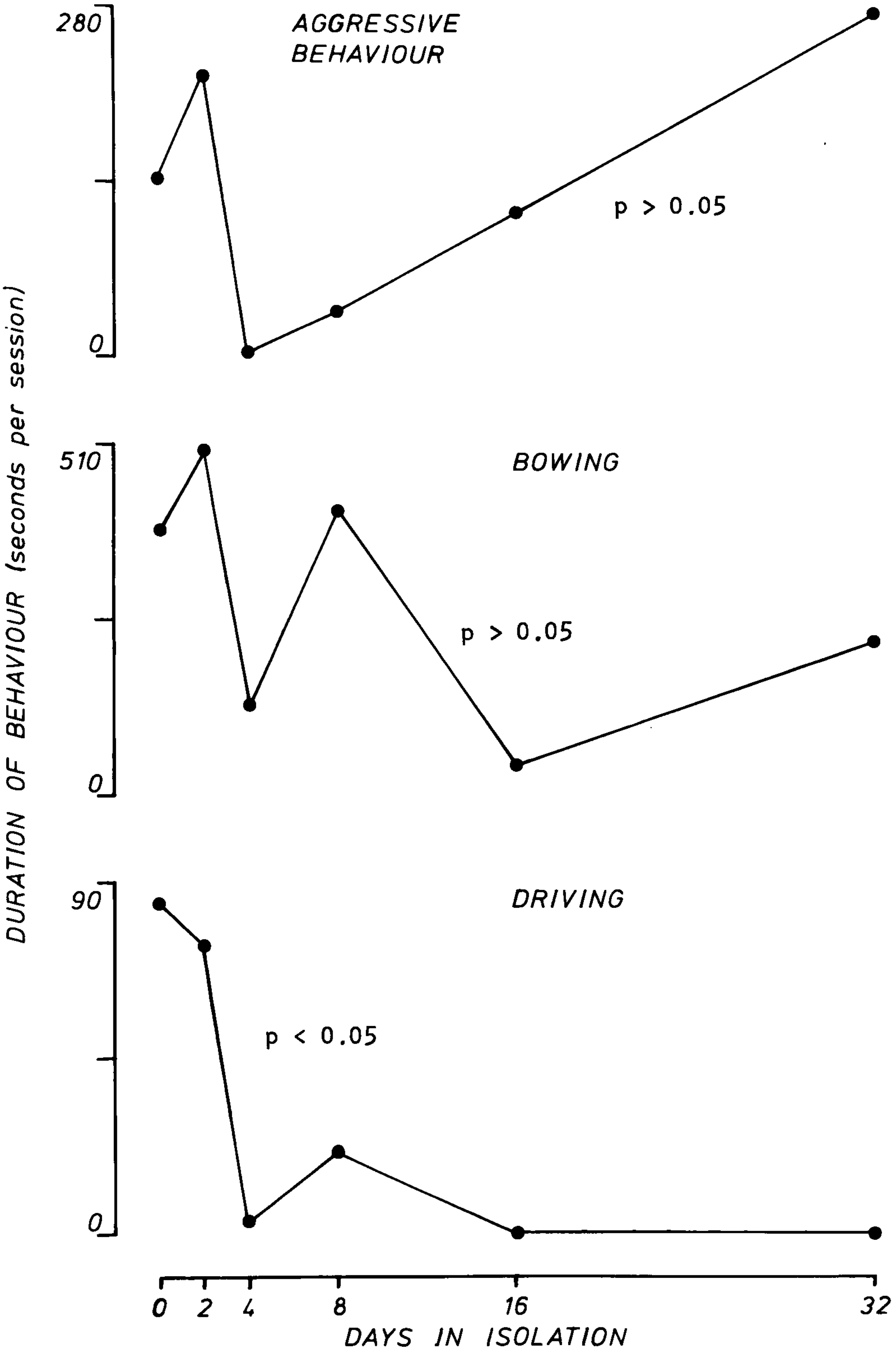

Fig. 4.2 P29. Graphs showing the duration of bowing, driving and aggressive behaviour, in seconds per session (ordinate), with increasing days in isolation. Driving showed a significant negative linear trend ($p < 0.05$) while bowing and aggressive behaviour showed no significance.

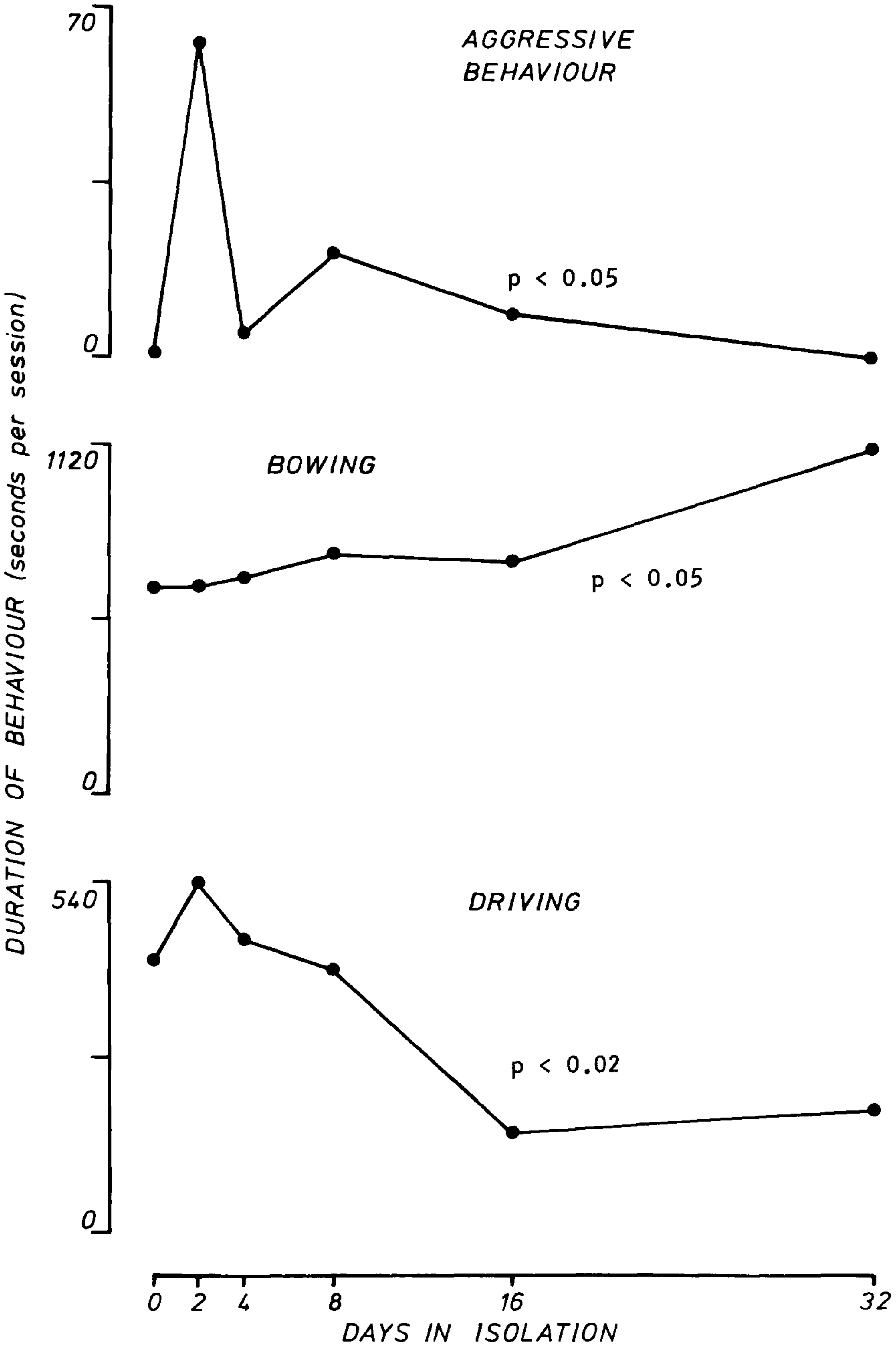

Fig. 4.3 P34. Graphs showing the duration of bowing, driving and aggressive behaviour, in seconds per session (ordinate), with increasing days in isolation. Bowing ($p < 0.05$), driving ($p < 0.02$) and aggressive behaviour ($p < 0.05$) all showed significant trends.

positive linear trend with increasing days in isolation ($p < 0.05$), while driving behaviour gave a significant negative linear trend ($p < 0.02$). Linear trend analysis supports the impressions conveyed in Fig. 4.3 with a significant negative linear trend ($p < 0.05$) for the graph for aggressive behaviour.

4.4 Discussion

Bowing showed a significant increment in two pigeons (P31 and P34), with increasing days in isolation. In the third pigeon (P29), the trend was not significant. Pigeons never perform bowing when alone, and the intensity with which they perform this behaviour after isolation suggests that the animals may have suffered from a low level of environmental stimulation (Welch, 1965). It is interesting to note that bowing is a conflict behaviour, and it is this behaviour and not aggressive behaviour which was performed most frequently after isolation. It is well known that conflict behaviour is performed as a result of the thwarting of a drive (Hinde, 1970), and it is possible that bowing was performed as a result of the thwarting of an aggressive drive.

There is evidence to suggest that driving behaviour is associated with courtship (Goodwin, 1955, 1956; Fabricius and Jansson, 1963). This suggests the possibility that there might be an association between Lehrman's results on gonadal hormone production in the barbary dove with the results presented here for driving behaviour performance with increasing days in isolation. Lehrman (1959, 1963) showed that gonadal hormone production decreased in isolated male barbary doves and that these reverted to a non-sexual phase. In two out of the three pigeons (P29 and P34) driving behaviour performance shows a significant decrement with increasing days in isolation. With the third pigeon (P31) the decrement is not significant; but the values for driving behaviour performance for days in isolation are much lower than for day 0.

Therefore a decrement in the performance of driving behaviour may reflect a change to a non-sexual phase with increasing isolation. A complication in the explanation of these results may be that the observed decrement is not brought about solely by the effect of isolation, but also by the absence of a mate, when the pigeons are placed in a social situation, in between each isolation period.

Aggressive behaviour showed a significant decline with increasing days in isolation, in one of the pigeons (P34, Fig. 4.3), in contrast to the results obtained by Franck and Wilhelmi (1973) working with Xiphophorus helleri (Pisces, Poeciliidae) males. The other two pigeons did not show any significant trends in their aggressive behaviour, with increasing days in isolation. Some studies show an increase of aggressive behaviour as a result of isolation (Courchesne and Barlow, 1971; Valzelli, 1969; Welch and Welch, 1969); others, however, show a decrement (e.g. Heiligenberg, 1964; Heiligenberg and Kramer, 1972; Ward, 1967). The results of this experiment do not give any clear indication as to which of these effects are shown by pigeons.

In conformity with his hydraulic model of motivation (Lorenz, 1950), Lorenz (1966) and others claim that animals have an aggressive drive which builds up spontaneously. This build-up of "action-specific energy" finds expression through the performance of aggressive behaviour. However, this model has been criticized on the grounds that the action-specific energy is 'used up' in the performance of the behaviour pattern, whereas most of the evidence suggests that behaviour patterns are terminated by various types of sensory feedback (Hinde, 1970, chpt. 8; Heiligenberg and Kramer, 1972).

The results obtained in this experiment do not suggest a build-up of an aggressive drive, over a period of time, which energizes fighting behaviour. If this were the case, the pigeons would have shown an increase in aggressive behaviour with increasing isolation.

On the issue of the effect of deprivation on the potentiality of an animal to perform a certain behaviour, McFarland (1971) suggests that "the change in motivational state induced in an animal deprived of appropriate external stimuli may be said to lead to an increase in the animal's potential to carry out the behaviour, and when the appropriate external stimuli are presented, the intensity of the behaviour is generally an increasing function of deprivation". One can tentatively suggest that this is shown by bowing behaviour.

However, it is quite clear that generalizations about the mechanisms controlling aggressive behaviour are hard to make. It is also clear, that these mechanisms differ in a number of ways from those of say, sexual behaviour, and generalizations about the control of one system can be applied to the other only with great reservations.

APPENDIX A

SEX DETERMINATION

SEX DETERMINATION

Feral pigeons lack secondary, morphological sex characteristics; and therefore the identification of the sex of immature, and sometimes mature birds is difficult. There are several tests for sex determination which do not involve any operative procedures; however, these are, to a certain extent, unsatisfactory. One of these tests is the observation of the frequency of occurrence of Bowing behaviour. Generally, this behaviour is always seen in male pigeons at a very early age (ref. section on Ontogeny), and young birds or birds which have been obtained through a dealer, which show this behaviour frequently are likely to be males. But the sexing of pigeons in this way can be unreliable and one can only be sure of positive sexing after thorough observation and understanding of pigeon behaviour.

Another more reliable method is that of cloacal examination. Fig. A.1 shows the urogenital systems of the male and female pigeons. Clearly, there are distinct differences in the form and number of openings e.g. the Ducta deferentia in the male, which are missing in the female, and the large vaginal opening in the female. For examination, a ring-lit magnifying lens is essential; and for convenience the pigeons are anaesthetised. The skin around the cloaca is turned outwards with a pair of large, blunt forceps, so that the cloaca itself is clearly visible.

However, the most reliable method of sex determination in pigeons is by abdominal surgery and gonadal examination. The birds are anaesthetised by an intra-muscular (Pectoral) injection of Equi-Thesin. The administered dose is 0.25 ml. per 100 grams body weight. The pigeons are laparotomized in the following manner: a lateral incision is made into the peritoneal cavity below the bottom end of the sternum, between the last intercostal spaces on either side of the pigeon. The intestines are moved to one side by means of one or two large spatulas, since the gonads lie dorsally in the

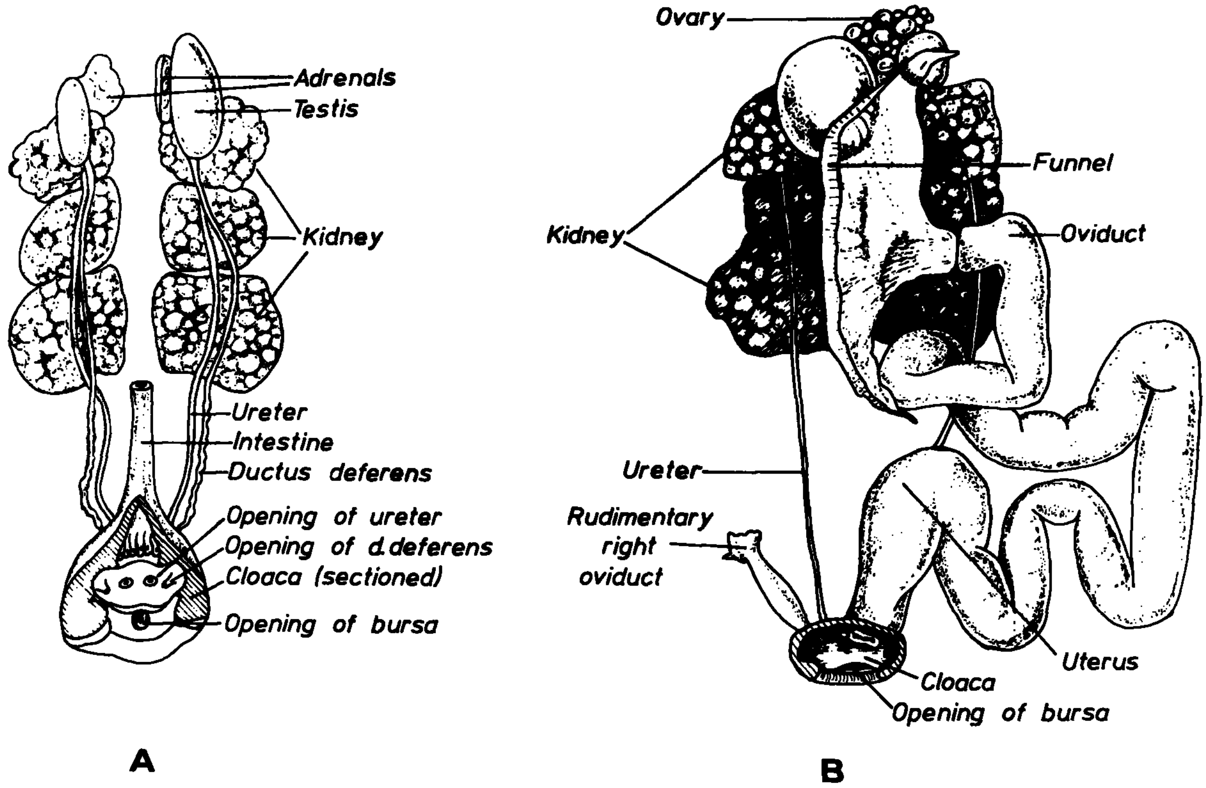

Figure A.1 Urogenital organs of the pigeon; A, male; B, female. The burse (of Fabricius) is a pouch of uncertain function, opening dorsally into the cloaca of birds. (A after Roseler and Lamprecht; B after Parker.) (Adapted from Romer, 1970).

bird. A 'spot-beam' of light is useful. Once positive identification is made, the intestines are replaced carefully and the incision is stitched up. The whole operative procedure should take no longer than 10 minutes and recovery from the anaesthetic is usually after two to three hours.

APPENDIX B

THE MATE

THE MATE

(A magnetic tape encoding keyboard for recording behavioural observations)

Ethology has brought new demands on the techniques of recording and processing behavioural data. What is required is a system capable of storing a large number of independent channels, on-off events of varying duration on a time basis, in format that is directly available to a computer. The system should be easily transportable.

The keyboard can contain up to 49 keys which can be used for recording behavioural data onto magnetic tape. The unit used throughout this study had thirty keys installed, only 18 of which were used at any one time. The keys have a double action: heavy finger pressure would lock any one key into a 'record' position until it is pressed for a second time. Light finger pressure would only activate a key as long as finger pressure is maintained.

Figure B.1 shows a simple block diagram for the Unit. Note that when the data is replayed through to the interface it first has to pass through a filtering and rectifying unit. This is a 'mains' operated unit which filters out any unwanted noise present on the pulses and magnetic tape, and rectifies the sinusoidal pulses into distinct square waves. Thus the pulse noise to background noise (signal to noise) ratio is large, and the possibility of an extraneous 'pulse' being played into the interface is minimal.

The datum (or double) pulses are produced every scan, and the scanning frequency depends on the multivibrator setting (frequency). At its present setting the keyboard is scanned every 0.3 seconds; that is, when no keys are depressed a double pulse is produced every 0.3 seconds, but finer or coarser settings are possible by modifying the multivibrator frequency so that the scanning frequency can be increased or decreased to the required

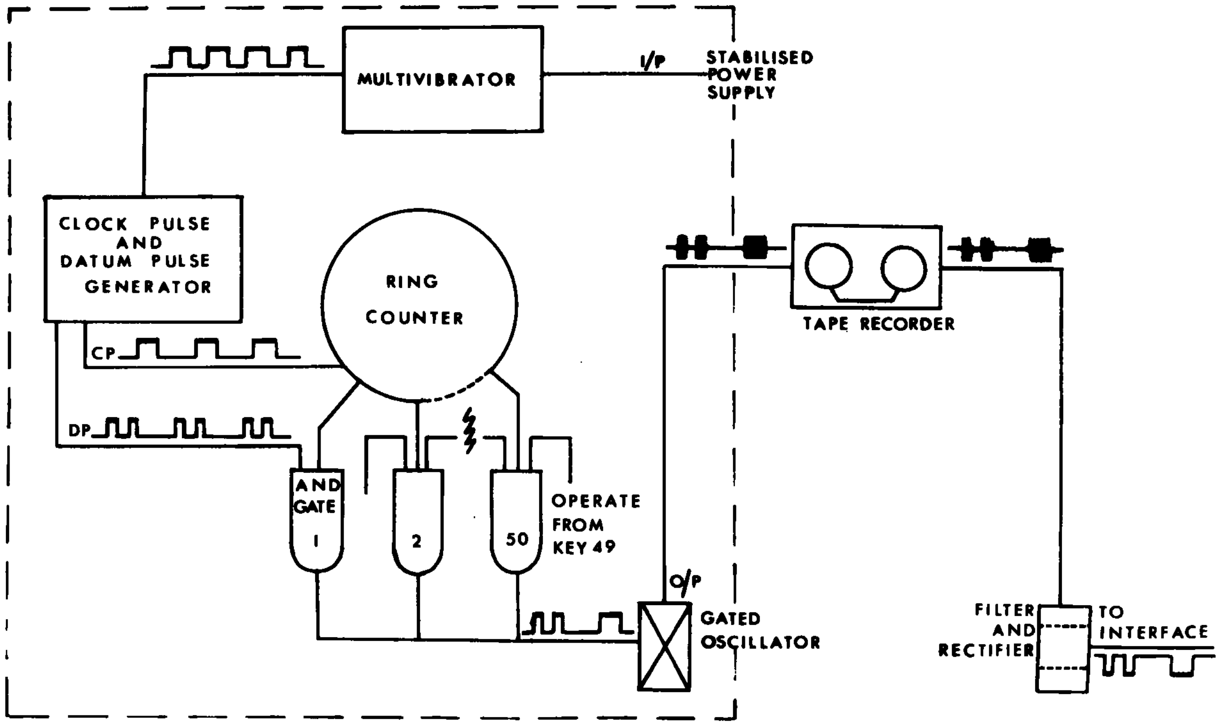

Figure B.1 Block diagram for the MATE system (enclosed by the dotted line), showing the main component groups involved in pulse generation. In addition to the recording output shown above, there are two further outputs: one is for datum pulse calibration and the other is the square wave output generally used for 'On-Line' experimental work.

setting. The double pulses function as markers with a fixed temporal spacing: when a key is depressed a clock (square wave) pulse is produced at a specific time interval after the double pulse, depending on which of the keys is depressed. If any key is held in a depressed position, the clock pulse is also scanned every 0.3 seconds.

The datum and clock pulses are recorded serially on to magnetic tape as 15 kHz. clicks having a sinusoidal waveform. The tape is replayed and the data is fed serially into the digital input of the WDV Interface to the computer. In addition to the 'record' output, the keyboard has two other outputs: one of the outputs can be used to feed square wave pulses directly into the interface (this facility is most useful when it is used for 'on line' experimentation and analysis of data; the other output is normally used for the temporal calibration of datum pulses. Analysed data can be stored both in the printed and the paper tape form. The 'Materials and Methods' section in Chapter 3 of this study will also include a brief description on the use of the MATE for the recording of behavioural data and the subsequent experimental analysis.

Ultimately, of course, keyboards or computer compatible event recorders must be suitable for the experimental work to be carried out apart from considering those sometimes limiting factors of cost and time. The Fernald/ Heinecke and WRATS systems have one major drawback in common and this is they both require AC power supply (this facility is not always readily available in the field). MATE can use either AC or DC power which probably makes it more suitable for field work. However, there is one main disadvantage in that the system is speed dependent i.e., data recorded on to one tape-recorder cannot be played back on another, since recording speeds vary from one instrument to the next.

White (1969, 1971), Lentz and Haith (1969), and Dawkins (1970), have described systems which can be used for recording behavioural observations on to magnetic tape. More recently Fernald and Heinecke (1974), describe a computer compatible multi-purpose event recorder which replaces magnetic tapes as the intermediate storage medium, punched paper tape. The main advantage of the Fernald and Heinecke system is that the data, recorded on paper tape, can be read directly by a digital computer at a much faster rate than the punching rate, or an encoded magnetic tape spanning the same length in time.

One of the drawbacks with the Fernald and Heinecke system is the large number of codes, which may give rise to some confusion during the recording of behavioural data. Moreover, coding has to be used for the recording of simultaneously occurring events, thus decreasing the maximum number of possible codes (unfortunately the authors do not list the maximum number of codes which could be employed when recording simultaneously occurring events).

The MATE system developed in this department is based on the principle of Pulse Code Modulation (see Mayo, 1968) and, to a certain extent, is similar to WRATS (White, 1971). However, I believe that the design and function of the system is basically simpler and more flexible.

This simplification in design, may, of course, have introduced certain drawbacks; but these can be easily overcome by modifying either the hardware or the software. For example, data can be recorded on the slowest tape speed and then played back for analysis at a faster speed of, say, $7\frac{1}{2}$ inches per second. Obviously this has the advantage of fast data processing coupled with a saving in computer time; so that by modifying the software, the encoded tapes may be played back at any speed the operator wishes to use. The multivibrator frequency can be changed to correspond with the frequency responses of the tape-recorder in use at the time. On the whole, however, the MATE's flexibility is far more dependent on software modification.

So, in conclusion, MATE is an ideal system for moderately long recording sessions (no longer than a few hours) and 'On-line' computation, and with slight modification to the hardware it can also be used as a multiple switch input for the automatic monitoring of pecking rates, movement etc.

APPENDIX C

ONTOGENY OF BEHAVIOUR

ONTOGENY OF BEHAVIOUR

In this Appendix I will outline the development of some behaviour patterns based on observations on seven squabs (4 male, 3 female), from hatching to four months of age, and an additional observation on two males and two females up to seven months of age.

On hatching, squabs are fed almost immediately by their parents although the former do not show any identifiable begging behaviour. As soon as a squab stretches its neck, the parent bird attending the nest immediately opens its bill to feed it. Sometimes the parent bird directs the squab's bill into its own mouth for feeding. The calls of day-old birds are barely audible and sound like 'cheeps'; as far as I could make out, the eyes were closed.

On the second day after hatching the eyes begin to open. Begging behaviour is still largely undirected and not very well defined, but as soon as a squab makes contact with the parent's beak, it pecks at the beak until it is fed. Between day 4 and day 7 the calls become more audible and the eyes open further. Moreover, the begging behaviour becomes more pronounced, and squabs show this behaviour in response to artificial stimulation (either by a glass rod or one's finger) of the ocular area. At about this time, feather growth is noticeable although the squab is still covered with fine yellow down, and preening-like actions are also seen.

Begging in response to artificial stimulation continues until the squabs are ten to eleven days of age, when they begin to show certain alarm behaviours such as outward movement of the wings, undirected aggressive pecking, crouching away from the author's hand and uttering low amplitude "clucks". Twelve to fifteen day old squabs continue to show these alarm responses; however, they sometimes show begging after prolonged stimulation of the area around the eyes. This behaviour is absent from the seventeenth day after hatching onwards. 2½ to 3 week old birds show such maintenance behaviours

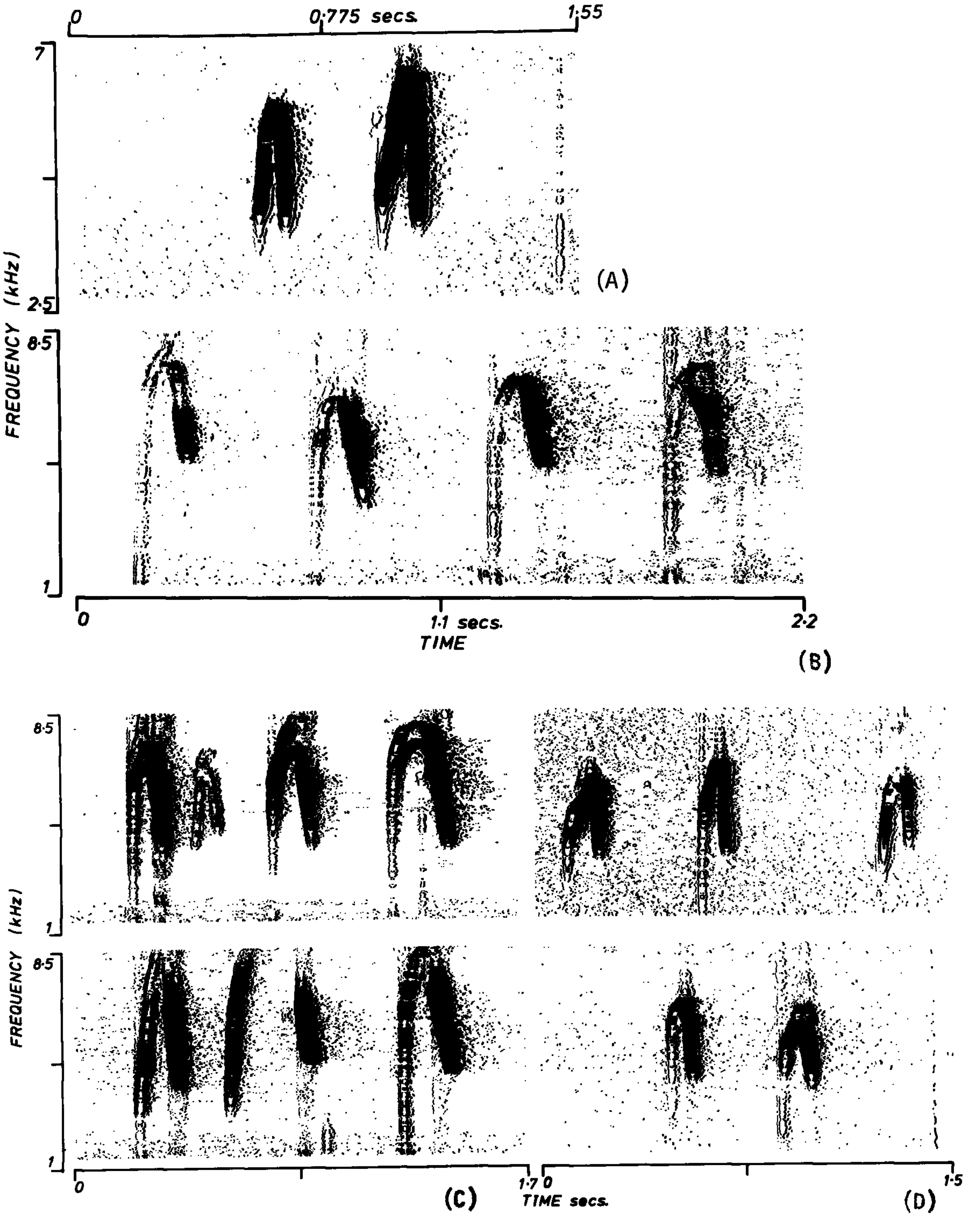

Figure C.1: Squab calls or 'cheeps'. (A) two cheeps of an 8 day old squab. (B) begging cheeps of a 4 day old squab; notice the 'clicks' at the beginning of each cheep (A: squab a; B: squab b). (C) begging cheeps of a 6 day old squab. (D) begging cheeps of a 4 day old squab. (C: squab b; D: squab c).

as wing and leg stretch, both wings stretch, preening and head-shaking. The development of these behaviours coincide with full feather cover. Aggressive pecking by three week old squabs is more directed, and male birds always show this behaviour somewhat earlier and more readily than female pigeons. Wing flicking is fully developed in 1½ month old birds, and again males show relatively more wing flicking than females.

The vocalisations of squabs sound like 'cheeps', and are very faint in day old chicks. By the fourth day the calls are audible enough to record. The spectrographs are very interesting (Fig. C.1 B & D): at the beginning of each call, one can identify a 'clicking' noise which is made by a squab when it opens its bill. This click disappears by the time the squabs are 8 days old. The calls themselves have a remarkably large frequency range; but this too becomes quite restricted as the squabs get older (Fig. C.1 A & C).

Young male pigeons utter calls similar to adult bowing calls but having a softer warble (unfortunately no sonograms are available for these calls), when these are three to four months of age; the fully developed bowing display is seen in four month old birds. At this time, female pigeons also produce a sort of bowing call, which sounds irregular in comparison to the male vocalisations. Two seven month old male pigeons showed full courtship behaviour, including driving, towards two adult females; but at seven months after hatching the two females were incapable of mating and had not yet laid any eggs.

APPENDIX D

Tables 1 to 5: Session totals (duration of behaviour, in seconds per session) presented in tables (i), and daily means (mean performance of behaviour in seconds per 32 minutes) presented in tables (ii), for Experimental Series 1 to Series 5 (Experiment 1, Chapter 3). The behaviours recorded during the experiment are coded as follows:-

Behaviour 1 ... Aggressive Pecking
Behaviour 2 ... Aggressive Billing
Behaviour 3 ... Body Pushing
" 4 ... Bowing
" 5 ... Nodding
" 6 ... Wing Vibration
" 7 ... Wing Flicking
" 8 ... Aggressive Intention Peck

TABLE 1

(i)

BEHAVIOUR DAY	SESSION	1	2	3	4	5	6	7	8
1	1	195	190	284	282	0	0	153	0
	2	176	90	271	294	3	0	55	0
	3	0	0	0	128	21	0	0	1
2	4	0	1	0	262	41	0	0	1
	5	0	0	0	290	88	12	9	0
	6	1	1	1	142	56	17	2	12
3	7	0	0	0	168	44	13	4	5
	8	0	0	0	144	32	27	4	5
	9	0	0	0	97	18	0	2	2
4	10	0	3	0	84	36	43	26	6
	11	43	53	58	247	49	13	157	5
	12	1	3	4	181	98	101	19	5
5	13	7	16	27	259	81	64	3	2
	14	1	13	15	238	60	121	20	6
	15	1	0	0	181	95	104	5	15
6	16	0	1	0	116	35	28	10	8
	17	12	46	85	500	205	0	70	13
	18	0	12	18	216	87	15	13	9
7	19	4	1	1	242	69	1	3	21
	20	2	0	0	273	69	11	2	38
	21	7	25	29	282	99	8	54	29
8	22	18	43	47	172	21	0	43	1
	23	0	0	0	106	53	40	0	7
	24	0	5	0	149	56	1	5	11
9	25	3	25	32	213	66	26	25	17
	26	2	2	0	158	21	27	2	50
	27	2	5	1	182	105	99	5	75
10	28	2	45	59	236	81	0	45	11
	29	0	0	0	148	47	0	0	31
	30	1	37	64	120	61	15	37	9

(ii)

BEHAVIOUR DAY	1	2	3	4	5	6	7	8
1	124	93	185	235	8	0	69	0
2	0	1	0	231	62	10	4	4
3	0	0	0	136	31	13	3	4
4	15	19	21	171	61	52	67	5
5	3	10	14	226	79	96	9	8
6	4	19	34	277	109	14	31	10
7	4	9	10	266	79	7	20	29
8	6	16	16	142	43	14	16	6
9	2	11	14	184	64	51	11	47
10	1	20	41	168	63	5	27	17

TABLE 2

(i)

BEHAVIOUR DAY	SESSION	1	2	3	4	5	6	7	8
1	1	481	201	228	286	1	0	114	1
	2	452	43	56	174	92	0	18	0
	3	350	44	36	70	31	0	62	0
2	4	564	26	27	128	130	57	24	0
	5	36	1	0	146	311	354	0	0
	6	22	0	0	31	109	177	0	0
3	7	39	1	0	46	544	1029	0	0
	8	560	25	26	75	276	171	39	0
	9	243	20	21	49	207	40	7	0
4	10	299	3	35	79	316	219	11	0
	11	302	57	42	88	54	0	22	0
	12	4	0	0	23	50	0	0	0
5	13	6	0	0	40	400	109	0	0
	14	3	0	0	176	459	16	23	23
	15	205	15	11	35	105	21	7	7
6	16	183	12	28	154	138	7	16	7
	17	0	0	0	47	54	0	0	3
	18	172	46	34	146	131	0	14	26
7	19	0	0	0	101	354	190	9	30
	20	18	91	98	88	215	8	74	48
	21	24	55	58	138	164	0	42	17
8	22	0	0	0	67	271	97	1	6
	23	0	0	0	22	61	0	3	14
	24	0	0	0	29	113	38	3	18
9	25	0	0	0	128	240	61	8	24
	26	88	201	229	178	128	13	93	24
	27	0	0	0	145	222	5	7	37
10	28	0	0	0	118	361	142	4	23
	29	0	0	0	69	177	4	5	38
	30	0	0	0	47	99	0	2	13

(ii)

BEHAVIOUR DAY	1	2	3	4	5	6	7	8
1	428	96	107	177	41	0	65	0
2	207	9	9	102	183	196	8	0
3	281	15	16	57	342	413	15	0
4	202	20	26	63	140	73	11	0
5	71	5	4	84	321	49	10	10
6	118	19	21	116	108	2	10	12
7	14	49	52	109	244	66	42	32
8	0	0	0	39	148	45	2	13
9	29	67	76	150	197	26	36	28
10	0	0	0	78	212	49	4	25

TABLE 3

(i)

BEHAVIOUR		1	2	3	4	5	6	7	8
DAY	SESSION								
1	1	89	1	0	1212	0	0	0	0
	2	89	258	307	440	150	16	98	2
	3	9	46	51	294	319	362	17	4
2	4	18	54	81	343	258	127	39	13
	5	5	8	8	300	181	108	3	68
	6	19	24	29	287	73	21	19	49
3	7	0	0	0	101	44	4	0	2
	8	5	0	0	311	104	56	0	22
	9	242	182	295	579	170	15	206	6
4	10	24	22	32	180	184	335	19	0
	11	13	13	18	282	216	209	23	10
	12	17	0	0	250	149	133	1	68
5	13	20	20	20	452	91	119	25	17
	14	57	20	26	205	190	342	53	15
	15	4	0	0	247	113	23	1	34
6	16	34	20	37	285	116	135	12	41
	17	43	29	57	127	105	20	23	4
	18	1	1	1	170	154	226	3	25
7	19	288	209	410	416	85	35	254	59
	20	323	288	526	168	99	0	406	0
	21	0	0	0	46	34	10	0	4
8	22	3	11	18	255	95	27	42	13
	23	138	66	144	256	103	72	107	6
	24	2	9	17	226	121	110	27	38
9	25	20	2	0	207	92	203	3	19
	26	3	25	39	119	81	39	22	1
	27	8	2	0	174	71	147	1	15
10	28	17	7	12	108	170	825	10	0
	29	137	61	124	249	210	867	81	0
	30	0	0	0	82	125	1073	0	0

(ii)

BEHAVIOUR	1	2	3	4	5	6	7	8
DAY								
1	62	102	119	649	156	126	38	2
2	14	29	39	310	171	85	20	43
3	82	61	98	330	106	25	69	10
4	18	12	17	237	183	226	14	26
5	27	13	15	301	131	161	26	22
6	26	17	32	194	125	127	13	23
7	204	166	312	210	73	15	220	21
8	48	29	60	246	106	70	59	19
9	10	10	13	167	81	130	9	12
10	51	23	45	146	168	922	30	0

TABLE 4

(i)

BEHAVIOUR		1	2	3	4	5	6	7	8
DAY	SESSION								
1	1	309	211	329	288	187	0	157	62
	2	49	186	281	38	126	3	222	1
	3	21	34	57	5	63	9	52	14
2	4	0	0	0	1	34	0	0	5
	5	0	0	0	21	131	192	7	39
	6	0	0	0	71	305	264	13	31
3	7	0	0	0	38	131	122	7	40
	8	27	23	62	127	263	302	41	29
	9	2	1	0	43	157	118	4	28
4	10	0	0	0	59	56	7	6	24
	11	17	39	62	180	232	72	49	31
	12	0	0	0	86	136	53	3	26
5	13	0	0	0	54	57	13	3	18
	14	1	0	0	152	153	133	25	52
	15	18	75	104	185	382	305	65	29
6	16	0	0	2	71	157	68	6	26
	17	0	0	0	96	96	43	10	42
	18	0	0	0	112	169	136	13	68
7	19	0	0	0	80	100	140	5	29
	20	2	23	24	93	136	100	17	33
	21	0	0	0	83	95	39	8	22
8	22	0	0	0	90	60	7	3	32
	23	5	27	49	155	178	176	21	23
	24	0	0	0	65	115	182	7	32
9	25	0	0	0	75	97	15	7	24
	26	0	0	0	59	87	45	6	28
	27	16	30	67	130	235	143	37	14
10	28	0	0	0	55	90	4	0	17
	29	0	0	0	65	106	0	10	25
	30	7	23	51	112	174	113	32	2

(ii)

BEHAVIOUR	1	2	3	4	5	6	7	8
DAY								
1	126	144	222	110	125	4	144	26
2	0	0	0	31	157	152	7	25
3	10	8	21	69	184	181	17	32
4	6	13	21	108	141	44	19	27
5	6	25	35	130	197	150	31	33
6	0	0	1	93	141	82	10	45
7	1	8	8	85	110	93	10	28
8	2	9	16	103	118	122	10	29
9	5	10	22	88	140	68	17	22
10	2	8	17	77	123	39	14	15

TABLE 5

(i)

BEHAVIOUR		1	2	3	4	5	6	7	8
DAY	SESSION								
1	1	84	43	110	165	88	0	82	2
	2	25	67	98	119	116	45	96	1
	3	102	16	32	96	90	29	96	7
2	4	0	0	0	53	212	155	15	12
	5	6	25	52	92	86	170	67	8
	6	33	32	65	96	237	474	105	5
3	7	0	0	0	46	127	113	5	4
	8	0	0	0	32	148	337	12	2
	9	14	27	50	155	283	252	50	10
4	10	0	0	0	31	161	250	5	1
	11	24	31	73	81	130	89	50	8
	12	40	65	121	206	202	58	47	7
5	13	9	27	53	124	148	121	45	1
	14	17	21	46	92	176	122	21	5
	15	20	27	33	138	270	97	47	2
6	16	1	3	4	61	90	108	4	0
	17	0	0	0	13	15	12	0	0
	18	0	0	0	31	45	0	0	0
7	19	39	36	57	270	242	79	79	1
	20	72	52	99	201	406	52	77	5
	21	21	36	46	198	430	73	55	1
8	22	15	19	28	172	442	269	32	3
	23	32	18	43	150	454	153	27	3
	24	66	53	88	103	507	258	80	1
9	25	33	13	20	98	567	319	52	8
	26	20	18	22	93	417	288	51	3
	27	34	21	31	121	436	109	38	12
10	28	11	7	17	155	398	204	17	3
	29	0	0	0	26	207	43	0	5
	30	29	32	30	73	211	44	50	5

(ii)

BEHAVIOUR	1	2	3	4	5	6	7	8
DAY								
1	70	42	80	127	98	25	91	3
2	13	19	39	80	178	266	40	8
3	5	9	17	78	186	234	22	5
4	21	32	65	106	164	132	34	5
5	15	25	44	118	198	113	38	3
6	0	1	1	35	50	40	1	0
7	44	41	67	223	359	68	70	2
8	38	30	53	142	468	227	46	2
9	29	17	24	104	473	239	47	8
10	13	13	16	85	272	97	22	4

TABLE 6

BEHAVIOUR	1	2	3	4	5	6	7	8
DAY								
1	162	95	143	260	86	31	81	6
2	47	12	17	151	150	89	16	16
3	76	19	30	134	170	173	25	10
4	52	19	30	137	138	105	29	13
5	24	16	22	172	185	114	23	15
6	30	11	18	143	107	53	13	18
7	53	55	90	179	173	50	72	22
8	19	17	29	134	177	96	27	14
9	15	23	30	139	191	103	24	23
10	13	13	24	111	168	222	19	12

Table showing the total daily means for all the behaviours over days (n = 50), for all the Experimental Series.

APPENDIX E

In the following Appendix, intercorrelations between behaviours for both session totals and daily means are presented systematically for all the Experimental Series (computed from Data presented in Appendix D). The word "Variable" in the correlation matrices, stands for "Behaviour", and the Behaviours recorded during the experiment are coded as follows:-

Behaviour 1 ... Aggressive Pecking
Behaviour 2 ... Aggressive Billing
Behaviour 3 ... Body Pushing
" 4 ... Bowing
" 5 ... Nodding
" 6 ... Wing Vibration
" 7 ... Wing Flicking
" 8 ... Aggressive Intention Peck

APPENDIX E

Tables E1 - E5: These correlation matrices show intercorrelations between behaviours (session totals, see Appendix D) over sessions (n = 30), for experimental series 1 to 5.

SPEARMAN CORRELATION TABLE

VARIABLE	1	2	3	4	5	6	7	8
1	1.000							
2	0.747^{+}	1.000						
3	0.793^{+}	0.914^{+}	1.000					
4	0.627^{+}	0.464^{*}	0.518^{*}	1.000				
5	0.126	0.076	0.176	0.378	1.000			
6	-0.159	-0.169	-0.208	-0.270	0.338	1.000		
7	0.595^{+}	0.831^{+}	0.781^{+}	0.420	0.151	-0.068	1.000	
8	0.075	-0.094	-0.109	-0.080	0.494^{*}	0.245	-0.151	1.000

Table E1: Correlation matrix showing intercorrelations between Behaviours over sessions (n = 30) for experimental series 1.
Degrees of freedom = 28.

$^{*}p < 0.01$

$^{+}p < 0.001$

SPEARMAN CORRELATION TABLE

VARIABLE	1	2	3	4	5	6	7	8
1	1.000							
2	0.802^{+}	1.000						
3	0.748^{+}	0.950^{+}	1.000					
4	0.318	0.490*	0.508*	1.000				
5	-0.227	-0.291	-0.340	0.148	1.000			
6	-0.031	-0.271	-0.351	-0.100	0.766^{+}	1.000		
7	0.557*	0.766^{+}	0.833^{+}	0.659*	-0.155	-0.294	1.000	
8	-0.599^{+}	-0.159	-0.094	0.262	0.175	-0.174	0.202	1.000

Table E2: Correlation matrix showing intercorrelations between behaviours over sessions (n = 30) for experimental series 2. Degrees of freedom = 28.

$^{*}p < 0.01$

$^{+}p < 0.001$

SPEARMAN CORRELATION TABLE

VARIABLE	1	2	3	4	5	6	7	8
1	1.000							
2	0.733^{+}	1.000						
3	0.694^{+}	0.980^{+}	1.000					
4	0.469^{*}	0.358	0.314	1.000				
5	0.117	0.263	0.304	0.146	1.000			
6	-0.135	-0.106	-0.108	-0.184	0.616^{+}	1.000		
7	0.663^{+}	0.899^{+}	0.898^{+}	0.311	0.287	-0.074	1.000	
8	-0.131	-0.196	-0.190	0.345	-0.043	0.004	-0.061	1.000

Table E3: Correlation matrix showing intercorrelations between behaviours over sessions (n = 30) for experimental series 3. Degrees of freedom = 28.

$^{*}p < 0.01$

$^{+}p < 0.001$

SPEARMAN CORRELATION TABLE

VARIABLE	1	2	3	4	5	6	7	8
1	1.000							
2	0.960^{+}	1.000						
3	0.903^{+}	0.932^{+}	1.000					
4	0.423	0.397	0.454	1.000				
5	0.553*	0.535*	0.566*	0.648^{+}	1.000			
6	0.124	0.086	0.096	0.344	0.661^{+}	1.000		
7	0.807^{+}	0.769^{+}	0.785^{+}	0.519*	0.618^{+}	0.250	1.000	
8	−0.123	−0.174	−0.188	0.354	0.294	0.363	0.109	1.000

Table E4: Correlation matrix showing intercorrelation between behaviours over sessions ($n = 30$) for experimental series 4. Degrees of freedom = 28.

$^{*}p < 0.01$

$^{+}p < 0.001$

SPEARMAN CORRELATION TABLE

VARIABLE	1	2	3	4	5	6	7	8
1	1.000							
2	0.753^{+}	1.000						
3	0.756^{+}	0.941^{+}	1.000					
4	0.677^{+}	0.714^{+}	0.701^{+}	1.000				
5	0.367	0.226	0.120	0.513^{*}	1.000			
6	-0.149	-0.156	-0.124	0.020	0.512	1.000		
7	0.803^{+}	0.787^{+}	0.780^{+}	0.572^{+}	0.216	0.034	1.000	
8	0.226	0.044	0.126	0.080	0.253	0.217	0.196	1.000

Table E5: Correlation matrix showing intercorrelation between behaviours over sessions ($n = 30$) for experimental series 5. Degrees of freedom = 28.

$^{*}p < 0.01$

$^{+}p < 0.001$

Tables E6 - E10: These correlation matrices show intercorrelations between the daily mean behaviour performance (daily means, see Appendix D) for all the behaviours, over days (n = 10), for Experimental Series 1 to 5.

SPEARMAN CORRELATION TABLE

VARIABLE	1	2	3	4	5	6	7	8
1	1.000							
2	0.610	1.000						
3	0.638	0.947^{+}	1.000					
4	0.293	0.302	0.159	1.000				
5	-0.162	0.043	-0.083	0.547	1.000			
6	0.046	-0.188	-0.208	-0.176	0.335	1.000		
7	0.512	0.597	0.555	0.467	-0.195	-0.389	1.000	
8	-0.135	0.019	0.000	0.152	0.762	0.220	-0.365	1.000

Table E6: Correlation matrix showing intercorrelations between behaviours (daily means) over days (n = 10) for Experimental Series 1. Degrees of freedom = 8.

$^{+}p < 0.001$

SPEARMAN CORRELATION TABLE

VARIABLE	1	2	3	4	5	6	7	8
1	1.000							
2	0.476	1.000						
3	0.476	1.000	1.000					
4	0.267	0.729	0.729	1.000				
5	-0.243	-0.340	-0.340	-0.370	1.000			
6	0.149	-0.302	-0.302	-0.596	0.602	1.000		
7	0.482	0.921^{+}	0.921^{+}	0.608	-0.024	-0.143	1.000	
8	-0.853^{*}	-0.038	-0.038	0.163	0.250	-0.301	-0.038	1.000

Table E7: Correlation matrix showing intercorrelations between behaviours (daily means) over days (n = 10) for Experimental Series 2. Degrees of freedom = 8.

$^{*}p < 0.01$

$^{+}p < 0.001$

SPEARMAN CORRELATION TABLE

VARIABLE	1	2	3	4	5	6	7	8
1	1.000							
2	0.809*	1.000						
3	0.867*	0.967^{+}	1.000					
4	0.261	0.492	0.370	1.000				
5	-0.340	-0.247	-0.243	0.182	1.000			
6	-0.491	-0.766*	-0.685	-0.455	0.596	1.000		
7	0.915^{+}	0.857*	0.879^{+}	0.394	-0.340	-0.648	1.000	
8	-0.539	-0.280	-0.394	0.067	0.286	-0.030	-0.406	1.000

Table E8: Correlation matrix showing intercorrelations between behaviours (daily means) over days (n = 10) for Experimental Series 3. Degrees of freedom = 8.

$^{*}p < 0.01$

$^{+}p < 0.001$

SPEARMAN CORRELATION TABLE

VARIABLE	1	2	3	4	5	6	7	8
1	1.000							
2	0.801*	1.000						
3	0.911^{+}	0.901^{+}	1.000					
4	0.465	0.800*	0.614	1.000				
5	0.239	0.003	0.186	0.030	1.000			
6	-0.202	-0.412	-0.353	-0.382	0.505	1.000		
7	0.913^{+}	0.875^{+}	0.960^{+}	0.665	0.272	-0.400	1.000	
8	0.000	-0.074	-0.085	0.345	0.365	0.491	0.006	1.000

Table E9: Correlation matrix showing intercorrelations between behaviours (daily means) over days (n = 10) for Experimental Series 4. Degrees of freedom = 8.

$^{*}p < 0.01$.

$^{+}p < 0.001$

SPEARMAN CORRELATION TABLE

VARIABLE	1	2	3	4	5	6	7	8
1	1.000							
2	0.894^{+}	1.000						
3	0.875^{+}	0.988^{+}	1.000					
4	0.912^{+}	0.879^{+}	0.855^{*}	1.000				
5	0.353	0.055	0.030	0.430	1.000			
6	-0.225	-0.273	-0.224	-0.261	0.418	1.000		
7	0.918^{+}	0.790^{*}	0.790^{*}	0.772^{*}	0.359	-0.043	1.000	
8	-0.132	-0.135	-0.117	-0.325	0.147	0.749	0.034	1.000

Table E10: Correlation matrix showing intercorrelations between behaviours (daily means) over days (n = 10) for Experimental Series 5. Degrees of freedom = 8.

$^{*}p < 0.01$

$^{+}p < 0.001$

Tables E11 - E12: These correlation matrices show intercorrelations between behaviours for the total number of sessions (n = 150) and the total number of days (n = 50) for all the experimental series.

SPEARMAN CORRELATION TABLE

VARIABLE	1	2	3	4	5	6	7	8
1	1.000							
2	0.815^{+}	1.000						
3	0.564^{+}	0.736^{+}	1.000					
4	0.031	0.185	0.040	1.000				
5	-0.022	-0.065	-0.062	0.098	1.000			
6	0.331^{+}	0.248^{*}	0.086	-0.100	0.305^{+}	1.000		
7	0.248^{*}	0.473^{+}	0.573^{+}	0.207	0.023	-0.076	1.000	
8	-0.232^{*}	-0.111	0.125	-0.134	0.010	-0.001	-0.015	1.000

Table E11: Correlation matrix showing intercorrelations between behaviours for the total number of sessions in the experimental series ($n = 150$). Degrees of freedom = 148.

$^{*}p < 0.01$

$^{+}p < 0.001$

SPEARMAN CORRELATION TABLE

VARIABLE	1	2	3	4	5	6	7	8
1	1.000							
2	0.726^{+}	1.000						
3	0.664^{+}	0.955^{+}	1.000					
4	0.245	0.494^{+}	0.414^{+}	1.000				
5	0.176	0.048	0.053	-0.361*	1.000			
6	0.060	-0.113	-0.110	-0.254	0.645^{+}	1.000		
7	0.543^{+}	0.825^{+}	0.843^{+}	0.467^{+}	0.034	-0.140	1.000	
8	-0.410*	-0.202	-0.163	0.041	0.061	-0.037	-0.179	1.000

Table E12: Correlation matrix showing intercorrelations between behaviours (total daily means) over days ($n = 50$), for all the Experimental Series. Degrees of freedom = 48.

$^{*}p < 0.01$

$^{+}p < 0.001$

APPENDIX F

Appendix showing raw data (tables F.1 to F.3) and data (tables F.4 to F.12) for linear trend analysis (after Still, 1967), for Experiment 2 (Chapter 4).

Tables F.1 to F.3

(Tables of raw scores, showing the duration of each behaviour (in seconds per 32 minute session) after isolation, for each pigeon).

Table F.1: P31.

BEHAVIOUR	AGGRESSIVE BEHAVIOUR	BOWING	DRIVING
DAYS IN ISOLATION			
0	92	334	717
2	138	262	28
4	71	330	21
8	165	515	264
16	91	1040	231
32	22	1034	420

Table F.2: P34.

BEHAVIOUR	AGGRESSIVE BEHAVIOUR	BOWING	DRIVING
DAYS IN ISOLATION			
0	1	660	422
2	63	664	540
4	5	695	453
8	21	772	406
16	9	752	151
32	0	1115	189

Table F.3: P29.

BEHAVIOUR	AGGRESSIVE BEHAVIOUR	BOWING	DRIVING
DAYS IN ISOLATION			
0	144	385	85
2	226	502	74
4	5	129	3
8	36	415	21
16	115	41	0
32	275	225	0

Tables F.4 to F.12: Linear trend analysis data on the scores presented in tables F.1 to F.3. The test is based on the Wilcoxon matched-pairs signed-ranks test.

Table F.4: P31. Trend analysis data for Bowing behaviour

Days in Isolation	0	2	4	8	16	32
Session* period						
1	129.1	116.1	141.3	90.6	199.4	137.6
2	34.7	103.9	153.5	115.0	151.6	159.0
3	3.3	34.4	14.0	76.9	99.8	174.2
4	7.3	0.0	21.0	76.2	174.6	162.4
5	6.2	7.3	0.0	66.2	11.3	157.6
6	99.8	0.0	0.0	84.7	133.5	150.9
7	53.6	0.0	0.0	0.0	150.2	12.2
8	0.0	0.0	0.0	2.5	19.9	79.9

*Each period was of 4 minutes duration

T = 0, Linear trend
significant
$p < 0.01$

Table F.5: P31. Trend analysis data for Driving behaviour

Days in Isolation	0	2	4	8	16	32
Session* period						
1	81.3	26.1	16.2	61.7	9.2	54.0
2	100.9	2.2	4.8	114.6	58.4	59.5
3	121.7	0.0	0.0	15.5	88.4	62.5
4	165.0	0.0	0.0	27.0	16.2	65.1
5	188.6	0.0	0.0	1.8	51.7	47.7
6	60.3	0.0	0.0	43.2	0.3	36.9
7	0.0	0.0	0.0	0.0	6.6	55.8
8	0.0	0.0	0.0	0.0	0.0	38.8

*Each period was of 4 minutes duration

T = 16, Linear trend
is not significant

Table F.6: P31. Trend analysis data for Aggressive Behaviour

Days in Isolation	0	2	4	8	16	32
Session* period						
1	4.4	68.2	33.5	77.1	6.2	5.1
2	30.3	52.3	30.7	9.9	6.9	8.1
3	14.4	14.0	0.0	58.2	0.0	0.0
4	21.0	0.0	7.7	3.0	1.4	0.0
5	11.0	0.0	0.0	13.1	2.5	0.0
6	10.3	0.0	0.0	3.9	18.7	1.8
7	0.0	0.0	0.0	0.0	14.6	0.0
8	0.0	0.0	0.0	0.0	40.9	7.0

*Each period was of 4 minutes duration

T = 15, Linear trend is not significant

Table F.7: P34. Trend analysis data for Bowing behaviour

Days in Isolation	0	2	4	8	16	32
Session* period						
1	57.3	61.7	83.9	107.6	174.6	171.6
2	103.9	101.7	95.0	143.9	156.1	191.6
3	154.2	106.9	113.9	119.4	143.5	155.7
4	118.0	79.9	108.3	103.2	124.6	194.9
5	112.0	82.8	88.4	76.5	59.9	136.1
6	64.3	89.9	86.9	74.3	9.6	179.8
7	38.1	77.3	78.4	69.5	83.6	77.3
8	12.2	64.0	39.9	77.6	0.0	8.1

*Each period was of 4 minutes duration

T = 3, Linear trend significant
$p < 0.05$

Table F.8: P34. Trend analysis data for Driving behaviour

Days in Isolation	0	2	4	8	16	32
Session* period						
1	86.9	121.7	113.9	100.2	38.8	61.7
2	143.9	60.6	65.8	51.0	31.0	17.0
3	61.4	34.7	80.6	53.6	18.4	21.8
4	38.4	68.4	43.2	33.6	34.0	12.9
5	49.2	86.2	98.4	49.2	0.0	0.7
6	17.3	33.2	41.4	71.7	0.0	2.5
7	17.0	98.7	5.9	33.2	29.2	64.0
8	8.1	36.2	3.6	13.6	0.0	8.5

*Each period was of 4 minutes duration

T = 1, Linear trend
significant
$p < 0.02$

Table F.9: P34. Trend analysis data for Aggressive behaviour

Days in Isolation	0	2	4	8	16	32
Session* period						
1	0.0	8.3	0.0	0.0	0.0	0.0
2	0.5	3.3	2.2	21.3	0.0	0.0
3	0.0	3.6	0.0	0.0	0.0	0.0
4	1.0	1.4	0.0	0.0	8.8	0.0
5	0.0	4.7	0.5	0.0	0.0	0.0
6	0.0	8.4	1.8	0.0	0.0	0.0
7	0.0	8.4	2.9	0.0	0.0	0.0
8	0.0	24.6	0.0	0.0	0.0	0.0

*Each period was of 4 minutes duration

T = 4, Linear trend
significant
$p < 0.05$

Table F.10: P29. Trend analysis data for Bowing behaviour

Days in Isolation	0	2	4	8	16	32
Session* period						
1	28.1	135.0	118.0	113.9	0.0	0.0
2	55.1	92.8	0.0	83.9	0.0	0.0
3	125.4	109.8	0.0	0.0	1.8	0.0
4	83.2	46.9	0.0	27.0	39.2	0.0
5	4.8	98.7	10.7	136.1	0.0	123.5
6	65.1	1.8	0.0	0.0	0.0	54.7
7	23.3	17.0	0.0	54.3	0.0	34.0
8	0.0	0.0	0.0	0.0	0.0	12.5

*Each period was of 4 minutes duration

T = 11, Linear trend is not significant

Table F.11: P29. Trend analysis data for Driving behaviour

Days in Isolation	0	2	4	8	16	32
Session* period						
1	15.1	31.4	2.9	18.4	0.0	0.0
2	59.9	4.0	0.0	2.2	0.0	0.0
3	0.0	31.8	0.0	0.0	0.0	0.0
4	2.5	7.0	0.0	0.0	0.0	0.0
5	0.0	0.0	0.0	0.0	0.0	0.0
6	7.0	0.0	0.0	0.0	0.0	0.0
7	0.0	0.0	0.0	0.0	0.0	0.0
8	0.0	0.0	0.0	0.0	0.0	0.0

*Each period was of 4 minutes duration

T = 0, Linear trend significant
$p < 0.01$

Table F.12: P29. Trend analysis data for Aggressive Behaviour

Days in Isolation	0	2	4	8	16	32
Session* period						
1	52.0	29.1	2.5	10.9	1.0	0.0
2	56.6	1.4	0.0	9.9	0.0	1.4
3	4.0	1.1	0.0	0.0	61.2	1.0
4	1.1	158.5	0.0	0.0	53.0	169.6
5	9.2	1.8	2.5	15.0	0.0	52.3
6	22.1	18.4	0.0	0.0	0.0	43.4
7	0.0	15.0	0.0	0.0	0.0	0.0
8	0.0	0.0	0.0	0.0	0.0	6.9

*Each period was of 4 minutes duration

T = 20, Linear trend is not significant

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