GENETIC ANALYSIS OF STRAIN DIFFERENCES IN PRE-LAYING BEHAVIOUR IN THE FOWL.

An ethological and genetic analysis of differences in the pre-laying behaviour of two strains of domestic fowl (Gallus gallus domesticus) confined in battery cages.

A study pertaining to the evolution and adaptiveness of behaviour
under conditions of natural and artificial selection.

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DECLARATION

I declare that this thesis has been composed by me and that the work described is my own.

TO MY PARENTS FOR THEIR UNFAILING SUPPORT

And with that word he flew down from the beams,
For it was day, and down his hens flew all,
And with a chuck he gave the troupe a call
For he had found a seed upon the floor.
Royal he was, he was no more afraid.
He feathered Pertelote in wanton play
And trod her twenty times ere prime of day.
Grime as a lion`s was his manly frown
As on his toes he sauntered up and down
He scarcely deigned to set his foot to ground
And every time a seed was found
He gave a chuck, and up his wives ran all.
Thus royal as a prince who strides his hall
Leave we this Chaunticleer engaged on feeding
And pass to the adventure that was breeding

Chaucer

The Nun`s Priest`s Tale

TABLE OF CONTENTS

PAGE

ABSTRACT

This thesis deals with the description and analysis of the pre-laying behaviour of two strains of domestic fowl (*Gallus gallus domesticus*) in battery cages. Hens from one of these strains, known as the S line, showed stereotyped pacing behaviour before laying. Hens from the other strain, known as the T line, showed little or no pacing behaviour and tended to sit.

Selection over two generations, for pacing in the S line and for sitting in the T line, consistently increased both variables: indicating genetic variation in the expression of the two traits.

Crosses between the two lines, extending to backcross and F1 generations, indicated that the tendencies to pace and to sit during the pre-laying period were inherited separately. The tendency to sit appeared to be inherited additively, whereas the tendency to pace (as opposed to not pacing) appeared to be inherited in a dichotomous fashion, controlled by a single gene or a polygenic threshold system. Neither trait was sex-linked.

It is suggested that the differences in the pre-laying behaviour of the two strains are due to differences in responsiveness to releasers for sitting behaviour. The T line generalise to sub-obtimal stimuli from the cage associated with the release of sitting behaviour; whilst the S line fail to do so, become frustrated, and in response to this frustration exhibit stereotyped pacing behaviour.

The differences in the pre-laying behaviour of the two strains did not appear to be related to their responses to aversive stimuli or the frustration of feeding behaviour, or to their ability to generalise to sub-optimal stimuli other than those associated with the release of sitting during the period before laying.

Theoretical aspects of the study relelated to the genetics of behaviour and its evolution are relevant to Tinbergen´s ´´derived`` activities hypothesis, which postulates that some visual displays have been derived from the behaviour shown in response to motivational conflict or thwarting.

Practical aspects of the study relate to the improvement of the welfare of domestic animals kept under intensive husbandry conditions by breeding domestic animals better adapted to life under such conditions than present day livestock.

INTRODUCTION.

i). Domestication and the behaviour of the chicken.

The domestic chicken is thought to be derived from one or all of the four species of jungle fowl endemic to S.E. Asia, and appears to have first been domesticated some five to six thousand years ago during the Neolithic period (Wood-Gush, 1959). Since first being domesticated the the chicken has been selected for a wide variety of traits encompassing virtually every aspect of its biology, with the result that the chicken is now a genetically diverse species with many morphs (strains) which differ from one another in respect of many characteristics. Yet despite this, although there are undoubtedly differences between strains of fowl in the thresholds for the release of particular behaviour patterns such as broodiness and aggression, the behavioural repertoire of the domestic chicken remains, as far as can be judged, essentially similar to that of its putative progenitors. However, within this century radical changes in poultry husbandry techniques have rendered many of these behaviour patterns redundant or inappropriate. One such set of redundant behaviour patterns, at least in the case of laying hens housed in battery cages, are the pre-laying and nesting behaviour patterns of the hen.

ii). The pre-laying and nesting behaviour of the domestic hen.

Knowledge of the pre-laying behaviour of feral fowl and fowl living under extensive conditions is scanty. There very few studies of the behaviour of ´´free-living`` fowl, and only two of these mention pre-laying and nesting behaviour. McBride et al, (1969) noted that the cockerel would often escort the hen to potential nest sites, and that having accepted a nest site the hen would throw twigs or other items of litter on to the site thereby constructing a simple nest. Duncan et al, (1978) reported that in the period before laying hens became restless and tended to distance themselves progressively from their flock mates, until finally moving off to their chosen nest sites. Beyond these observations, knowledge of the pre-laying and nesting behaviour of ´´free-living`` fowl is restricted to descriptions of the nest site, and the construction of the nest. The control and expression of pre-laying and nesting behaviour under artificial conditions has, however, been extensively studied by Wood-Gush and his co-workers at the A.R.C.`s Poultry Research Centre, and from these studies it is possible to develop a comprehensive model of the pre-laying and nesting behaviour of the domestic hen (see Wood-Gush, 1975a for a review of this subject).

In common with most gallinaceous species the nest of the domestic chicken is a simple structure, rarely more than a shallow scrape with a scanty lining of feathers or litter. However, in choosing her nest site and constructing her nest the hen exhibits a complex and well defined sequence of behaviour patterns.

The expression of this pre-laying and nesting behaviour is largely under hormonal control, and is part of a process which begins with the ovulation of the egg to be laid the following day. Following ovulation, the release of the hormones progesterone and oestrogen from the post-ovulatory follicle leads to the start of pre-laying behaviour about twenty-four hours later when the egg is normally, but not necessarily, ready to be laid (Wood-Gush, 1963; Wood-Gush and Gilbert, 1964; Gilbert and Wood-Gush, 1965; Wood-Gush and Gilbert, 1969a). The first sign of the onset of the pre-laying period is that the hen becomes restless and starts to move about more than usual, and tends to orientate herself away from her flock mates. At the same time she may start to give a characteristic pre-laying call (Wood-Gush and Gilbert 1969a). This period of restlessness is followed by a phase known as nest-examination (Wood-Gush, 1963), during which the hen moves about apparently examining potential nest sites, usually walking between these sites with a characteristic high-stepping gait (Wood-Gush, 1975a). Eventually the hen chooses a particular nest site, frequently one at which she has laid on previous occasions, and having selected the site performs a characteristic set of nest building behaviour patterns. These are:

(a) rotation:- the hen crouches, such that her keel is kept low and her tail raised, and then rotates herself simultaneously pushing her feet out backwards and sideways. If she is nesting in loose material such as wood shavings,this combination of posture and movement have the effect of scraping a hollow in the litter surrounded by a rim of displaced material, which serves as the basis of the nest.

(b) litter-tossing:- the hen picks up pieces of litter and drops them on her back, from where they tend to fall on to the rim of the nest whilst she is sitting.

Once the nest is constructed the hen tends to sit firmly, although she may from time to time rise and shuffle around a little. During the time she is sitting the hen frequently performs more litter-tossing, and a third nest building behaviour, known as litter-gathering, in the course of which she rakes litter towards herself with her bill (Wood-Gush,1975a).

(iii). The pre-laying behaviour of domestic hens housed in battery cages.

Domestic hens housed in battery cages can perform none of the behaviour patterns described above in a functional form; their choice of nest site is extremely limited, they cannot excavate a scrape in the wire floor of the cage, and they have no materials from which to construct a nest. As a consequence of this every time a hen housed in a in a battery cage ovulates she is motivated to carry out, some twenty-four hours later, pre-laying and nesting behaviour which she cannot perform, and therefore suffers the thwarting (blocking) of these behaviour patterns. This thesis is devoted to the study of the behaviour patterns shown by hens housed in battery cages, during the period when under other circumstances they would be showing pre-laying and nesting behaviour.

Wood-Gush and Gilbert, (1969b) observed that hens from two strains of domestic fowl showed marked differences in their pre-laying behaviour when confined in battery cages; hens from one strain (hereafter refered to as the S line) showed stereotyped pacing in the period before laying - a behaviour which is now known to be indicative of frustration (Duncan, 1970) - whereas hens from the other strain (hereafter refered to as the T line) typically sat during the pre-laying period. In two subsequent studies Wood-Gush, (1972 and 1975) carried out experiments, involving modifications to the battery cage, such as altering the slope of the cage floor and replacing the wire mesh floor of the cage with a solid floor covered with litter, the results of which indicated that the differences in the pre-laying behaviour of the two strains were due to differences in responsiveness to releasers for sitting behaviour. The aim of this study was to elucidate something of the ethological and genetic basis of this difference.

From a practical view point such a study is of interest because it relates to the possibility of improving the welfare of domestic animals kept under intensive husbandry conditions by breeding animals better adapted to life under such conditions. From an academic view point it is of interest because it is relevant to current theories concerning the evolutionary origins of visual displays.

(iv). The pre-laying behaviour of domestic hens housed in battery cages and the evolution of visual displays.

The connection between the pre-laying behaviour of domestic hens housed in battery cages and the evolution of visual displays lies in Tinbergen`s (1952) ``derived`` activities hypothesis which postulates that many visual displays have evolved from the behaviours shown by animals in response to motivational conflict (the simultaneous activation of two incompatible behavioural drives, such as attack and flight) and thwarting (the blocking of one particular behavioural drive, for example such as occurs when a hungry animal is presented with food it can see but cannot obtain). Although thwarting and motivational conflict may at first sight appear to be rather different phenomena, since thwarting involves the arousal of only a single tendency, whilst motivational conflict requires arousal of at least two such tendencies; animals respond to both situations in similar ways (see Manning, 1979 for a discussion of this point), and in discussing these responses I will employ the term conflict situation to describe both phenomena.

In conflict situations animals tend to show one or more of a characteristic set of behavioural responses (Hinde,1970; Manning, 1979; Lewis and Gower, 1980) which include;

(a):- intention movements: the initial phases of movements, or movement sequences of a particular behaviour pattern (Daanje, 1950).

(b). Alternation:- the alternate employment of acts representative of two competing behaviour patterns (Lewis and Gower, 1980; Wood-Gush and Guiton, 1967).

(c). ambivalence:- the combination of the intention movements or components of two incompatible behaviour patterns into a single movement. (Tinbergen, 1953).

(d). compromise behaviour:- the expression of a behaviour common to two conflicting tendencies (Andrew, 1956).

(e). Redirection:- the direction of behaviour (most frequently aggression) at substitute objects (Tinbergen, 1952 and 1959).

(f). Displacement activites:- the performance of an activity which is apparently irrelevant to the context in which it occurs and the tendencies aroused (McFarland, 1966; Tinbergen, 1952).

(g). Vacuum behaviour:- the performance of a behaviour pattern in the absence of any of the stimuli normally required for its elicitation. (Lorenz, 1935; Hinde, 1970; Tinbergen, 1952).

(h). Stereotypies:- a movement or series of movements which is repeated regularly, and which serves no apparent function. (Hediger, 1950: Morris, 1964 and 1966).

(i). Autonomic responses:- such as pilo-errection and vaso-dilation (see Manning, 1979 for a summary of the causation of such responses).

The essence of Tinbergen`s ``derived`` activities hypothesis is that interactions between animals frequently lead to conflict situations, and that during the course of evolution some of the responses shown to these conflicts have come to fulfil a communicative function. For examples; the ground pecking threat display of the male chicken appears to have been derived from displacement feeding behaviour shown in in response to a conflict between the tendencies to attack and to flee from an opponent (Feekes, 1972); and the upright threat posture of the herring gull (Larus argentatus) from the ambivalent posture adopted in response to a conflict between attack and escape (Tinbergen, 1959).

The process by which behaviour shown in response to conflict comes to fulfill a communicative function, called semanticization by Wickler, (1967), typically involves changes of two types, known respectively as ritualisation (Huxley, 1914) and emancipation (Tinbergen, 1952). Ritualisation frequently involves the exaggeration, simplification, and stereotyping of movements (Cullen, 1972), and is frequently accompanied by the aquirement of anatomical structures such as tufts, plumes, and bright colours which enhance the conspicuousness of the nascent display (Cullen, 1972). All of which serves to lessen the possibility of ambiguity in the signals, and makes them more distinguishable from signals carrying different messages (Cullen, 1966). Emancipation involves changes in the neurophysiological mechanisms controlling the expression of the behaviour patterns of the nascent display, affecting the thresholds for their release, and making their expression less dependent on the factors originally underlying them and more dependent on the context in which the display occurs (Tinbergen, 1952).

The evidence in support of the ´´derived activities`` hypothesis comes from three sources. These are;

a). The similarity between the motor patterns of many displays and the conflict behaviour from which they are thought to have been derived (see Tinbergen, 1952 for examples).

b). In some cases the expression of a display can be influenced by the presence or absence of the stimuli originally associated with the release of the conflict behaviour from which it was derived. For example, in agonistic encounters hungry domestic cocks ground peck more frequently in the presence of food than they do in its absence, or when satiated (Feekes, 1972).

c). Comparative studies of the behaviour of closely related species which show the stages in which an original conflict behaviour shown by a phylogeneteically primitive species has become modified, through the processes of ritualisation and emancipation, to serve as a display in more advanced species. For example male zebra finches show displacement bill wiping during courtship. In the related striated finch however this behaviour appears to have been elaborated into a ritualised courtship bow (Morris, 1958).

However, although these arguments are convincing in themselves, one fundamental premise of the derived activities hypothesis - the existence of genetic variation in the behavioural responses shown in conflict situations, upon which natural selection could act so as to modify them to function as displays - has not yet been substantiated. However, as mentioned above domestic hens confined in battery cages show considerable variability in their behavioural responses to the thwarting of their normal pre-laying and nesting behaviour. Demonstration that this variability is at least to some degree under genetic control - the aim of this study - would therefore further substantiate the ´´derived`` activities hypothesis.

(v). The relevance of pre-laying behaviour in battery cages to the improvement of animal welfare.

That hens should exhibit stereotyped pacing in the period before laying when confined in battery cages is undesirable on two counts. From an economic view point it is undesirable because it involves unneccesary expenditure of energy, which may inturn lead to increased food consumption (Wood-Gush, 1972). In terms of the birds` welfare it is undesirable since the behaviour pattern is indicative of the birds being frustrated (Duncan, 1970), and increases the possibility of their suffering abrasions as a consequence of coming into contact with the cage sides.

The occurence of stereotyped pacing in the period before laying has been reported by several authors (e.g. Brantas, 1980; Duncan, 1970; von Heil et al, 1982; and Wood-Gush, 1969), and is currently considered to be a major welfare problem (Hughes, pers. comm.). Setting aside abolishing the use of the battery cage for the housing of domestic hens and replacing it with some alternative husbandry system, two solutions to this problem exist. These are; either to modify the design of of battery cages so as to incorporate stimuli which elict sitting behaviour; or alternatively to breed strains of birds (like the T line) which do not exhibit stereotyped pacing in the period before laying (Wood-Gush, 1972). This study will hopefully shed light on the practicality of selecting against stereotyped pacing during the pre-laying period on a commercial scale.

Chapter 2. General materials and methods.

(I) The animals.

All the animals used in this study (with twelve exceptions - see chapter 11.) were members, or were the descendents of an original population of thirty-one S strain birds (nine males and twenty-two females) and forty T strain birds (twelve males and twenty-eight females). The S strain is a light strain originally derived from White Leghorn stock. The T strain is a medium light strain originally derived from a Rhode Island Red x Light Sussex cross. These two strains, which were originally obtained from commercial suppliers, have been maintained as closed populations at the A.R.C. Poultry Research Centre, Roslin, Midlothian for over 12 years, and are descendents of birds from the strains used by Wood-Gush (1972) in his study of strain differences in the pre-laying behaviour of domestic fowl housed in battery cages.

(II) Breeding of animals.

With the exception of the original population of seventy one birds and the twelve birds mentioned above, which were drawn from the Poultry Research Centre`s stocks and whose genetic lineage can only be traced back to the dam, all the animals used in this study were obtained from matings between known pairs of males and females, and their pedigrees can be traced back over one or two generations. Full details of pedigrees are given in Appendix 3.

Each breeding pair was housed in a top tier cage of a commercial three tier battery cage system measuring 54 (h back), 61 (h front) X 123 (w) X 46 (d) cm. Food and water were available *ad* *libitum*. Temperature in the poultry house in which the cages were located was thermostatically controlled. The photo-period was 14L : 10D.

Seven to fourteen days after the males had been introduced to the females, a number of eggs were collected from each female, and their fertility assessed using the ´´agar flake staining technique`` (full details of this technique are given in Appendix 2). If at this time, any female was laying only infertile eggs, her mate was ´´milked`` using the technique described by Lake, (1957) in order to determine whether or not he was producing semen. If the male was producing semen, artificial insemination was used to fertilise the female (see Anon., 1973, for technique). If the male was infertile he was replaced with another male.

Once all the females were laying fertile eggs, eggs were collected for incubation. On collection each egg was marked, in indelible ink, with the identities (wing band numbers) of the sire and dam. The eggs were then stored under refrigeration until seven to fourteen eggs had been collected from each female. At this point the eggs were set and incubated. The eggs were candled at periodic intervals during incubation, and infertile eggs or eggs containing dead embryons removed. On day eighteen of incubation the remaining viable eggs were transferred to a ´´hatcher`` incubator, the eggs from each mating being placed in separate isolated sections of the incubator, and left until day twenty-one of incubation when the chicks hatched.

When it was considered that sufficient eggs had been collected from each mating, the male and female were separated. If the female was to be used in a subsequent mating she was returned to her home cage and kept ´´celibate`` for twenty-one days . Birds which were not required for further matings or other purposes were culled. In the case of hens required for subsequent crossings, separation of matings by twenty-one days was necessary because the sperm of domestic fowl remain capable of fertilising eggs for up to fourteen days following ejaculation by the male (Lorenz, 1954), and are ´´stored`` by the hen in ´´sperm nests`` in the infundibulum of the oviduct (Parker, 1931). Therefore two to three weeks must elapse before it can be assumed safely that stores of sperm from previous matings have been exhausted, or that the sperm from these matings have become inviable.

(III) Husbandry. Animals less than sixteen weeks of age.

On the day of hatching each chick was wing-banded. Its wing band number was then recorded together with its genotype (S line, T line, F1 etc.), the identities of its sire and dam, and its hatch date. The chicks were then sexed by examination of the genital eminence (see Blount, 1945 for a description of the technique used). Male chicks surplus to requirement for the breeding of subsequent generations were then culled.

After sexing, the chicks were randomly divided into mixed sex groups of between thirty and forty. Each group of chicks was then transfered to a compartment of an ´Eltex` battery brooder, measuring 33 (h) X 96 (w) X 42 (d) cm. Food and water were available *ad libitum*. The photo-period was 14L : 10D. The temperature in the brooder was regulated by thermostatic control.

At three weeks of age when the chicks no longer required ´´brooding`` they were transferred to pens measuring 154 (w) X 215 (d) cm. Each pen contained between thirty and forty chicks. The pens had solid plywood sides to a height of 1m, with wire mesh above, and had wood shavings on the floor. The temperature in the poultry house in which the pens were located was thermostatically controlled. Food and water were available ad libitum. The photo-period was 14L : 10D.

All the animals were vaccinated against Marek´s disease when one day old, and against Newcastle disease at twenty-one days and one hundred and twelve days old.

(IV) Husbandry. Animals over sixteen weeks of age.

At sixteen weeks of age the birds were transferred from pens to individual cages in a three tier battery cage system. Females were housed in cages on the middle or bottom tiers of the battery, measuring 46 (h, back), 54 (h, front) X 31 (w) X 46 (d) cm. Males were housed in cages on the top tier of the battery, measuring 54 (h, back), 61 (h, front) X 31 (w) X 46 (d) cm. Within these limitations, the animals were assigned to cages at random. These cages were the animals´ home cages and they lived in them throughout the course of this study unless being used for breeding. Food and water were available ad libitum. Food (the P.R.C.`s layers mash) was available from troughs located at the front of the cage. Water was available from ´nipple` drinkers located at the back of the cage. Each bird had neighbours in at least two of the three cages adjacent to its home cage, and most birds had neighbours in all three of the adjacent cages. The poultry house in which the battery cages were located was artificially illuminated. The photo-period was 14L : 10D. Temperature in the poultry house was thermostatically controlled.

(V) Observation of pre-laying behaviour.

All the animals were observed when between twenty-six and fifty-two weeks of age. The observer, who was in full view of the birds, sat approximately 1 m. in front of the cage of the bird under observation. All observations were made within eight hours of ´dawn` (lights on) in the poultry house.

The major difficulty associated with making observations of the pre-laying behaviour of domestic fowl is determining at what time of day a given bird will lay. Domestic hens lay eggs in clutches of variable numbers, each clutch normally being separated by one or two resting (non-laying) days. Even within a clutch the time of day at which each egg is laid is not constant from day to day. The time interval, by which two successive eggs in a clutch differ from twenty-four hours (which is known as the ´lag`, Gilbert and Wood-Gush, 1964), is affected by at least three different factors. These are;

(a). The number of eggs in the clutch. The lag is usually positive (i.e. greater than twenty-four hours) but tends to regress towards zero as the number of eggs in the clutch increases; and if the number of eggs in the clutch is very large it may be negative (i.e. less than twenty-four hours) - Heywang (1938).

(b) The position (1st, 2nd, 3rd, etc.) of the egg in the clutch. Eggs laid early in a clutch tend to be separated by greater lag times than eggs laid in the middle of, or towards the end of a clutch, with the exception of the last egg which is usually separated from the penultimate egg by a long positive lag - Heywang (1938).

(c) Variability between individuals. Given hens, even when laying clutches of similar length, may vary considerably in their lag times (personal observation).

This variability in lag times means that it is impossible to predict, with any great accuracy, when a hen is likely to lay on a given day. The best that can be achieved is an approximate estimate based on a record of laying times on previous days. In this study, a daily record of laying times (accurate to the nearest hour) was kept for all the hens, from the time they came into lay until they had been scored for pre-laying pacing and sitting. On the day that a bird was to be observed, its expected time of lay was estimated from its previous laying history, and observations commenced approximately thirty minutes before the expected time of lay. This method although generally satisfactory was far from perfect since many potential observations were lost because birds laid earlier than expected, and much time was wasted because hens laid considerably later than expected.

(VI) Measurement and quantification of pre-laying pacing and sitting.

Wood-Gush (1972) quantified the expression of pre-laying pacing and pre-laying sitting by counting the number of paces taken and the proportion of time spent sitting in the hour prior to laying. Preliminary observations made during the early stages of this investigation showed that the expression of both pacing and sitting tended to peak in the fifteen minutes or so prior to laying (see figures 12a, 12b, and 12c, and the discussion of this phenomenon in Chapter 12), and that the differences between the S and T lines in the expression of these two traits could be demonstrated on the basis of the birds` behaviour during the ten minutes prior to laying (see Chapter 5). Accordingly, in this study the expression of pre-laying pacing was quantified by calculating the average number of paces taken per minute in the ten minutes before laying (total number of paces taken, divided by ten), and the expression of pre-laying sitting by calculating the proportion of time spent sitting in the same ten minute period (total sitting time divided by total observation time). One pace was scored every time the bird lifted and lowered its foot from and to the floor of the cage; with the exception of such movements performed in the course of body scratching, food scratching, making nesting scrapes or jumping at the sides of the cage (see chapter.3). For a bird to be classified as sitting it had to adopt a posture such that the hocks were fully retracted against the body, and the shanks held parallel to the floor of the cage.

Reducing the required observation time from the one hour used by Wood-Gush, (1972) to the ten minutes used in this study has three advantages. These are :-

(a) The potential number of birds which can be scored on one day is greatly increased. This is of importance since for the purposes of a study in behavioural genetics it is desirable that as many animals as possible be scored at similar ages.

(b) Since it is not possible to predict exactly when a bird will lay, it is almost inevitable that some birds will lay within the required observation time and that the data collected will be valueless. With an observation period of ten minutes, if this does happen, little time and effort has been wasted. With an observation period of one hour the potential wastage is considerable.

(c) Because the expression of pre-laying pacing and pre-laying sitting tends to reach a peak in the fifteen minutes or so before laying (see chapter. 12), casual observations of the birds' behaviour can be used as a short-term predictor of their likely time of lay. This is of considerable value when attempting to assess the order in which birds expected to lay at similar times should be scored.

The number of paces taken and the amount of time spent sitting by each animal was recorded by direct observation (see (V) above) using an event recorder. Two types of event recorder were used during the course of this study. These were: a four channel Rustrak event recorder (model no. 92), and a twenty channel Esterline Angus event recorder (model no. A620). The chart speed of each machine was known and constant:- 1`` per minute in the case of the Rustrak, and 0.75`` per minute in the case of the Esterline Angus. The amount of time spent sitting was recorded on a single channel, continuous deflection of the pen representing a period of time spent sitting. The number of paces taken was recorded on three channels, one discrete pen deflection representing one pace. Use of more than one channel to record the number of paces taken was necessary because the rate at which paces were taken frequently exceeded the key recovery time of both machines. At the end of each observation period, ie. at the time at which the bird layed, the chart was marked with a particular combination of pen deflections and labelled with the bird´s wing band number.

At the end of each day´s observations the record chart was removed from the event recorder and divided up into sections representing the observations of each bird. The proportion of each tape representing the ten minutes before laying was then identified, and the number of steps taken and proportion of time spent sitting in this period calculated. Obviously, if information about the time spent sitting in excess of the ten minutes before laying was required, it could be obtained by reference to the appropriate portion of the event recorder tape.

Statistical analysis of results.

Many of the data collected in this study were not normally distributed about their respective means, because of this I have as far possible avoided the use of parametric statistics in the analysis of results and have relied on non-parametric tests. Further in preparing figures comparing the expression of pre-laying pacing and pre-laying sitting between various genotypic types I have shown not only the means scores of each type but also their median scores.

Chapter 3. Qualitative descriptions of pre-laying behaviour in battery cages.

Introduction.

In this chapter I make qualitative descriptions of the pre-laying behaviour patterns which are characteristic of hens from the Poultry Research Centre`s S and T lines, when housed in battery cages. It is not my intention at this point to make rigorous definitions of pre-laying behaviour patterns for use in quantitative analyses - these will be given in subsequent chapters as and when is appropriate - but rather to provide an overview of pre-laying behaviour in battery cages, and to develop a system of nomenclature for these behaviour patterns which will be used consistently throughout this thesis. In developing this system of nomenclature I have, whenever possible employed the terminology used by Kruijt (1964), Morris (1956), and Wood-Gush (1955, 1971, and 1975a).

Materials and methods.

The observations described here were made incidentally whilst scoring S and T line hens for the expression of pre-laying pacing and pre-laying sitting. The birds were housed in individual battery cages located on the middle or bottom tiers of a three tier battery cage system. Each bird had neighbours in at least two of the three cages adjacent to its own, and most birds had neighbours in all three adjacent cages. Full details of the birds` histories and husbandry conditions are given in Chapter 2. Observation periods were of variable duration because of the difficulties associated with predicting exactly when a bird would lay (see Chapter 2 for a full discussion of this point). No observation period had a duration of less than ten minutes, and many were in excess of several hours.

Results. Qualitative descriptions of pre-laying behaviour in battery cages.

In both the S and T lines the onset of pre-laying behaviour is frequently marked by a phase during which the hen stands still, sometimes giving the impression of being disturbed or nervous. Hens in this phase will normally adopt one of three postures. These are:
(i) The relaxed standing posture (figure 3a.), in which the plumage is relaxed, the neck partially extended, and the legs slightly bent.
(ii) The hunched standing posture (figure 3b.), in which the plumage is ruffled, the neck fully retracted, and the legs bent in a manner such that the hocks are held close against the body.
(iii) The alert standing posture (figure 3c.) (Kruijt 1964), in which the neck is extended almost vertically, the plumage is sleek, and the legs held almost straight. The alert posture is usually adopted from one of the other two postures in response to sudden noises or movements, and is often accompanied by scanning of the surroundings with short jerky movements of the head.

Hens adopting these postures maintain them for variable periods of time, which may be as brief as a matter of seconds or as long as several minutes. The standing phase is terminated by the hen becoming increasingly restless and starting to move about the cage more than is usual. At the same time she may start to give a particular pre-laying call, which Wood-Gush and Gilbert (1969a), describe as sounding like ´´qwa-a-a-a``, when given at high intensity and ´´qwa-qwa-qwa`` when given at low intensity.

The hen`s general restlessness gradually gives way to a phase which appears to correspond to the phase called ´´nest-examination`` by Wood-Gush (1963), in his treatise on the nesting behaviour of domestic fowl housed in pens, since many of the behaviour patterns described by Wood-Gush (ibid.) as being characteristic of hens in the ´´nest-examination`` phase are also shown by birds in cages at this time.

During this phase the bird moves about her cage, apparently examining the cage corners and sides, usually walking with a high stepping gait, her neck stretched out horizontally (figure 3d.), or with her neck and body held at an acute angle to the floor (figure 3e.). She may also appear to examine the roof of the cage by raising her keel up high and extending her neck vertically, usually resting one foot on the side of the cage (figure 3f.). From time to time she will also adopt this posture in order to put her head over the division between her own cage and an adjacent one giving the impression that she would like to ´escape` from her own cage.

It is at the end of this ´´nest-examination`` phase that the differences in the pre-laying behaviour of S and T line hens become manifest. Towards the end of the ´´nest-examination`` phase T line hens, typically alternate exploratory behaviour with brief periods of sitting, and as time progresses the duration of these periods of sitting gradually increases until the bird is sitting almost continually. In the case of S line birds however, the end of the ´´nest-examination`` phase is marked not by an increasing tendency to sit, but by an increase in locomotor activity which ultimatly develops into stereotyped escape behaviour.

During the period she is sitting, a hen may adopt any one of three postures. These are;

(i) The relaxed sitting posture (figure 3g.), in which the hen sits with her neck retracted in a manner such that her head is held slightly above the level of her body, and her wings held down and forward. The plumage is usually relaxed.

(ii) The slouched sitting posture (figure 3h.). This posture differs from the relaxed sitting posture only in the position of the head, which is lowered below the level of the body. Occasionally a bird adopting this posture will rest its head on the floor of the cage.

(iii) The alert sitting posture (figure 3i.), in which the bird sits with its neck extended almost vertically. The plumage is sleek, and the wings held in their normal folded position. Like the alert standing posture, the alert sitting posture is usually adopted in response to environmental disturbance, and is usually accompanied by scanning of the environment.

From time to time, birds adopting the relaxed or slouched sitting postures exhibit waves of feather raising during which the erection of the dorsal plumage varies between being relaxed and fluffed.

The stereotyped escape behaviour, which is characteristic of S line hens, consists of continuously-repeated pacing, back and forth along one or more sides of the cage; which may be accompanied by jumping at the sides of the cage, attempts to climb over the partitions between the home cage and adjacent cages, and attempts to squeeze through the bars of the cage front. Sometimes a hen will pace ´´on the spot``, repeatedly showing the intention movements of starting to move off in one direction and then apparently ´´change her mind``, and turning round as if to move off in the opposite direction. The expression of these escape movements tends to increase in intensity as the point of lay approaches (see Chapter 12 for a discussion of this point).

During the pre-laying period both S and T line hens may exhibit nest-building behaviour. This nest-building behaviour manifests itself in the expression of three behaviour patterns, all of which are described by Wood-Gush (1975a). These are:

(i) Rotation (figure 3j.). The hen adopts a characteristic ´´keel down-tail up`` posture, such that her keel forms an acute angle to the floor, her rump is raised, and her chest is in contact with the floor. After adopting this posture she rotates herself through an angle of 90 degrees or more, often at the same time making scraping movements with her legs (see ii. below).

(ii) Scraping (figure 3k.). The hen adopts the ´´keel down-tail up`` posture or half crouches, and then pushes her feet out backwards and sideways.

(iii) Litter-gathering (figure 3l.). Litter-gathering is performed either when the hen is sitting or half crouching. The hen extends her neck so that her head is moved down and forwards. She then retracts her neck so that her head is drawn back towards her body, with her bill slightly above or just making contact with the floor of the cage. This series of movements is usually performed very quickly several times in succession.

In pens with wood-shavings on the floor, these nest-building movements are used to excavate a shallow hollow in the litter, surrounded by a rim of displaced material which constitutes the nest (Wood-Gush 1975a). In the battery cage they have no functional value, and since they occur in the absence of the appropriate environmental stimuli may be regarded as **examples of** vacuum activities (Lorenz, 1935; Tinbergen, 1951).

At the time of laying, S and T line hens will almost invariably adopt one of two postures. These are:

(i) The upright or ´´penguin`` posture (figure 3m.). The bird completely retracts its neck, straddles its legs, and by swinging its head and keel up and backwards brings its body into an upright position. This results in the opening of the cloaca being positioned vertically above the floor of the cage. The plumage surrounding the vent is erected so as to be held clear of the vent. (ii) The squat or hunched posture (figure 3n.). In this posture the neck is retracted, the head is held back and above the level of the body, the keel is slightly raised, the legs are held with the hocks close against the body and the shanks in contact with the floor of the cage. The feathers of the nape are usually fluffed, and the plumage of the vent region is erected so as to be held clear of the cloaca. All of this results in the hen having a short or hunched appearance.

In addition to the behaviour patterns described above, both S and T line hens may exhibit feeding, drinking and grooming behaviour during the pre-laying period. No descriptions of these behaviour patterns are given here, since they have already been described in detail by Kruijt (1964), Duncan (1980b), and Wood-Gush (1955 and 1971). Feeding and grooming occur frequently, but are usually shown in bouts of short duration. Drinking, however, may occupy a substantial part of a hens time, some birds spend considerable periods of time drinking immediately prior to laying (see also chapter 8).

Another behaviour pattern which is shown frequently during the pre-laying period is head-shaking (sometimes called head-flicking). Head-shaking, which involves rapidly repeated movements of the head from side to side (Kruijt, 1964) is usually performed by birds adopting the alert standing or alert sitting postures. and may be shown at any time during the pre-laying period. There is however a tendency for the frequency of head-shaking to decrease as the point of lay approaches (personal observation, B.O. Hughes, pers.

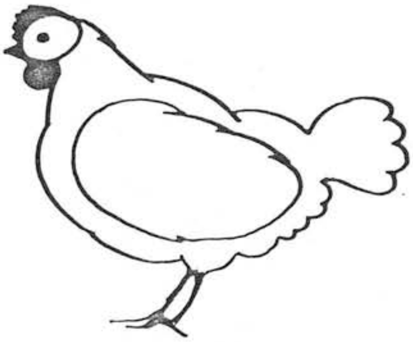
comm.).

Post-laying behaviour may involve standing in the alert posture, and cackling (Wood-Gush 1971) ; and, if the egg has not rolled out of the cage, egg rolling (Wood-Gush 1975a). During egg rolling (figure 3o.) the hen stands with her head upside down, her comb sometimes in contact with the floor of the cage and set at right angles to her body, so as to hook her bill around the egg, and then rolls the egg towards her breast. There is however considerable inter-individual variability in the expression of both cackling and egg rolling ; many birds do not exhibit cackling, and many will ignore their egg even if it does not roll from the cage.

Figure 3a (top). The relaxed standing posture.

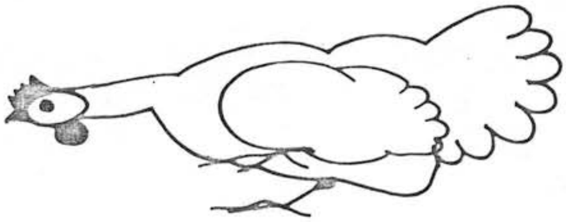
Figure 3b (middle). The hunched standing posture.

Figure 3c (bottom). The alert standing posture.



Figures 3d (top) and 3e (middle). Postures adopted by the hen when walking with a high stepping gait during nest-examination.

Figure 3f (bottom). Posture adopted by the hen when apparently investigating the roof of the cage during nest-examination.



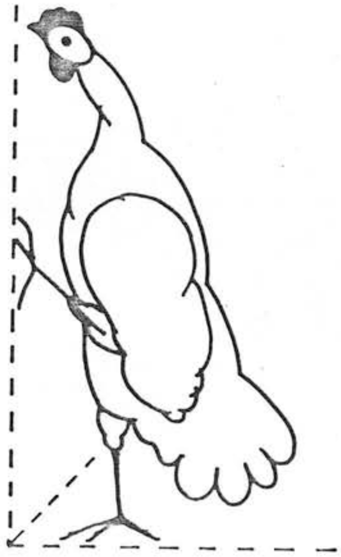


Figure 3g (top). The relaxed sitting posture.

Figure 3h (middle). The slouched sitting posture.

Figure 3i (bottom). The alert sitting posture.

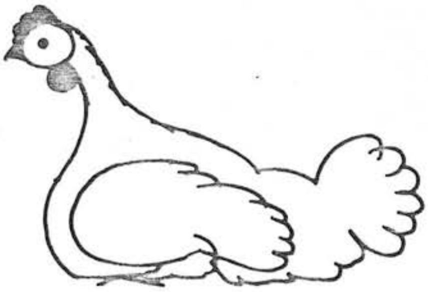
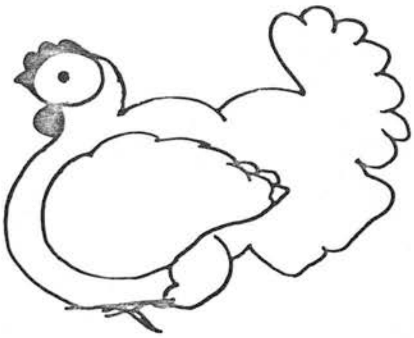


Figure 3j (top). The ´´keel down-tail up`` posture adopted by the hen during rotation.

Figure 3k (bottom). The posture and movements of scraping.



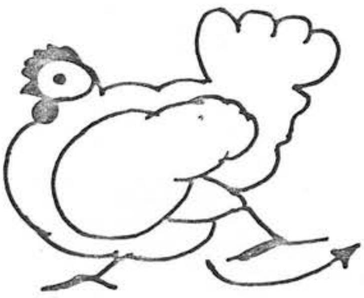


Figure 31. The movements of litter-gathering.

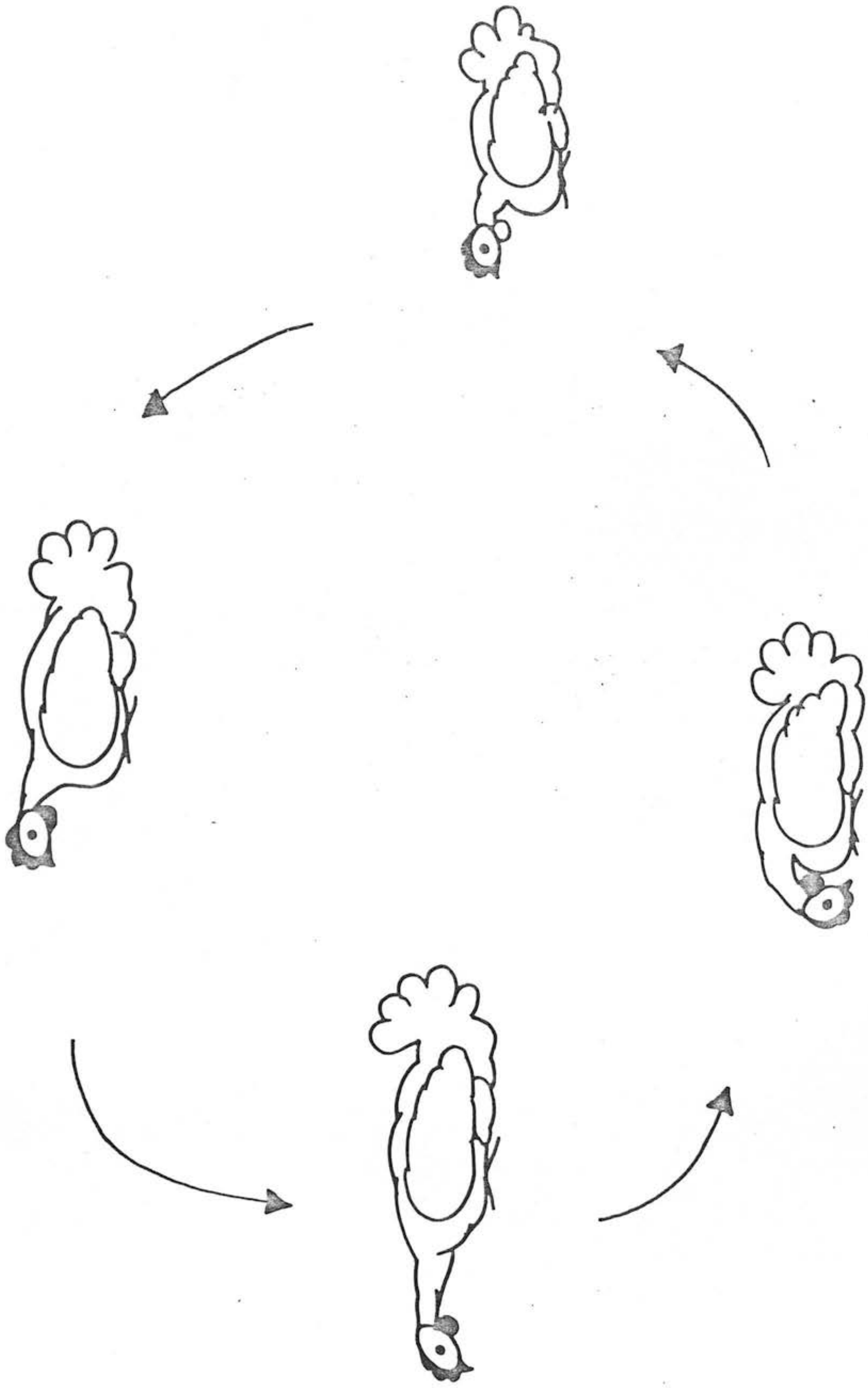
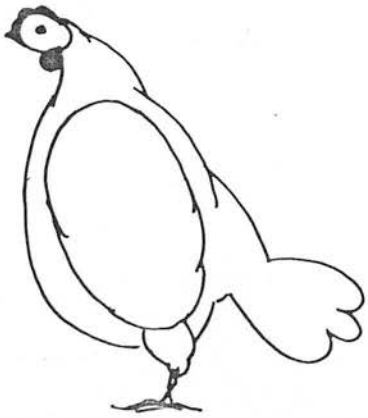
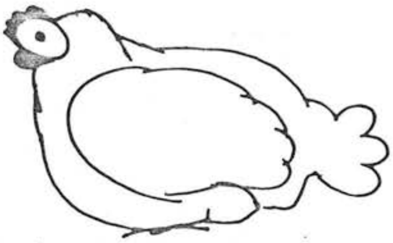


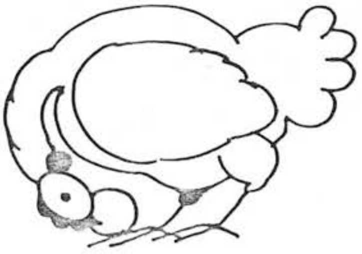
Figure 3m (top). The upright or ´´penguin`` laying posture.

Figure 3n. (middle). The squat or hunched laying posture.

Figure 3o (bottom). The posture adopted during egg rolling.







Chapter 4. Genetic analysis of pre-laying pacing and pre-laying sitting. I. Individual consistency in pre-laying pacing and pre-laying sitting.

Introduction.

As the pre-laying behaviour of the hen is repeated every time the bird lays, before attempting to investigate the genetics of pre-laying pacing and pre-laying sitting, it is necessary to obtain an estimate of the magnitude of the contribution of the within-individuals components of variance to the total phenotypic variance of each of these two traits. Since, if the within individuals component of variance is high, then each animal must be scored several times before an accurate assessment of its true phenotypic value can be made; whereas if the within individuals component of variance is low, making multiple measurements achieves little gain in accuracy, and wastes considerable time and effort.

The aim of the experiments described here was to obtain separate estimates of the within individuals component of variance of pre- laying pacing and pre-laying sitting by investigation of the degree of individual consistency in the expression of the two traits.

Experiment 4(i). The correlation between paired individual scores on two days, for pre-laying pacing and pre-laying sitting, respectively.

Materials and methods.

Twelve S strain and thirteen T strain hens, selected at random from the original population of fifty hens, were scored for the expression of pre-laying pacing and pre-laying sitting. Husbandry and scoring methods were as described in chapter 2. All animals were scored within a three month period.

Within strains correlations between the two scores for pacing, and the two scores for sitting were computed using the Spearman rank correlation coefficient (r_s), as described by Siegel, (1956).

Results.

The correlations between paired scores for pacing are shown in table 4(a)., and the correlations between paired scores for sitting in table 4(b). The raw data are presented in tables 4.i., 4.ii., 4.iii., and 4.iv. of appendix 1.

Experiment 4(ii). The repeatability of pre-laying pacing and pre-laying sitting.

Five S strain birds and five T line birds, selected at random from the original population of fifty hens, were each scored five times for the expression of pre-laying pacing and pre-laying sitting. Husbandry and scoring techniques were as described in chapter 2. Within strains repeatabilities for each trait were then calculated according to the formula:

$$r = \frac{\sigma^2_b}{\sigma^2_b + \sigma^2_w} \qquad \text{(Falconer, 1964)}$$

where r = repeatability

σ^2 b = the between individuals component of variance

σ^2 w = the within individuals component of variance

The between and within individuals components of variance were estimated from the results of an analysis of variance, as described by Snedecor,(1956).

Results.

Analyses of variance of scores for pre-laying pacing and pre-laying sitting in the S and T lines are shown in tables 4c., 4d., 4e., and 4f., respectively. Between individuals and within individuals components of variance, and repeatabilities for pre-laying pacing are shown in table 4g. Between individuals and within individuals components of variance, and repeatabilities for pre-laying sitting are shown in table 4h. The untreated data are shown in tables 4.v., 4.vi., 4.vii., and 4.viii. of appendix 1.

Discussion.

The high values of the between scores correlations , and repeatabilities for both pre-laying pacing and pre-laying sitting show that, in respect of these two traits at least, S and T line hens show relatively little variation in their pre-laying behaviour between successive ovipositions and that the contribution of the within individuals component of variance to the total phenotypic variance of either trait is small. Given this it is justifiable, when carrying out investigations into the genetics of pre-laying pacing and pre-laying sitting, to base individual phenotypic values for either trait on measurements made during observation of a single oviposition, since making multiple measurements will achieve little gain in accuracy. Accordingly, throughout the course of this study individual scores for pre-laying pacing and pre-laying sitting were based on observations of a single oviposition.

One further point which arises from these findings is the question, why are individual birds so consistent in their pre-laying behaviour? Discussion of this matter is left to chapter 12.

TABLE 4a. Spearman rank correlation coefficients (rs) between paired scores for pre-laying pacing on two occasions.

Strain	rs	p
S	0.86	<0.01
T	0.77	<0.01

Table 4b. Spearman rank correlation coefficients (rs) between paired individual scores for pre-laying sitting on two occasions.

Strain	rs	p
S	0.84	<0.01
T	0.90	<0.01

Table 4c. Analysis of variance of scores for pre-laying pacing of each of five S strain birds on five occasions.

SOURCE OF VARIATION	SUM OF SQUARES	DEGREES OF FREEDOM	MEAN SQUARES
Between individuals	1454.19	4	363.55
Within individuals	0381.73	20	19.09
Total	1832.92	24	

Table 4d. Analysis of variance of scores for pre-laying pacing of each of five T line birds on five occasions.

SOURCE OF VARIATION	SUM OF SQUARES	DEGREES OF FREEDOM	MEAN SQUARES
Between individuals	3187.28	4	796.82
Within individuals	740.30	20	37.82
Total	3927.58	24	

Table 4e. Analysis of variance of scores for pre-laying sitting of each of five S line birds on each of five occasions.

SOURCE OF VARIATION	SUM OF SQUARES	DEGREES OF FREEDOM	MEAN SQUARES
Between individuals	0.6571	4	0.1643
Within individuals	0.1254	20	0.0063
Total	1.6957	24	

Table 4f. Analysis of variance of scores for pre-laying sitting of each of five T strain birds on five occasions.

SOURCE OF VARIATION	SUM OF SQUARES	DEGREES OF FREEDOM	MEAN SQUARES
Between individuals	1.4205	4	0.3551
Within individuals	0.2752	20	0.0138
Total	1.6957	24	

Table 4g. The between individuals (σ^2 b) and within individuals (σ^2 w) components of variance , and repeatability of pre-laying pacing.

STRAIN	σ^2b	σ^2w	REPEATABILITY
S line	68.74	19.09	0.78
T line	151.96	37.02	0.80

Table 4h. The between individuals (σ^2 b) and within individuals (σ^2 w) components of variance, and repeatability of pre-laying sitting

STRAIN	σ^2b	σ^2w	REPEATABILITY
S line	0.0316	0.0063	0.8338
T line	0.0683	0.0138	0.8319

Chapter 5. Genetic analysis of pre-laying pacing and pre-laying sitting. II. Between and within strains variance in the expression of pre-laying pacing and pre-laying sitting.

Introduction.

Although it is clear from the findings of Wood-Gush (1969 and 1972), and Wood-Gush and Gilbert (1969b), that there are marked strain differences between the S and T lines in the expression of pre-laying pacing and pre-laying sitting, it is also clear, both from the data presented by these authors and from the results presented in chapter 4 of this thesis that there is considerable variation within the S and T lines in the expression of the two traits.

The aims of the experiment described in this chapter were, firstly - to investigate the extent of the behavioural divergence with respect to pre-laying pacing and pre-laying sitting, between the S and T lines, and secondly - to obtain an indication of the magnitude of the differences between individuals within each of the two strains in the expression of these two traits.

Materials and Methods.

Twenty-two S line hens and twenty-eight T line hens were each scored for the expression of pre-laying pacing and pre-laying sitting. These animals were drawn at random from the Poultry Research Centre`s stocks, and together with their male sibs constituted the original population of animals from which all but twelve of the animals used in this study were descended (see Chapter 2.). Husbandry and scoring techniques were as described in Chapter

2.

Between-lines comparisons of the expression of pacing and sitting respectively, were made using the Mann-Whitney U test (two tailed), as described by Siegel, (1956). Within strains, distributions of scores for pacing and sitting were prepared as scattergrams (Lehner, 1979) of individuals` scores for pacing plotted against their scores for sitting. Scores for sitting were plotted on the abscissa, scores for pacing on the ordinate.

Results.

During the ten minutes before laying, S line hens (when the two strains were each considered collectively) paced significantly more than T line hens and spent considerably less time sitting. The mean (+/- S.E.) number of paces taken per minute by S line hens was 27.76 +/- 4.34 compared to the 6.64 +/- 2.30 taken by T line hens ($p < 0.001$; Figure 5a.). The mean (+/- S.E.) proportion of time spent sitting by S line hens was 0.18 +/- 0.05 compared to the 0.55 +/- 0.09. of T line hens ($p < 0.001$; Figure 5b.).

However, as can be seen from figures 5c and 5d, which show the distributions of scores for pre-laying pacing and pre-laying sitting in the S and T lines respectively, there was considerable variation in the expression of the two traits within both strains. S line hens varied considerably in the number of paces taken per minute, and T line hens in the proportion of time spent sitting. Further, there were some S line birds which sat, some T line birds which paced, a number of birds in both strains which exhibited only low levels of both behaviour patterns, and in the S line a number of birds which sat for quite substantial periods but also exhibited pacing behaviour.

The scores for pacing and sitting of the S and T line birds, from which Figures 5a., 5b., 5c., and 5d. were compiled are shown in Tables 3.i. and 3.iv. of appendix 3.

Discussion.

The findings presented in this chapter have at least two implications. These are :-

i) Although there are significant differences between the S and T lines in the expression of pacing and sitting, (i.e.: most S line birds pace and do not sit, most T line birds sit and do not pace) there is considerable within-strains variation in the expression of both traits, and there is a degree of overlap between the two strains in their expression. Given this, and the considerable within-strain variation in the expression of both pacing and sitting, if there is genetic variation in the expression of these traits, it should be possible to increase the behavioural divergence between the S and T lines by selecting for pacing in the S line and sitting in the T line. This hypothesis is tested in Chapter 6.

ii) Pacing and sitting are not mutually exclusive. Clearly, a bird which paces throughout the pre-laying period cannot sit, and vice-versa, but it is possible for a bird to spend part of its time pacing and part of its time sitting.. Further, it is possible for a bird to show neither behaviour pattern. These points are discussed in detail in Chapter 12.

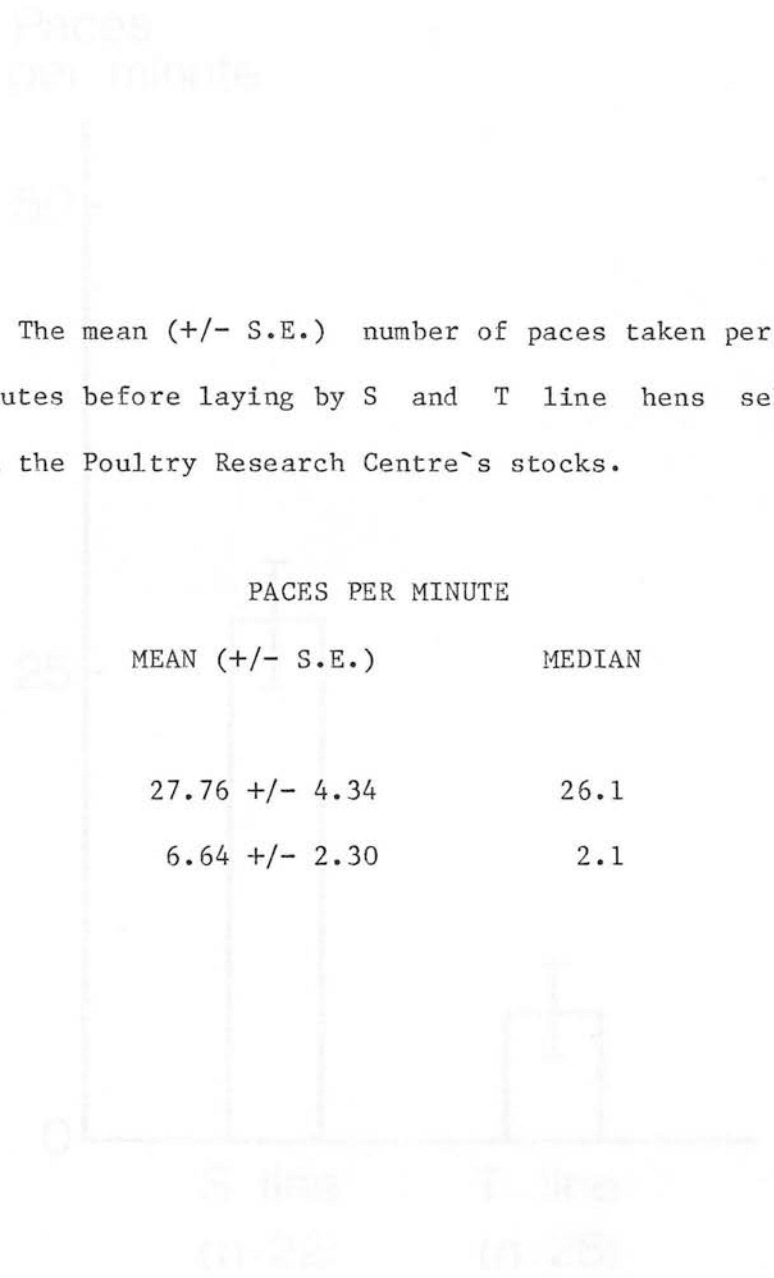


Figure 5a. The mean (+/- S.E.) number of paces taken per minute in the ten minutes before laying by S and T line hens selected at random from the Poultry Research Centre`s stocks.

LINE	PACES PER MINUTE	
	MEAN (+/- S.E.)	MEDIAN
S	27.76 +/- 4.34	26.1
T	6.64 +/- 2.30	2.1

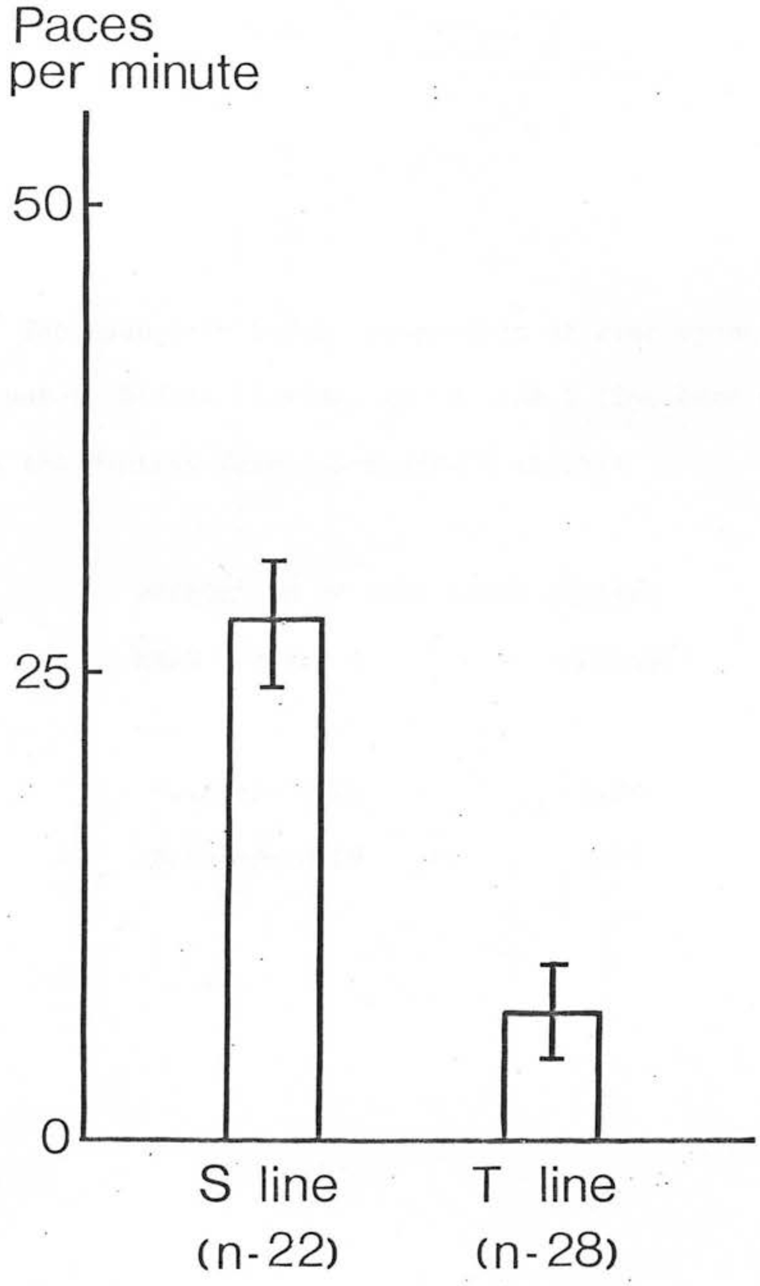

Paces
per minute
50
25
0
S line
(n-22)
T line
(n-28)

Figure 5b. The mean (+/- S.E.) proportion of time spent sitting in the ten minutes before laying by S and T line hens selected at random from the Poultry Research Centre`s stocks.

LINE	PROPORTION OF TIME SPENT SITTING	
	MEAN (+/-S.E.)	MEDIAN
S	0.18 +/- 0.05	0.08
T	0.55 +/- 0.09	0.77

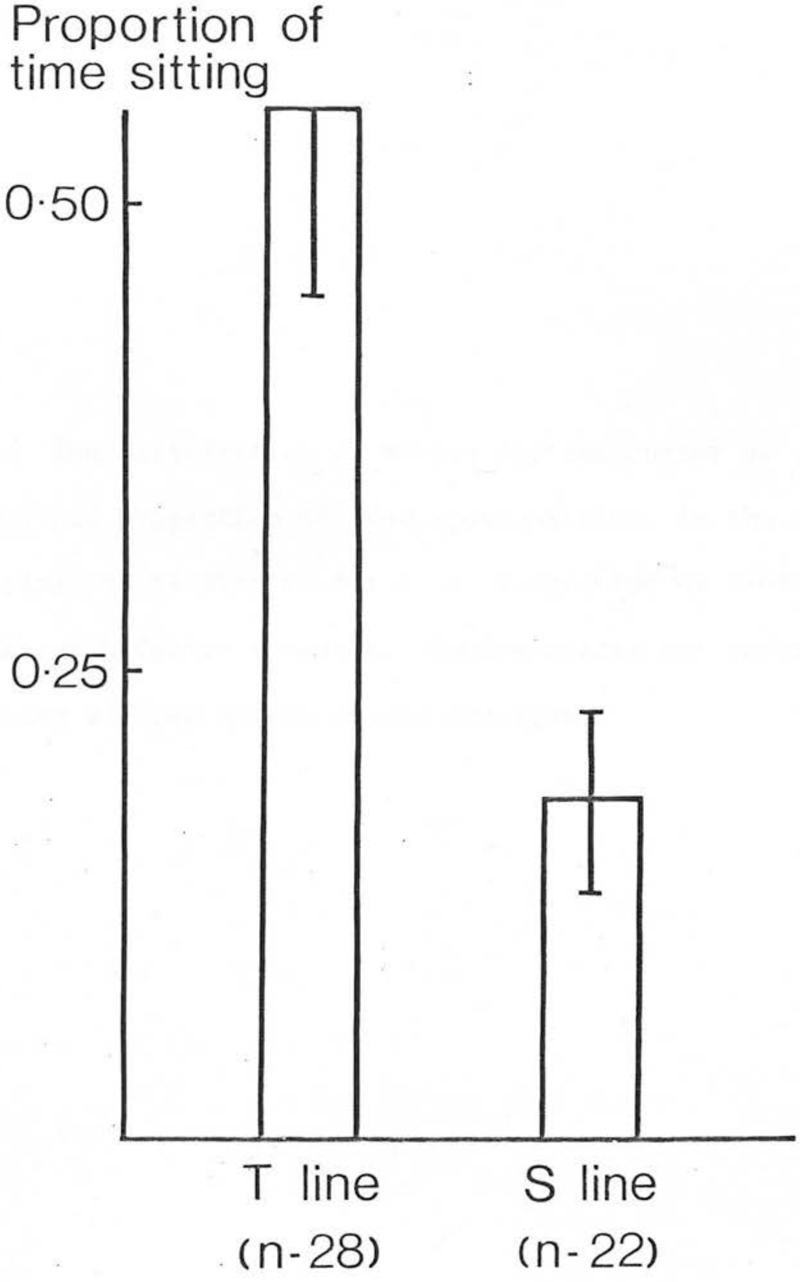

Proportion of time sitting
0·50
0·25
T line
(n-28)
S line
(n-22)

Figure 5c. The distribution of scores for the number of paces taken per minute, and proportion of time spent sitting, in the ten minutes before laying, of twenty-two S line hens selected at random from the Poultry Research Centre`s stocks. Pacing scores are plotted on the ordinate, and sitting scores on the abscissa.

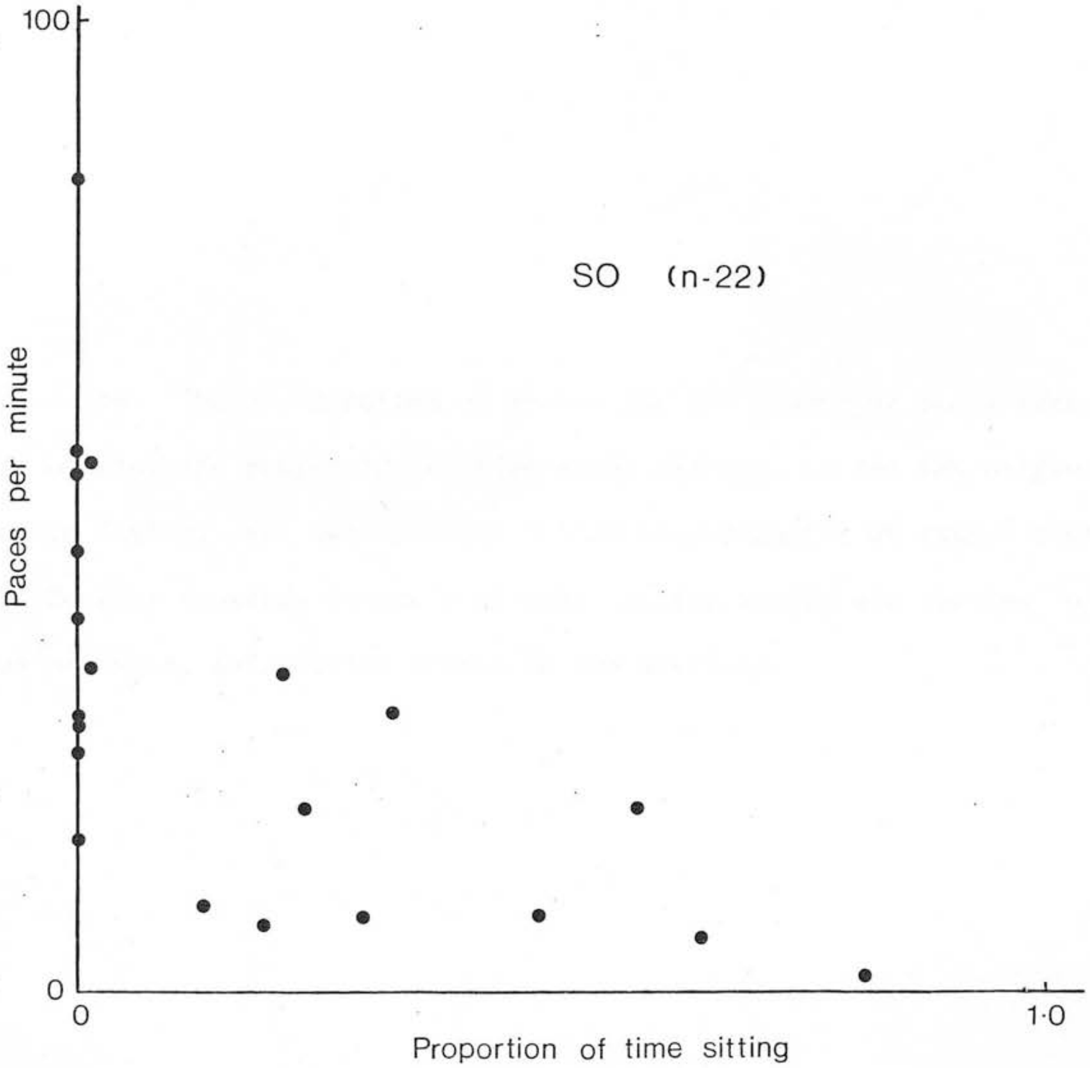
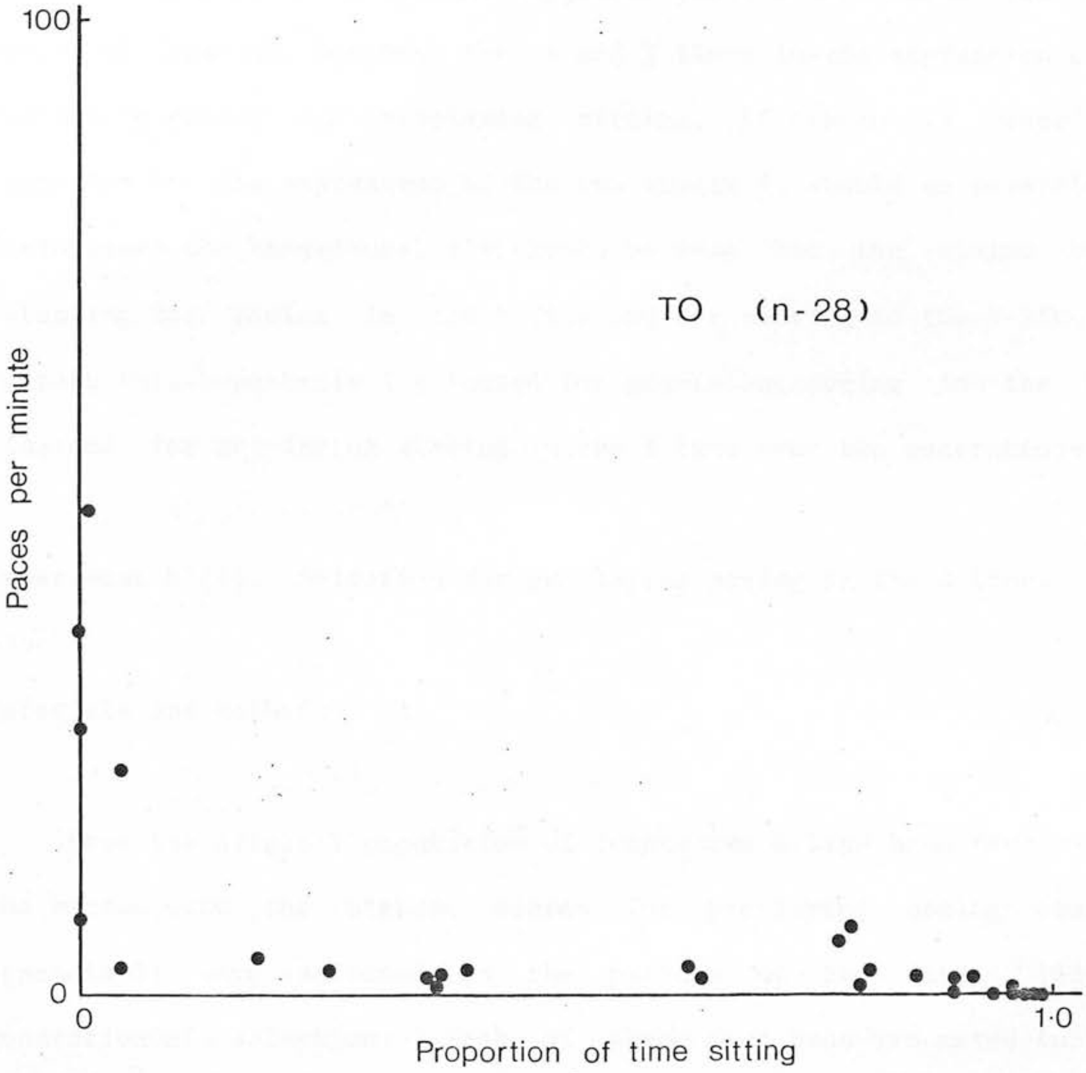

100
Paces per minute
SO (n-22)
0
0
1·0
Proportion of time sitting

Figure 5d. The distribution of scores for the number of paces taken per minute, and proportion of time spent sitting, in the ten minutes before laying, of twenty-eight T line hens selected at random from the Poultry Research Centre`s stocks. Pacing scores are plotted on the ordinate, and sitting scores on the abscissa.


100
0
Paces per minute
TO (n-28)
0
1·0
Proportion of time sitting

Chapter 6. Genetic analysis of pre-laying pacing and pre-laying sitting .III. Selection for pacing and sitting.

Introduction

In chapter 5. it was suggested that, since there was a degree of overlap between the S and T lines in the expression of pre-laying pacing and pre-laying sitting, if there is genetic variation in the expression of the two traits it should be possible to increase the behavioural divergence between the two stains by selecting for pacing in the S line and for sitting in the T line. To test this hypothesis I selected for pre-laying pacing in the S line and for pre-laying sitting in the T line over two generations.

Experiment 6 (i). Selection for pre-laying pacing in the S line.

Materials and methods

From the original population of twenty-two S line hens four of the birds with the highest scores for pre-laying pacing (see appendix 3) were selected as the parents of the first (S1) generation of selection. Each of these four hens was mated to a male drawn at random, except for a prohibition against full sib matings, from the male sibs of the original twenty-two S line hens. Breeding and husbandry techniques were as described in chapter 2.

Ten female S1 progeny of the four selected hens were scored for the expression of pre-laying pacing and pre-laying sitting using the methods described in chapter 2, and five of the S1 hens with the highest scores for pre-laying pacing (see appendix 3) were selected as parents of the second (S2) generation of selection. Each of these five hens was mated to a male sib of one of the four other selected females. Breeding and husbandry techniques were as described in chapter 2.

Twenty female (S2) progeny of the five selected S1 hens were scored for the expression of the pre-laying pacing and sitting using the methods described in chapter 2.

Between generations comparisons of the expression of pre-laying pacing and pre-laying sitting were made using the Mann-Whitney U test (two-tailed) as described by Siegel, (1959). Within generations distributions of scores for pacing and sitting are presented as scattergrams (Lehner, 1979) of individuals` scores for pre-laying pacing plotted against their scores for pre-laying sitting. Scores for sitting being plotted on the abscissa, scores for pacing on the ordinate.

Results

After one generation of selection for pre-laying pacing the mean (+/- S.E.) number or paces taken per minute by S line hens during the ten minutes prior to laying had increased - although not significantly at the 5% level - from 27.76 +/- 4.34 to 30.01 +/- 5.42 ($p = 0.28$; figure 6a), and the mean (+/- S.E.) proportion of time spent sitting in that period had fallen - again not significantly at the 5% level - from 0.1800 +/- 0.0520 to 0.0669 +/- 0.0362 ($p = 0.13$; figure 6b).

After two generations of selection the mean (+/- S.E.) number of paces taken per minute had increased to 50.89 +/- 4.40, a significant increase over both the S0 and S1 generations ($p = 0.0007$, and $p < 0.02$, respectively; figure 6a). The mean (+/- S.E.) proportion of time spent sitting by the S2 birds was 0.0721

+/- 0.0393. This was less than the time spent sitting by the S0 birds, but slightly greater than the time spent sitting by the S1 birds (p = 0.25, and p > 0.1 respectively; figure 6b).

Figures 6c and 6d show the distributions of scores for pre-laying pacing and pre-laying sitting in the S1 and S2 generations.

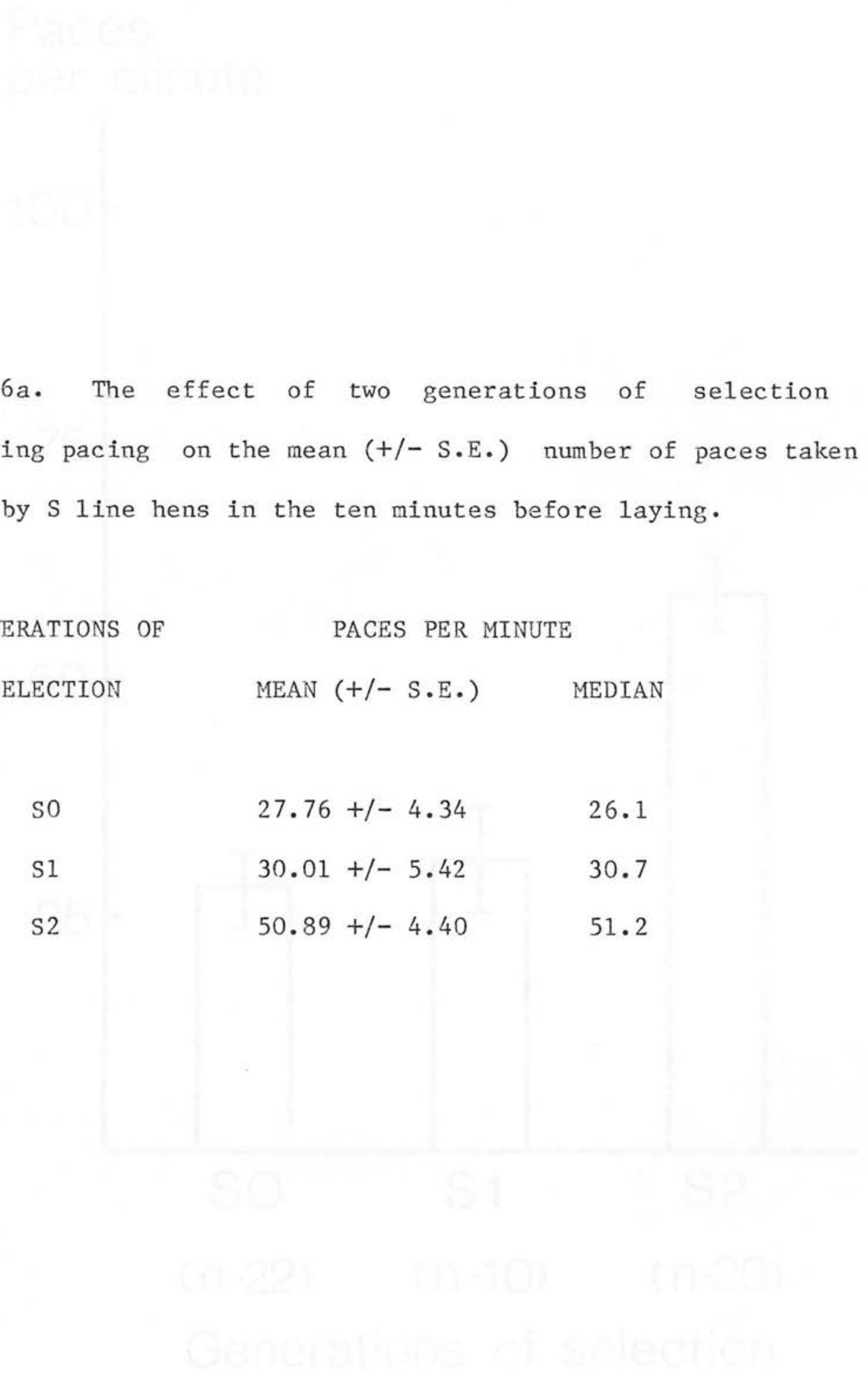


Figure 6a. The effect of two generations of selection for pre-laying pacing on the mean (+/- S.E.) number of paces taken per minute by S line hens in the ten minutes before laying.

GENERATIONS OF SELECTION	PACES PER MINUTE MEAN (+/- S.E.)	MEDIAN
S0	27.76 +/- 4.34	26.1
S1	30.01 +/- 5.42	30.7
S2	50.89 +/- 4.40	51.2

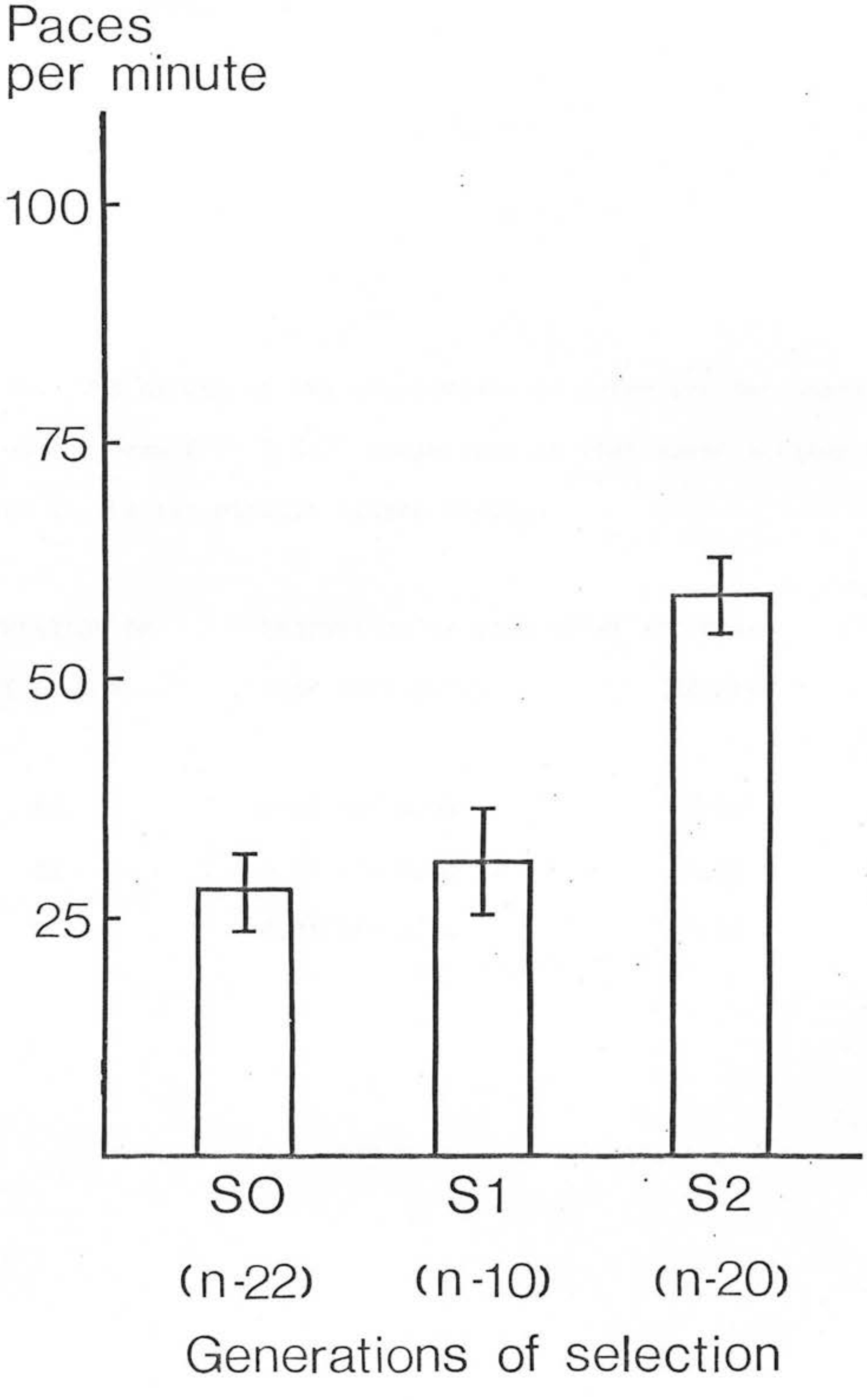

Paces per minute
100
75
50
25
SO
(n-22)
S1
(n-10)
S2
(n-20)
Generations of selection

Figure 6b. The effect of two generations of selection for pre-layng pacing on the mean (+/- S.E.) proportion of time spent sitting by S line hens in the ten minutes before laying.

GENERATION OF SELECTION	PROPORTION OF TIME SPENT SITTTING MEAN (+/- S.E.)	MEDIAN
S0	0.18 +/- 0.05	0.08
S1	0.07 +/- 0.04	0.00
S2	0.07 +/- 0.04	0.00

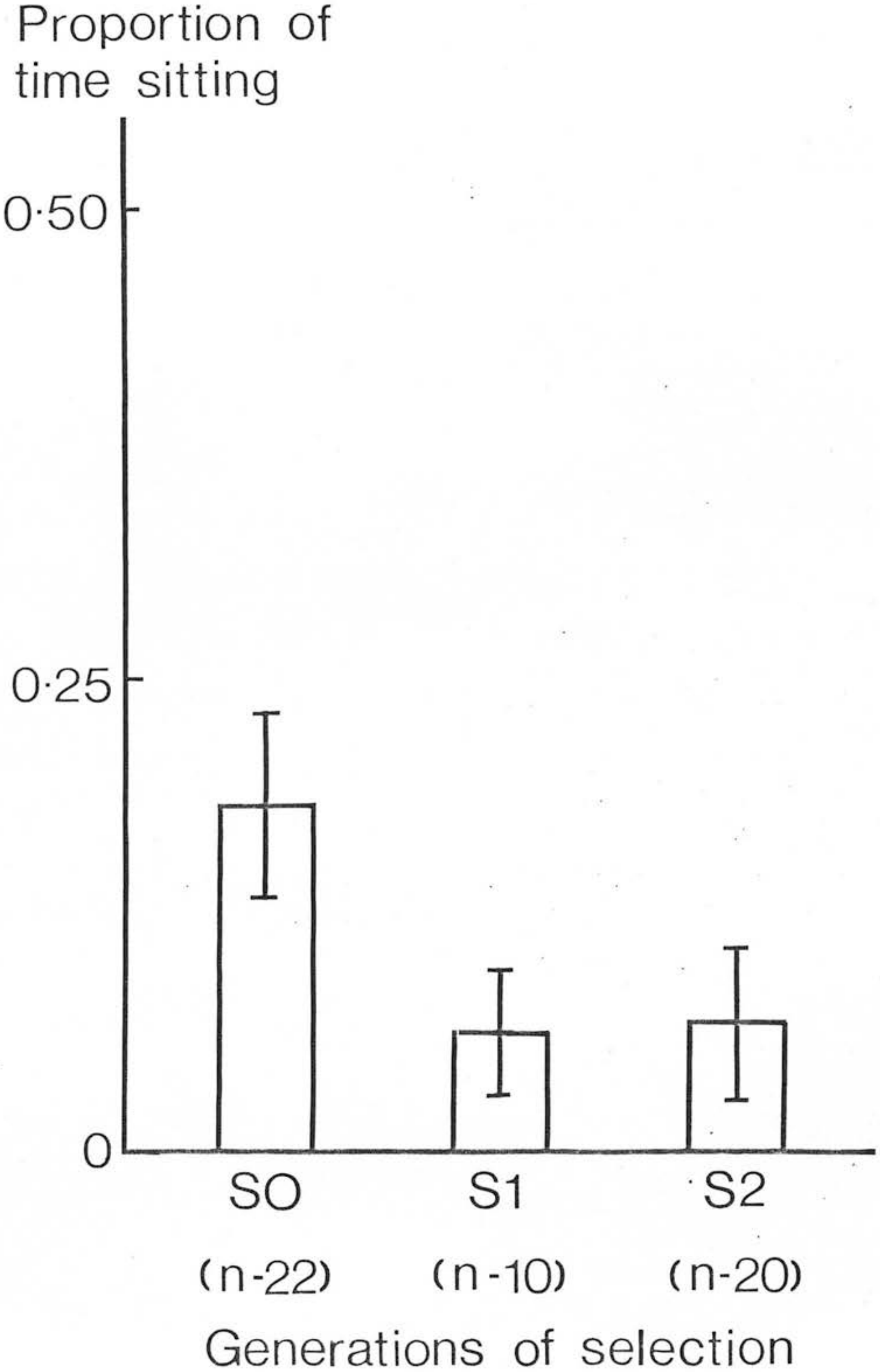

Proportion of time sitting
0·50
0·25
0
SO
(n-22)
S1
(n-10)
S2
(n-20)
Generations of selection

Figure 6c. The distribution of scores for the number of paces taken per minute, and proportion of time spent sitting during the ten minutes before laying of ten S line hens after one generation of selection for pre-laying pacing. Pacing scores are plotted on the ordinate, sitting scores on the abcissa.

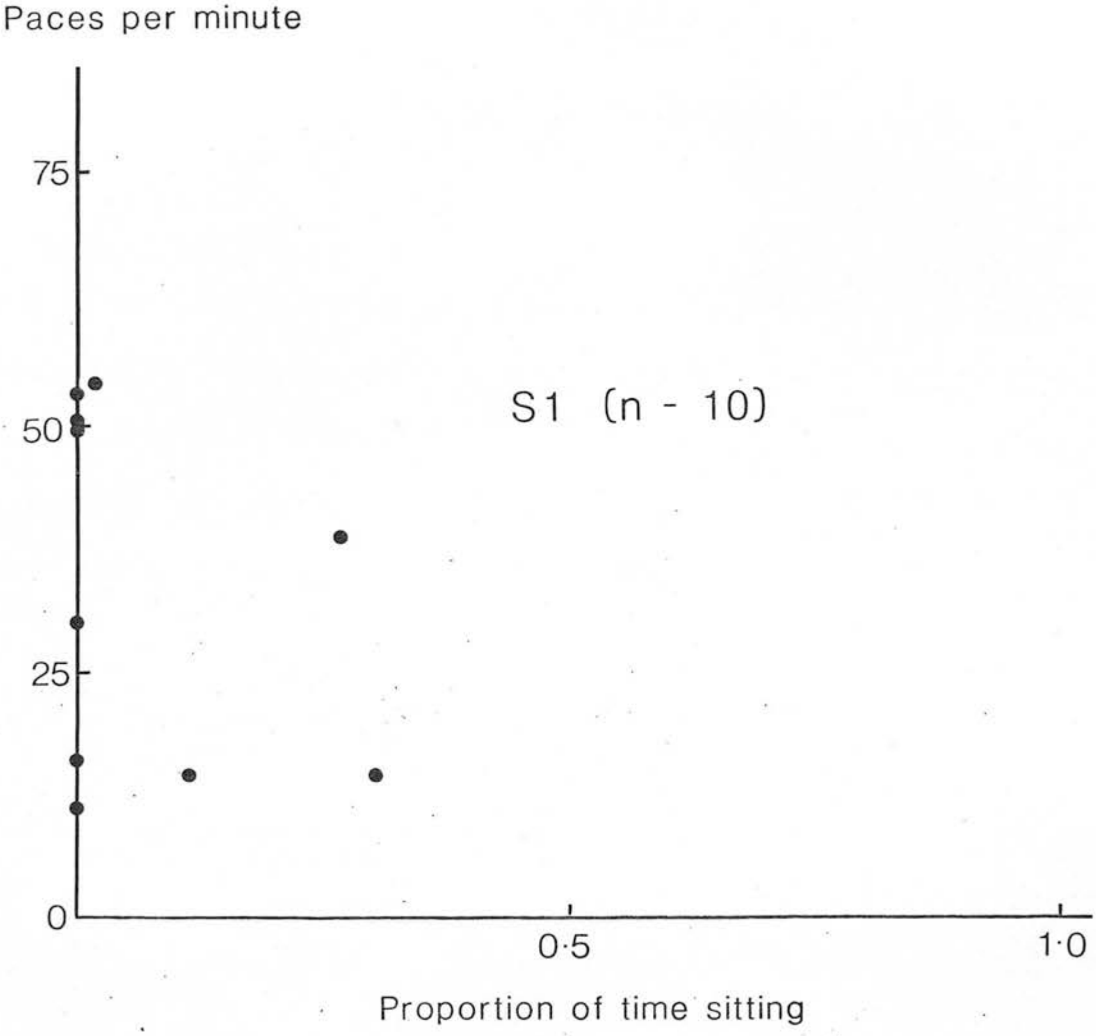
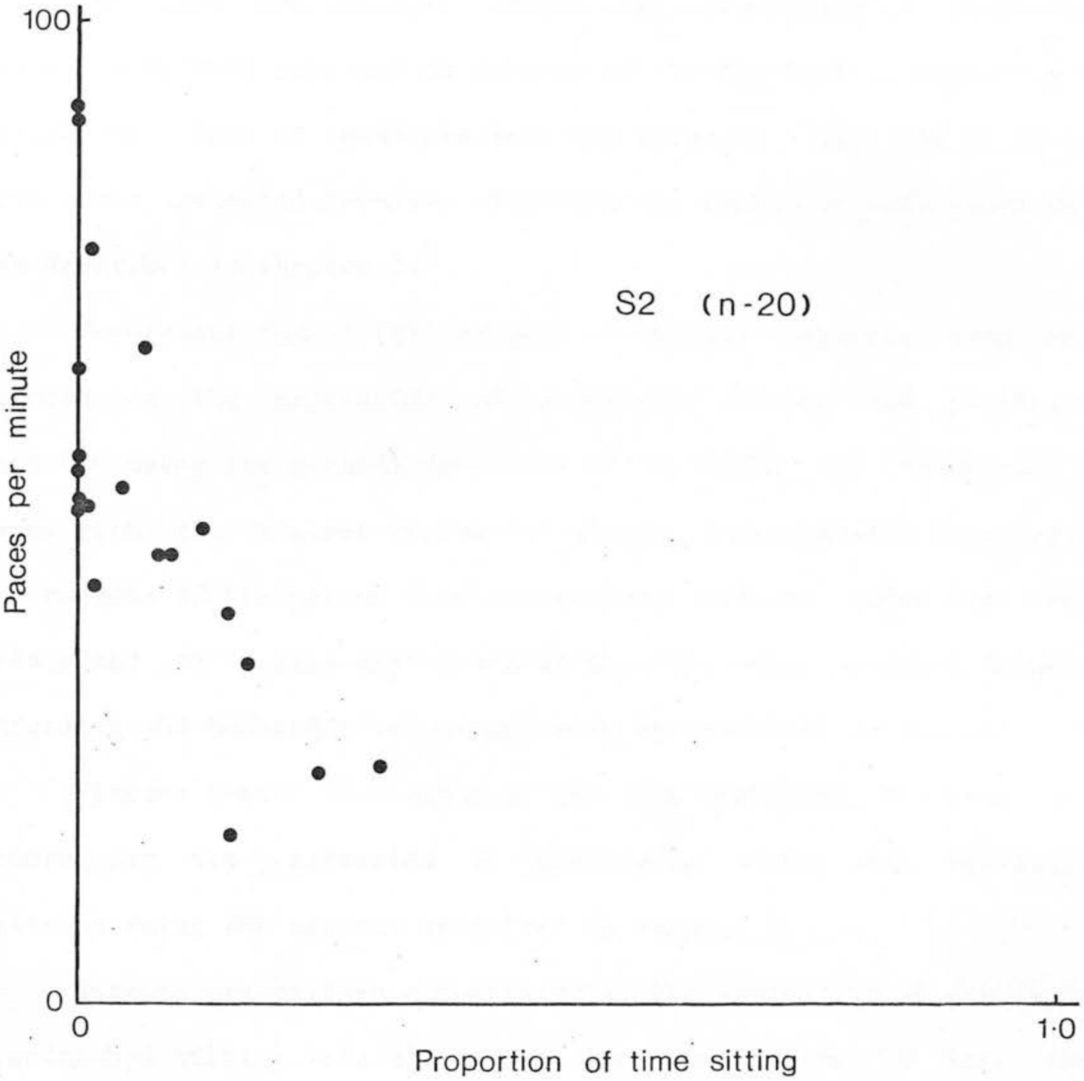

Paces per minute
75
50
25
0
S1 (n - 10)
0·5
1·0
Proportion of time sitting

Figure 6d. The distribution of scores for the number of paces taken per minute, and proportion of time spent sitting in the ten minutes before laying of twenty S line hens after two generations of selection for pre-laying pacing. Pacing scores are plotted on the ordinate, sitting scores on the abscissa.


100
0
Paces per minute
S2 (n-20)
0
1·0
Proportion of time sitting

Experiment 6 (ii). Selection for pre-laying sitting in the T line.

Materials and methods

From the original population of twenty-eight T line hens six of the hens with the highest scores for pre-laying sitting (see appendix 3) were selected as parents of the first (T1) generation of selection. Each of these six hens was mated to a male sib of one of the other selected females. Breeding and husbandry techniques were as described in chapter 2.

Twenty-one female (T1) progeny of the six selected hens were scored for the expression of pre-laying pacing and pre-laying sitting using the methods described in chapter 2, and six of the T1 hens with the highest scores for sitting (see appendix 3) selected as parents of the second (T2) generation. Each of these six hens was mated to a male sib of one of the five other selected females. Breeding and husbandry techniques were as described in chapter 2.

Sixteen female T2 progeny of the six selected T1 hens were scored for the expression of pre-laying pacing and pre-laying sitting using the methods described in chapter 2.

Between generations comparisons of the expression of pre-laying pacing and sitting were made using the Mann-Whitney U test (two tailed), as described by Siegel, (1956). Within generations distributions of scores for pacing and sitting were prepared as scattergrams (Lehner, 1979) of individuals scores for pre- laying pacing plotted against their scores for sitting. Scores for sitting were plotted on the abscissa, scores for pacing on the ordinate.

Results

After one generation of selection for pre-laying sitting the mean (+/- S.E.) proportion of time spent sitting in the ten minutes prior to laying had increased - but not significantly so at the 5% level - from 0.5513 + 0.0939 to 0.6320 + 0.1485 ($p = 0.30$, figure 6e), and the mean number of paces taken per minute in that period had fallen - again not significantly at the 5% level - from 6.64 +/- 2.30 to 4.21 +/- 1.36 ($p = 0.49$, figure 6f).

After two generations of selection the mean +/- (S.E.) proportion of time spent sitting had increased to 0.7112 +/- 0.0754 (figure 6e), and the mean number of paces taken per minute had fallen to 2.99 +/- 1.10. The proportion of time spent sitting by the T2 individuals was not however significantly greater, at the 5% level, than that spent sitting by either the T0 or T1 individuals ($p = 0.13$, and 0.27, respectively), nor was the number of paces taken by the T2 birds significantly less, at the 5% level, than that taken by the T0 and T1 ($p = 0.15$ and 0.19, respectively).

Figures 6g and 6h show the distributions of scores for pre-laying pacing and pre-laying sitting in the T1 and T2 generations.

Discussion.

The facts that selection for pacing in the S line and for sitting in the T line consistently increased both variables over two generations, and that by the second generations of selection for these characters there was almost complete behavioural divergence between the two lines - no S line bird sat for any substantial period of time, and no T line bird showed stereotyped pacing behaviour (figures 6d and 6h) - strongly implies genetic variation in the expression of both traits.

However it could be argued that since the number of generations of selection is relatively small and there are no control populations against which the performances of the selected lines can be compared, the increases in pacing in the S line, and in sitting in the T line might be attributable to environmental effects. However two factors mediate against this being the case. First, the S and T line birds were raised communally and it is unlikely that environmental factors which led to an increase in pacing in the S line would also lead to an increase in sitting in the T line. Second, the radical changes in population structures between the unselected and selected lines. The unselected S line contained individuals which sat, and the unselected T line contained individuals which paced. As mentioned above by the second generation of selection such ``atypical`` individuals had been eliminated from both populations. It is unlikely that this would have occured simultaneously in both lines simply as a consequence of chance or environmental effects.

Given as demonstrated above that there is genetic variation in the expression of both pacing and sitting, and that both characters respond to selection, it is in theory possible to work out realised heritabilities (Falconer,1964) for either trait. However computation of these values necessitates making assumptions about the breeding values of males, which in this study cannot be justified because of the small numbers of animals involved and the considerable variability in the expression of pre-laying pacing and pre-laying sitting within families in the unselected lines (see Appendix 3 for examples). I point this out only to show that the omission of realised heritabilities for pacing and sitting from this chapter is a deliberate action, rather than an oversight on my part.

Figure 6e. The effect of two generations of selection for pre-laying sitting on the mean (+/- S.E.) proportion of time spent sitting by T line hens in the ten minutes before laying.

GENERATION OF SELECTION	PROPORTION OF TIME SPENT SITTING	
	MEAN (+/- S.E.)	MEDIAN
T0	0.55 +/- 0.09	0.77
T1	0.63 +/- 0.15	0.79
T2	0.71 +/- 0.08	0.87

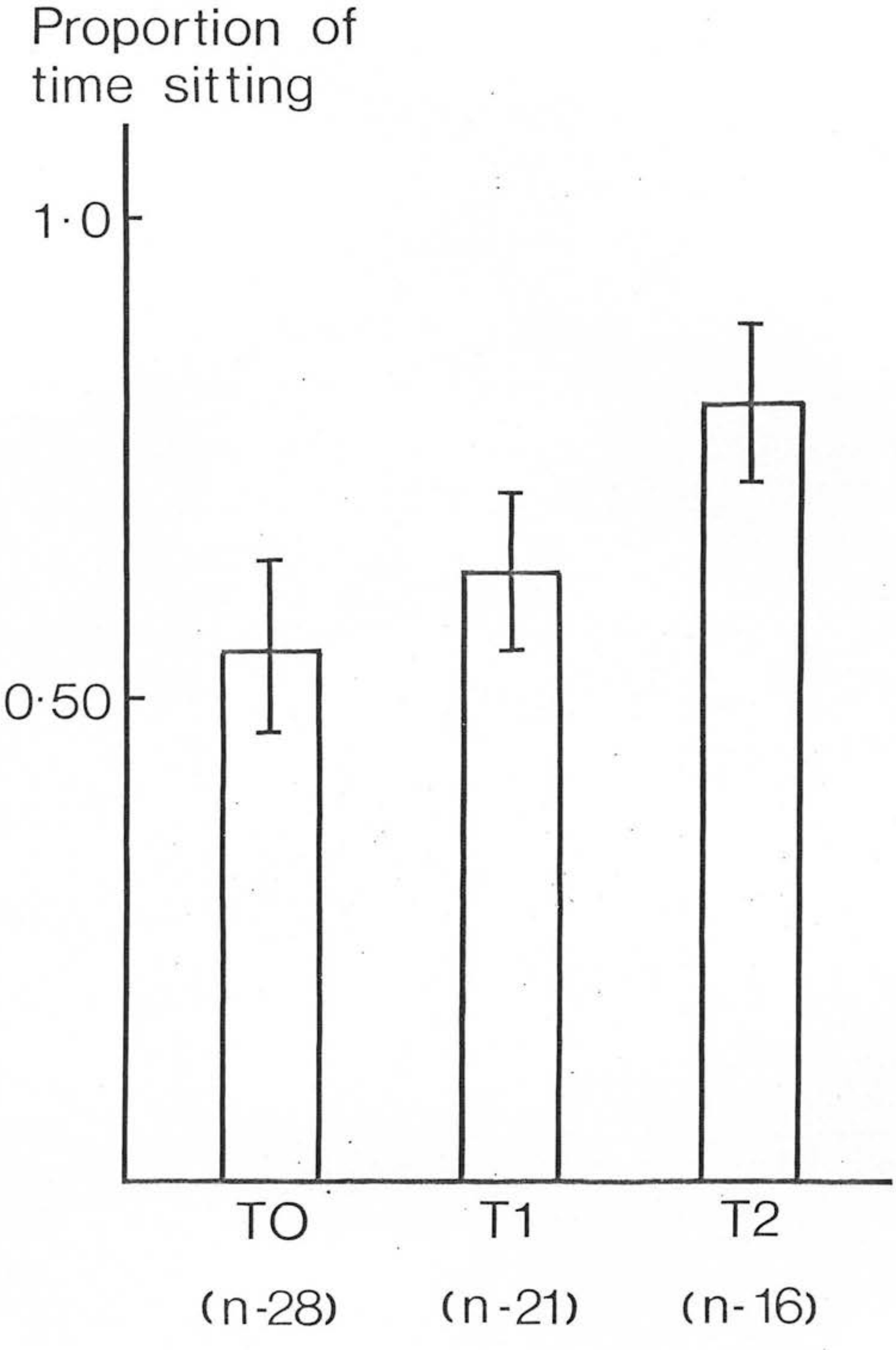

Proportion of time sitting
1·0
0·50
TO
(n-28)
T1
(n-21)
T2
(n-16)
Generations of selection

Figure 6f. The effect of two generations of selection for pre-laying sittng on the mean (+/- S.E.) number of paces taken per minute by T line hens in the ten minutes before laying.

GENERATION OF SELECTION	PACES PER MINUTE MEAN (+/- S.E.)	MEDIAN
T0	6.64 +/- 2.30	2.1
T1	4.21 +/- 1.36	2.4
T2	2.99 +/- 1.10	1.1

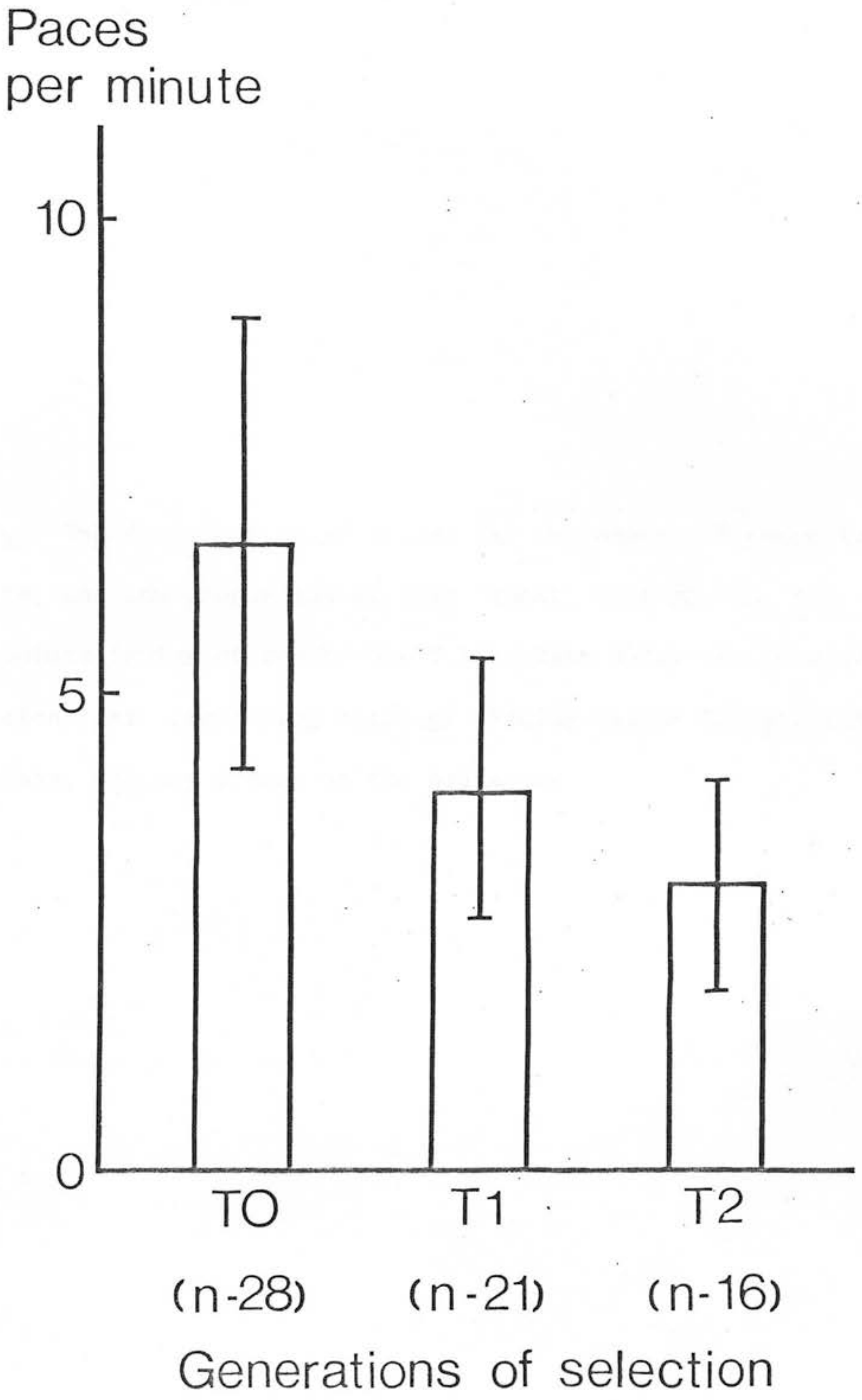

Paces
per minute
10
5
0
TO
T1
T2
(n-28)
(n-21)
(n-16)
Generations of selection

Figure 6g. The distribution of scores for the number of paces taken per minute, and the proportion of time spent sitting in the ten minutes before laying of twenty-one T line hens after one generation of selection for pre-laying sitting. Pacing scores are plotted on the abscissa, sitting scores on the ordinate.

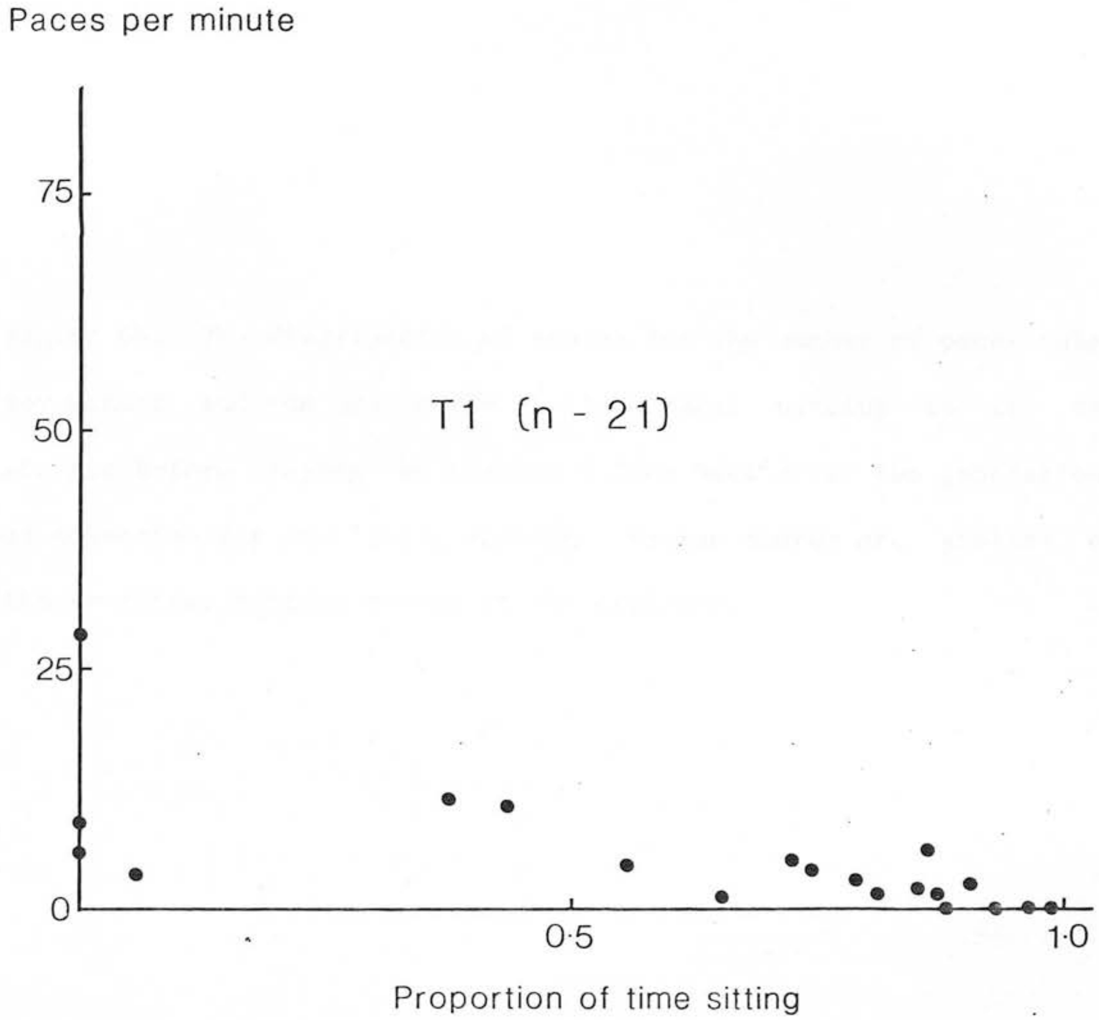
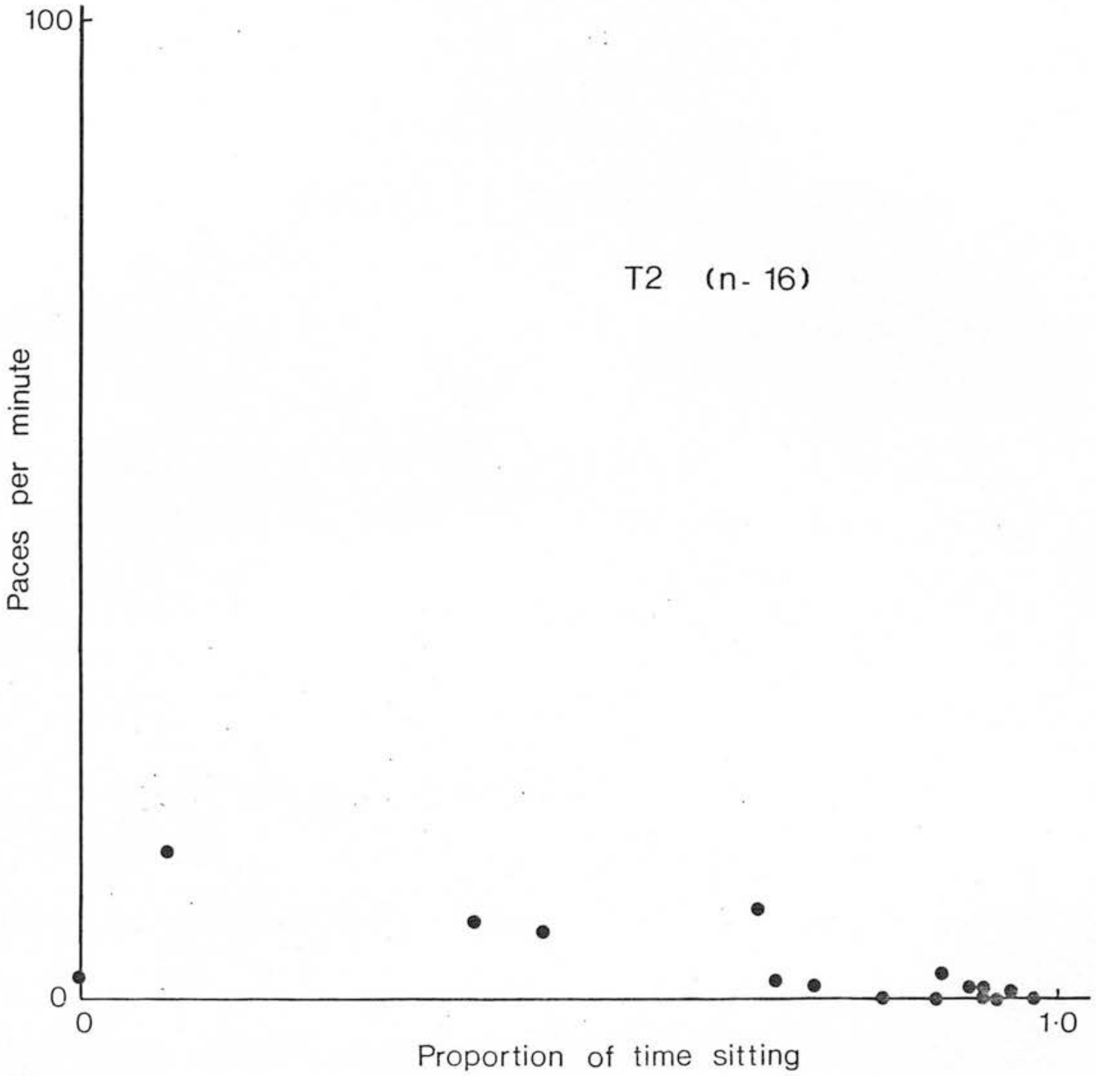

Paces per minute
75
50
25
0
T1 (n - 21)
0·5
1·0
Proportion of time sitting

Figure 6h. The distribution of scores for the number of paces taken per minute, and the proportion of time spent sitting in the ten minutes before laying of sixteen T line hens after two generations of selection for pre-laying sitting. Pacing scores are plotted on the abscissa, sitting scores on the ordinate.


100
0
Paces per minute
T2 (n- 16)
0
1·0
Proportion of time sitting

Chapter 7. Genetic analysis of pre-laying pacing and pre-laying sitting. IV. Strain crosses.

Introduction.

Although the findings presented in the previous chapter demonstrate that there is genetic variation in the expression of pre-laying pacing and pre-laying sitting in both the S and T lines, they reveal little about the nature of this variation. In an attempt to determine something of the mode of inheritance of pre-laying pacing and pre-laying sitting I carried out a series of crosses between the S and T lines.

Experiment 7(i). The initial ´investigatory` F1 cross.

Introduction.

Since nothing was known about the inheritance of either pre-laying pacing or pre-laying sitting in the S and T lines it seemed prudent, before attempting a large scale crossing experiment to carry out a small scale ´investigatory` study, the results of which would, hopefully, indicate the most appropriate design for a further large scale experiment.

Materials and methods.

Five S line hens and five S line cockerels, and five T line hens and five T line cockerels were drawn at random from the original unselected populations. Each S line hen was mated with a T line cock, and each T line hen with a S line male. Full details of these pairings are given in appendix 3. Breeding and husbandry techniques were as described in chapter 2.

Seven Fl`s derived from matings between S line males and T line females, and fourteen Fl`s derived from matings between T line males and S line females were scored for the expression of pre-laying pacing and pre-laying sitting. The pedigrees of these animals are given in appendix 3. Scoring and husbandry techniques were as described in chapter 2.

Comparisons of scores for pre-laying pacing and pre-laying sitting of the reciprocal Fl`s were made using the Mann-Whitney ´U` test (two tailed), as described by Siegel (1956). Distributions of scores for pre-laying pacing and pre-laying sitting were plotted seperately as frequency histograms.

Results.

The mean scores for pre-laying pacing and pre-laying sitting of the two reciprocal Fl`s are shown in figure 7a. There were no significant differences between the reciprocal Fl`s in the expression of either pacing or sitting ($U = 39$, $p > 0.1$, and $U = 45.5$, $p > 0.1$ respectively) The scores of the two reciprocal Fl`s were therefore combined to give single sets of values for pacing and sitting. The distributions of scores for pre-laying pacing and pre-laying sitting of the Fl`s and the unselected parental lines are shown in figures 7b. and 7c.

Discussion.

Although the number of Fl hybrids scored is rather low, it is possible to draw certain tentative conclusions from the results of this cross. These are;

i). Since there is no significant difference in the expression of pre-laying pacing or pre-laying sitting between the F1`s derived from matings between S line males and T line females and the F1`s derived from the reciprocal cross, it follows that neither trait is sex linked (see figure 10a).

ii). The distribution of scores for pre-laying sitting of the F1´s is intermediate to those of the two parental lines (see figure 10c) which implies additivity in the expression of pre-laying sitting. The expression of pre-laying sitting could therefore be under polygenic control with additive variance, or alternatively under the control of a single gene with incomplete dominance.

iii). The distribution of scores for pre-laying pacing of the F1`s is essentially similar to that of the T line parental generation. This has two implications. First, it implies, in view of (ii) above, that pacing and sitting are inherited separately. Second, it implies that the tendency to exhibit pre-laying pacing is apparently recessive to the tendency not to pace, irrespective of whether the animal sits or not.

There are at least three possible interpretations of this finding. These are: -

a). The expression of pre-laying pacing is under polygenic control, the S line being homozygous recessive and the T line homozygous dominant at virtually all loci affecting this behaviour. This is unlikely because the S and T lines are not true breeding for the expression of ´pacing` and ´non-pacing`. There is in fact considerable variation in the expression of pacing even within families in the unselected S and T lines (see tables 3(i) and 3(iv) of appendix 3).

b). The expression of pre-laying pacing is under the control of a single gene, dominant ´non-pacing` alleles of this gene being at high frequency in the T line and recessive ´pacing` alleles at high frequency in the S line.

c). The expression of pre-laying pacing is under polygenic control at the level of the genotype, but phenotypic expression of the behaviour is dependent on what Wright, (1934) has called a threshold effect. This interpretation implies that there is some sort physiological scale of genetically determined tendencies to pace and not to pace, and that on this scale there is a critical point (the threshold). Animals which fall on one side of the threshold show stereotyped pacing before laying, animals falling on the other side of the threshold do not. S line hens would thus typically lie on one side of the threshold and T line hens on the other side of the threshold. Given this, if the T line was in general genetically further removed from the threshold than the S line on the physiological scale, then the Fl´s, although in fact genetically intermediate between the two lines would tend to fall on the the non-pacing side of the threshold, thereby giving the impression that pacing and non-pacing are dichotomous traits and that pacing is recessive to non-pacing.

It is not possible on the basis of this Fl cross to distinguish between the single gene and threshold models for the inheritance of pre-laying pacing outlined above. However, one property of the threshold system of inheritance is that backcrosses tend to be closer to the parental types with the result that apparent dominance in an Fl cross can apparently be reversed when the Fl´s are backcrossed to the supposedly homozygous recessive line (Fuller and Thompson, 1960). A single gene model, however predicts that backcross to the homozygous recessive line will exhibit segregation, containing individuals which are homozygous and individuals which are heterozygous; in this particular case individuals which pace and individuals which do not. This point is pursued further in experiment 7(ii).

Experiment 7(ii). Backcross analysis.

Introduction.

In the discussion of experiment 7(i) it was suggested that the tendencies to exhibit pre-laying pacing and pre-laying sitting were inherited seperately. The expression of pre-laying sitting being under the control of a gene or genes with additive effects. The expression of pre-laying pacing being controlled either by a single gene effect or by a polygenic threshold system.

The aim of this experiment was to confirm the findings of experiment 10(i), and to attempt to distinguish between the single gene and polygenic threshold models for the inheritance of pre-laying pacing by repeating the Fl cross on a larger scale, and by backcrossing to the two parental lines.

If the expression of pre-laying pacing is controlled by a major autosomal gene, then given that S line birds are homozygous for the recessive ´´pacing`` allele of the gene, and that T line birds are homozygous for the dominant ´´non-pacing`` allele of the gene, then Fl hybrids will be heterozygous and should not pace. Backcrosses to the S line (Fl x S) will be either homozygous recessive or heterozygous and therefore half the birds should exhibit pre-laying pacing and half should not. Backcrosses to the T line will however be homozygous dominant or heterozygous and therefore should not pace. Whereas if a polygenic threshold system controls the expression of pre-laying pacing then a variety of outcomes is possible from the backcross to the S line. Examples are; (i). reversal of apparent dominance of pacing to non-pacing in backcrosses to the S line, arising because the backcrosses to the S line lie closer to the S line parent than do the Fl´s and therefore fall predominantly on the non-pacing side of the threshold. (ii). All backcrosses to the S line do not exhibit pacing, because the T line is so much further removed from the threshold than the S line that the backcrosses although in fact intermediate between the S line and the T line, the Fl´s still fall on the non-pacing side of the threshold. Either of these two findings would strongly argue against a single gene controlling the expression of pre-laying pacing.

Materials and methods.

Fl`s (three males and six females derived from matings between S line males and T line females, and five males and three females derived from matings between T line males and S line females) drawn at random from the Fla generation were backcrossed to hens, or their male sibs, selected from the Sl or Tl generations. Hens from the Sl generation being selected for high levels of pre-laying pacing and hens from the Tl generation for high expression of pre-laying sitting. The Sl and Tl birds used in these matings were then crossed to produce a second generation of Fl`s - the Flb generation, and were then used to breed the second generations of pure bred animals - the S2 and T2 generations. Full details of the animals used and the pairings made can be found in appendix 3. Breeding and husbandry techniques were as described in chapter 2.

Twenty S line backcrosses (Fla x Sl), twenty-one T line backcrosses (Fla x Tl), sixteen Flb´s derived from matings between S line males and T line females, twenty-one Flb´s derived from matings between T line males and S line females, the twenty S2 hens, and the sixteen T2 hens were scored for the expression of pre-laying pacing and pre-laying sitting. Husbandry and scoring techniques were as described in chapter 2. Between groups comparisons of scores for pre-laying pacing and pre-laying sitting were made using the Mann - Whitney U test (two tailed), as described by Siegel,(1956). Distributions of scores for pre-laying pacing and pre-laying sitting of each of the groups were plotted seperately as frequency histograms.

Results.

There was no significant difference between the reciprocal F1`s in the expression of pre-laying pacing and pre-laying sitting ($z = 0.736$, $p = 0.46$, and $z = 1.54$, $p = 0.124$ respectively; figure 7d.). The scores of the two reciprocal F1`s were therefore combined to give a single set of values for pre-laying pacing and pre-laying sitting respectively. The distributions of scores for pre-laying pacing of the S2, T2, Flb, Fla x S1, and Fla x T1 generation hens are shown in figures 7e, 7f, 7g, 7h, and 7i. The distributions of scores for pre-laying sitting of the S2, T2, Flb, Fla x S1, and F1 x T1 generations are shown in figures 7j, 7k, 7l, 7m, and 7n.

Discussion.

The results of the second F1(b) cross confirmed the results of the initial F1(a) cross. There was no significant difference between the reciprocal F1(b) hybrids in the expression of either pre-laying pacing or pre-laying sitting confirming that neither trait was sex-linked. The distribution of scores for pre-laying sitting of the Flb`s was intermediate to those of the S2 and T2 generations confirming additivity in the inheritance of this trait. The distribution of scores for pre-laying pacing of the Flb`s was similar to that of the T2 generation indicatiing apparent dominance of ´pacing` to non-pacing.

The results of the backcrosses, however, failed to distinguish between the single gene and polygenic threshold models for the inheritance of pre-laying pacing.

The S line backcross consistent with the single gene model contained both presumably homozygous recessive pacing individuals, and presumably heterozygous non-pacing individuals. Whereas the T line backcross, again consistent with the single gene hypothesis contained only non-pacing heterozygous and homozygous dominant individuals. These observations are not however incompatible with the polygenic threshold model. Since the bimodal distribution of scores for pre-laying pacing of the S line backcrosses could have arisen because some of the animals fell on each side of the threshold, Whereas all the T line backcrosses, being even closer to the T line parents than the Fl´s, all fell on the non-pacing side of the threshold.

It is not therefore possible to decide on the basis of the data presented here whether a single gene or polygenic threshold hypothesis should be employed to explain the inheritance of pre-laying pacing in the S and T lines. This question could probably be resolved by repeated backcrossing to the supposedly homozygous recessive S line (Fuller and Thompson, 1960). Unfortunately, simple lack of time precludes the possiblity of attempting such a test in this study.

Figure 7a. The mean (+/- S.E.) number of paces taken per minute, and mean (+/- S.E.) proportion of time spent sitting in the ten minutes before laying by reciprocal F1´s of the unselected S and T lines.

CROSS	PACES PER MINUTE	PROPORTION OF TIME SPENT SITTING
	MEAN (+/- S.E.)	
S♂ x T♀	7.93 +/- 3.78	0.32 +/- 0.16
T♂ x S♀	14.02 +/- 4.16	0.28 +/- 0.09
	MEDIAN	
S♂ x T♀	6.00	0.00
T♂ X S♀	15.00	0.24

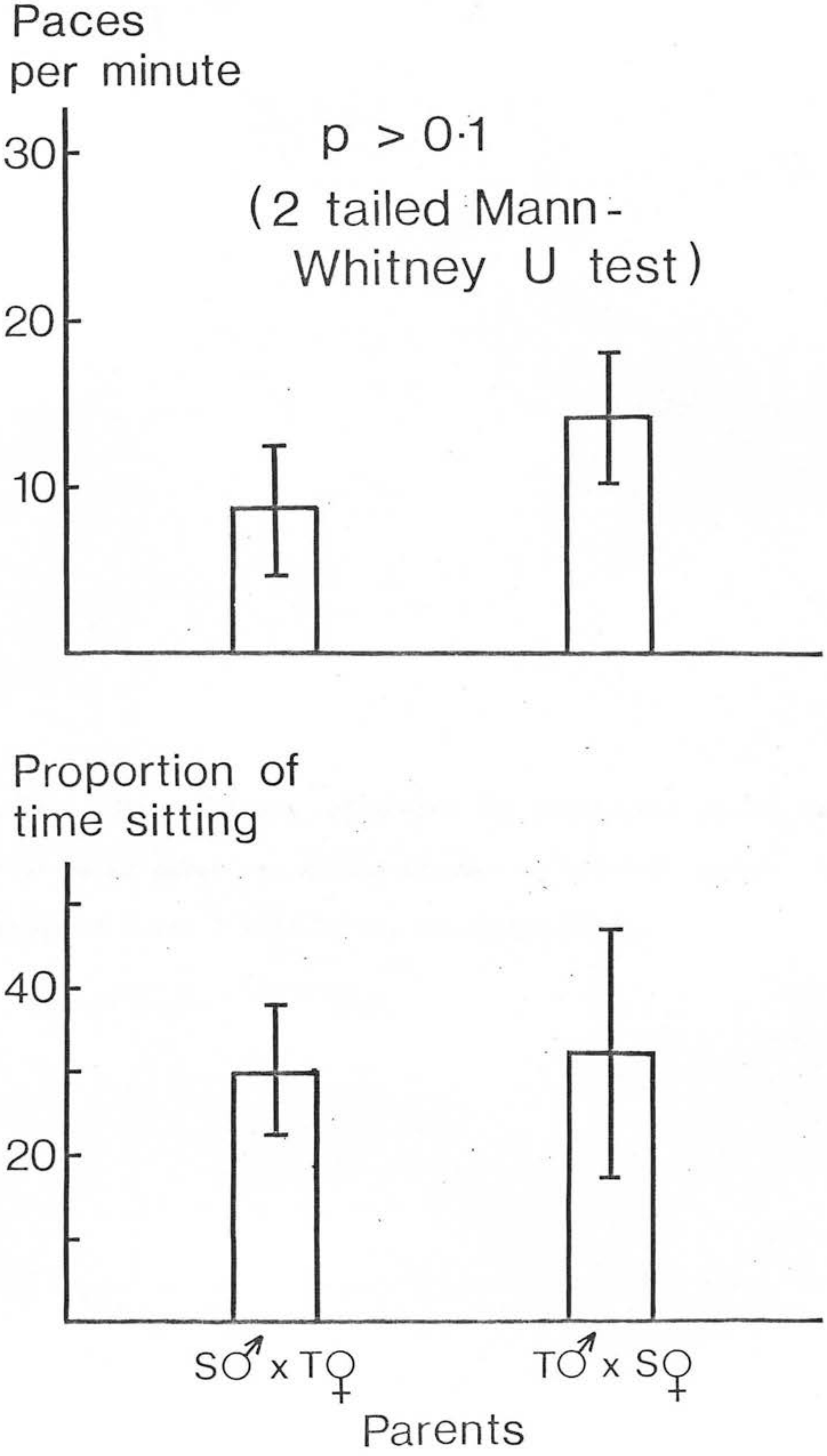
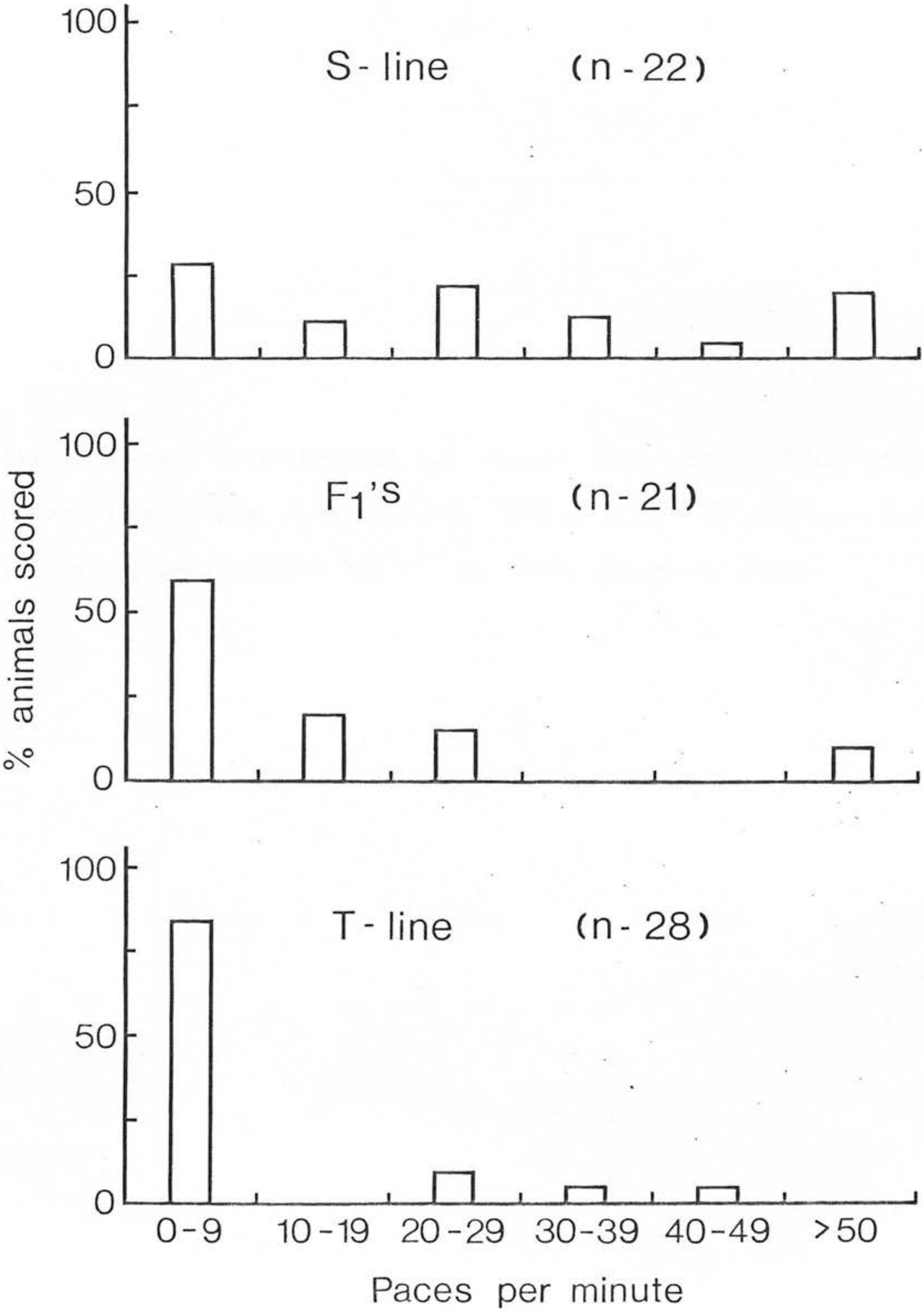
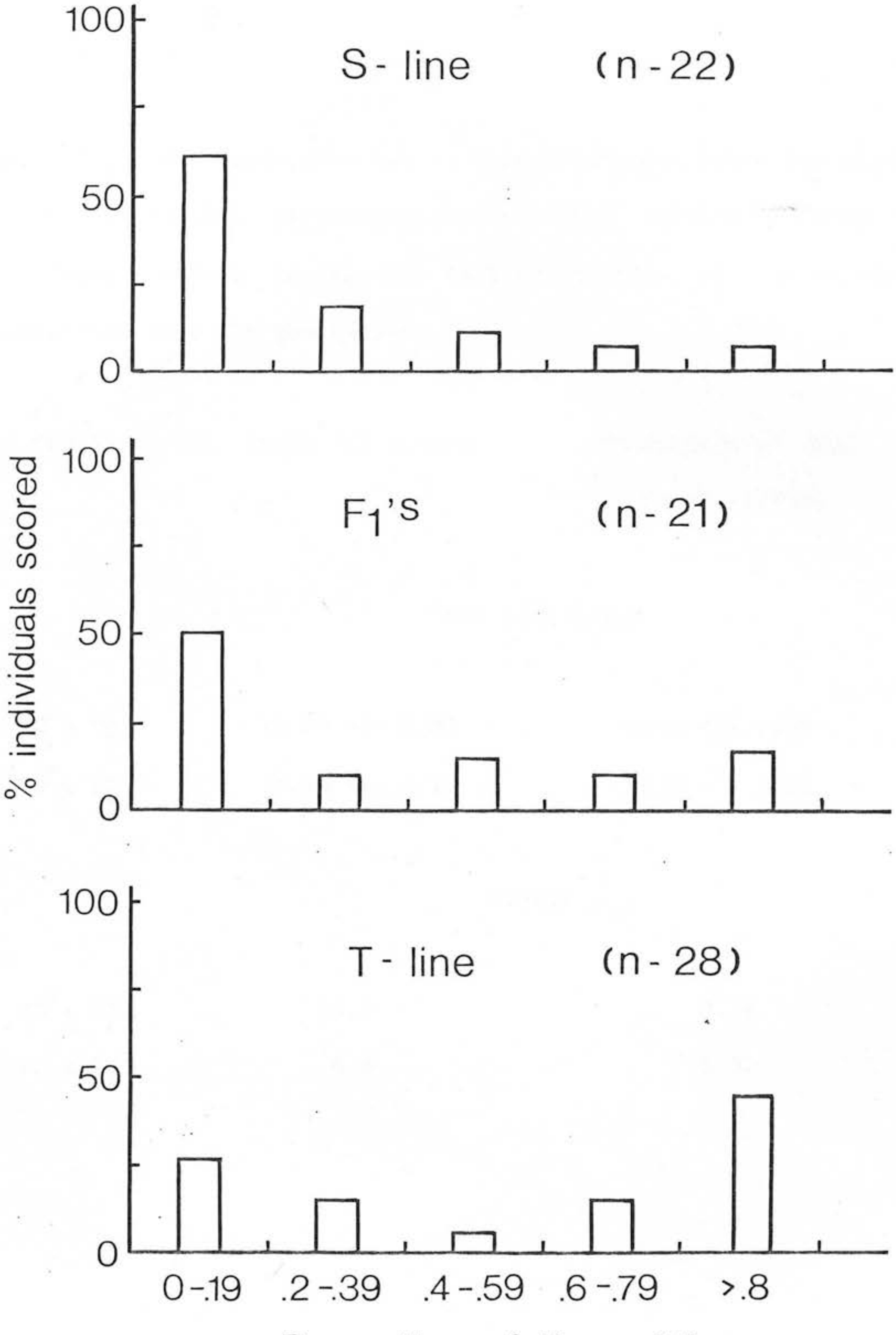

Paces
per minute
30
20
10
p > 0·1
(2 tailed Mann-Whitney U test)
Proportion of
time sitting
40
20
S♂ x T♀
T♂ x S♀
Parents

Figure 7b. Distributions of scores for pre-laying pacing (average number of paces taken per minute in the ten minutes before laying) of unselected S and T line birds, and their F1`s.



100
S - line
(n - 22)
50
0
100
F1's
(n - 21)
50
% animals scored
0
100
T - line
(n - 28)
50
0
0 - 9
10 - 19
20 - 29
30-39
40-49
>50
Paces per minute

Figure 7c. Distributions of scores for pre-laying sitting (proportion of time spent sitting during the ten minutes before laying) of unselected S and T line, birds and their Fl`s.



S- line (n-22)
F1'S (n-21)
T- line (n-28)
% individuals scored
100
50
0
0-.19
.2-.39
.4-.59
.6-.79
>.8
Proportion of time sitting

Figure 7d. The mean (+/- S.E.) number of paces taken per minute, and mean (+/- S.E.) proportion of time spent sitting, during the ten minutes before laying by reciprocal F1´s of the S1 and T1 generations (the F1b generation).

CROSS	PACES PER MINUTE	PROPORTION OF TIME SPENT SITTING
	MEAN (+/- S.E.)	
S♂ x T♀	10.49 +/- 2.83	0.32 +/- 0.09
T♂ x S♀	11.46 +/- 2.13	0.45 +/- 0.52
	MEDIAN	
S♂ x T♀	13.9	0.19
T♂ x S♀	6.8	0.52

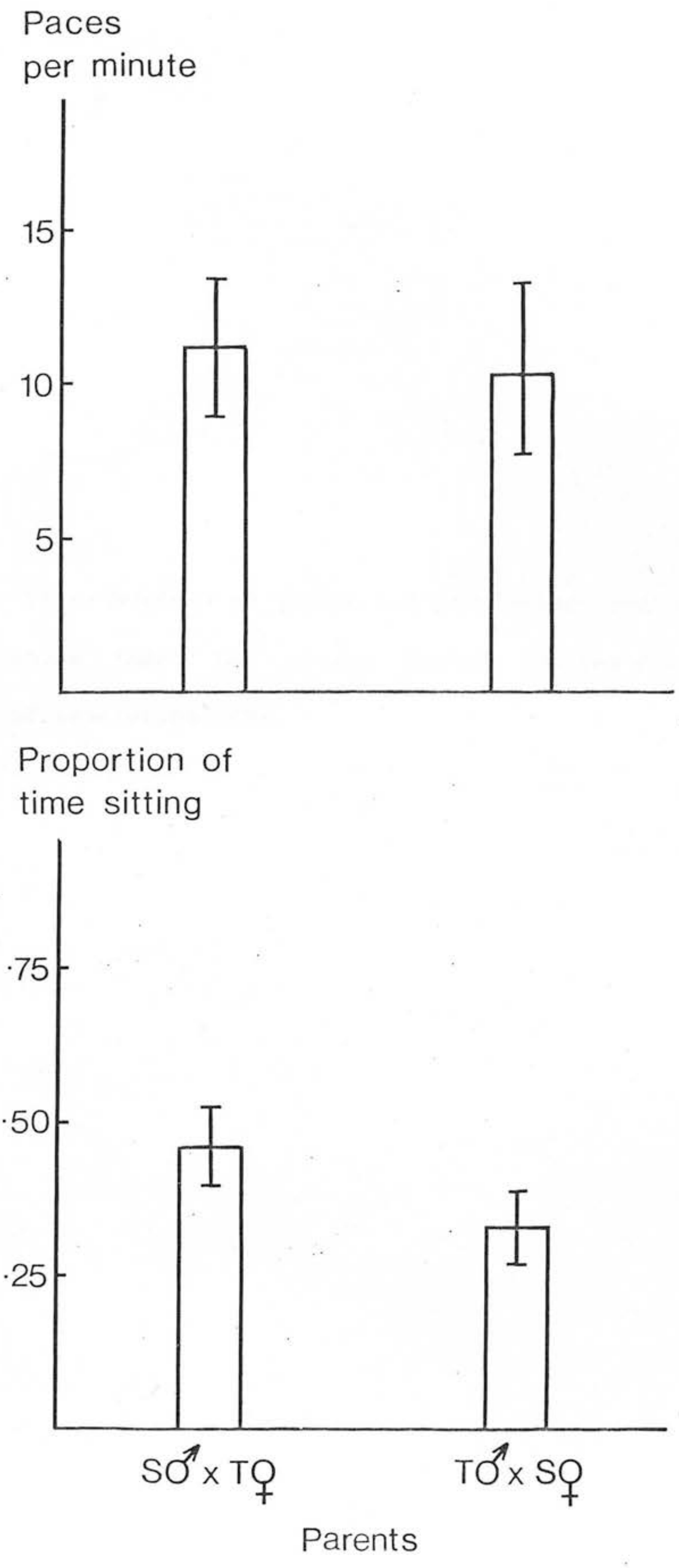

Paces
per minute
15
10
5
Proportion of
time sitting
·75
·50
·25
S♂ x T♀
T♂ x S♀
Parents

Figure 7e. Distributions of scores for pre-laying pacing (average number of paces taken per minute during the ten minutes before laying) of S2 generation hens.

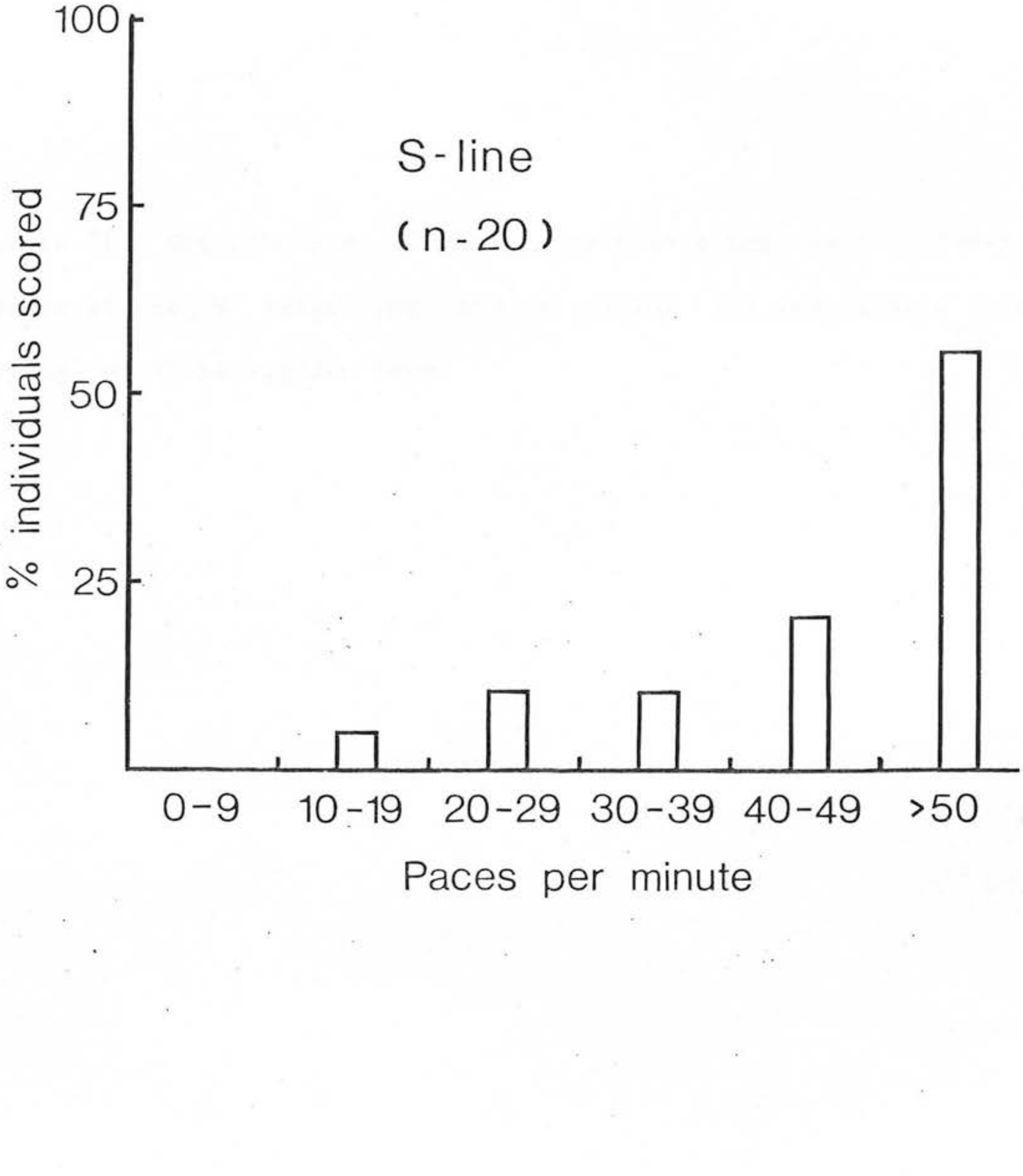

100
75
50
25
% individuals scored
S-line
(n-20)
0-9
10-19
20-29
30-39
40-49
>50
Paces per minute

Figure 7f. Distributions of scores for pre-laying pacing (average number of paces taken per minute during the ten minutes before laying) of T2 generation hens.

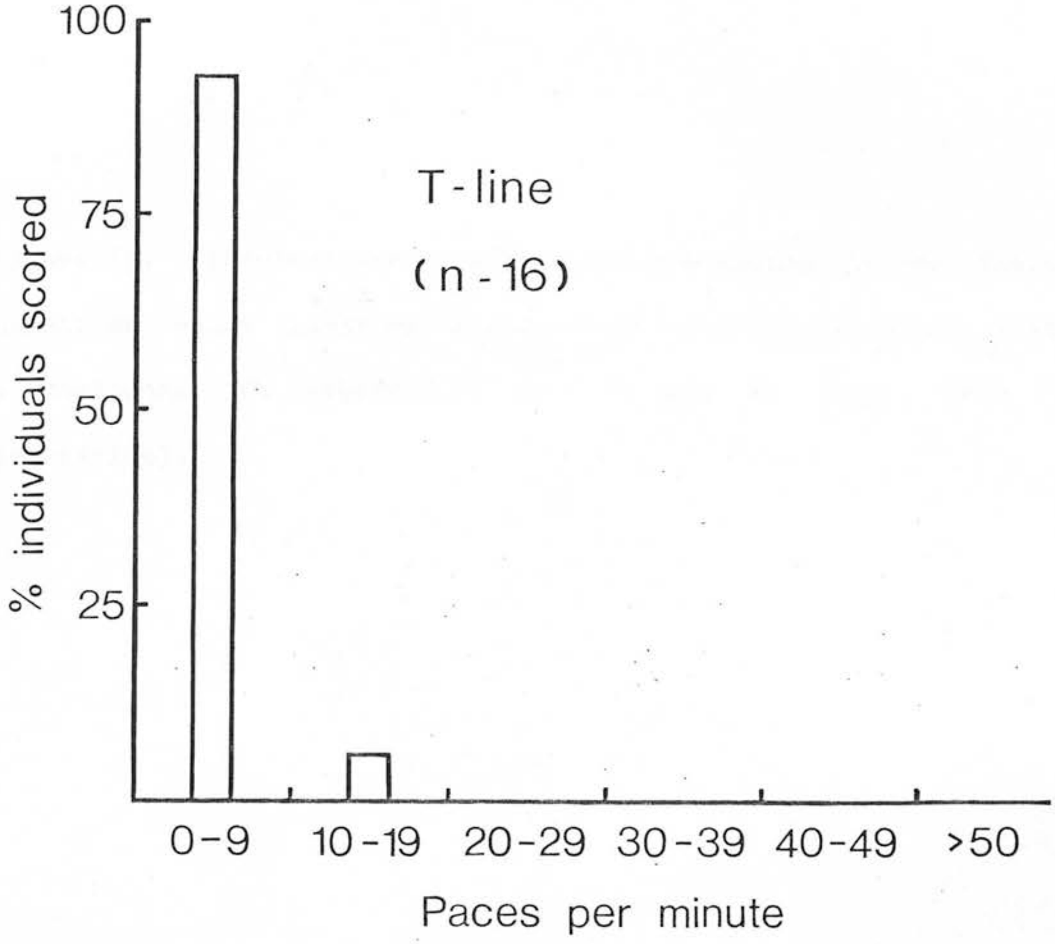

100
75
50
25
% individuals scored
T-line
(n - 16)
0-9
10-19
20-29
30-39
40-49
>50
Paces per minute

Figure 7g. Distributions of scores for pre-laying pacing (average number of paces taken per minute in the ten minutes before laying) of reciprocal F1 hybrids of the S1 and T1 lines (the F1b generation).

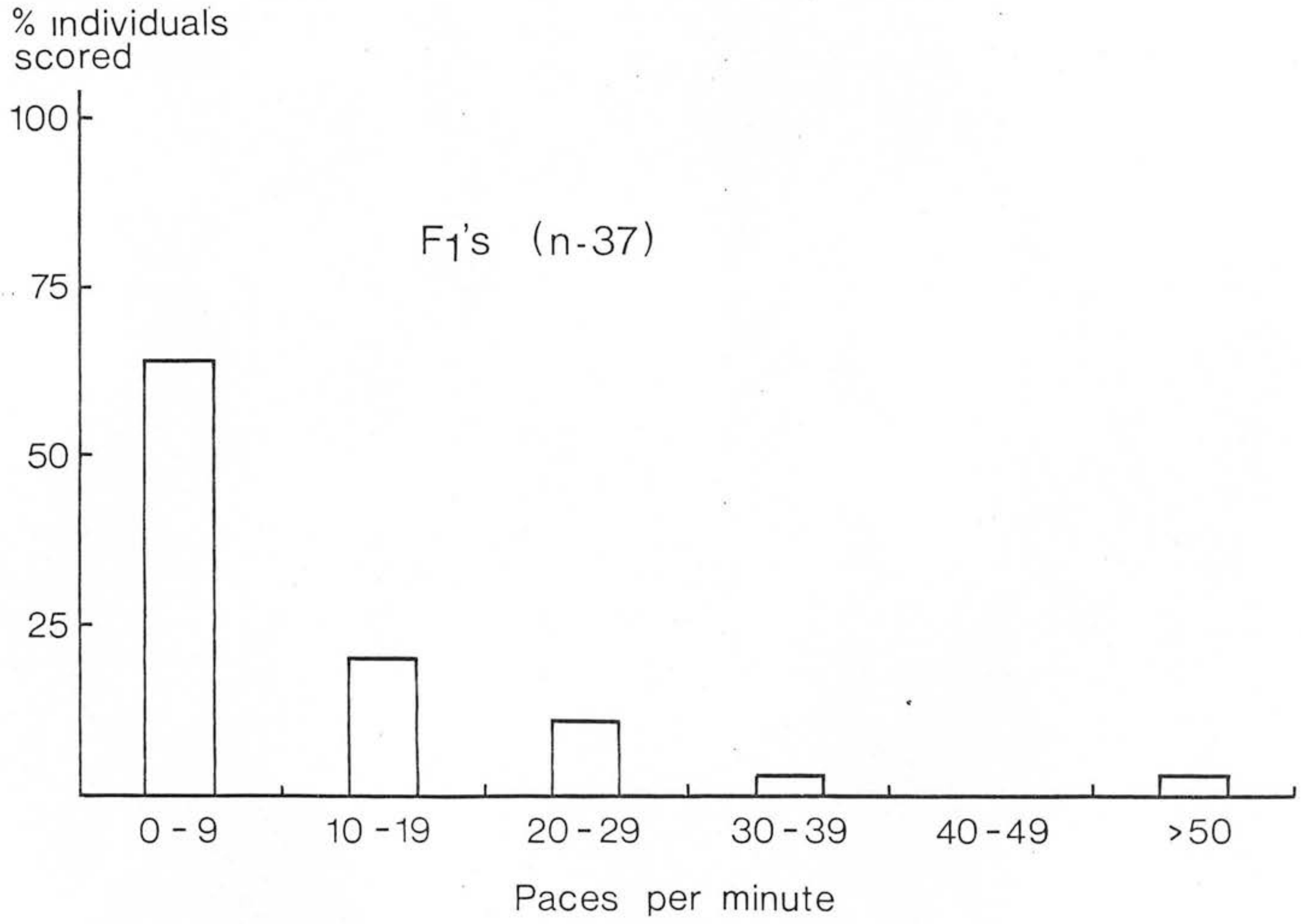

% individuals scored
100
75
50
25
F$_1$'s (n-37)
0 - 9
10 - 19
20 - 29
30 - 39
40 - 49
>50
Paces per minute

Figure 7h. Distributions of scores for pre-laying pacing (average number of paces taken per minute during the ten minutes before laying) of backcross to the S1 line (F1 x S).

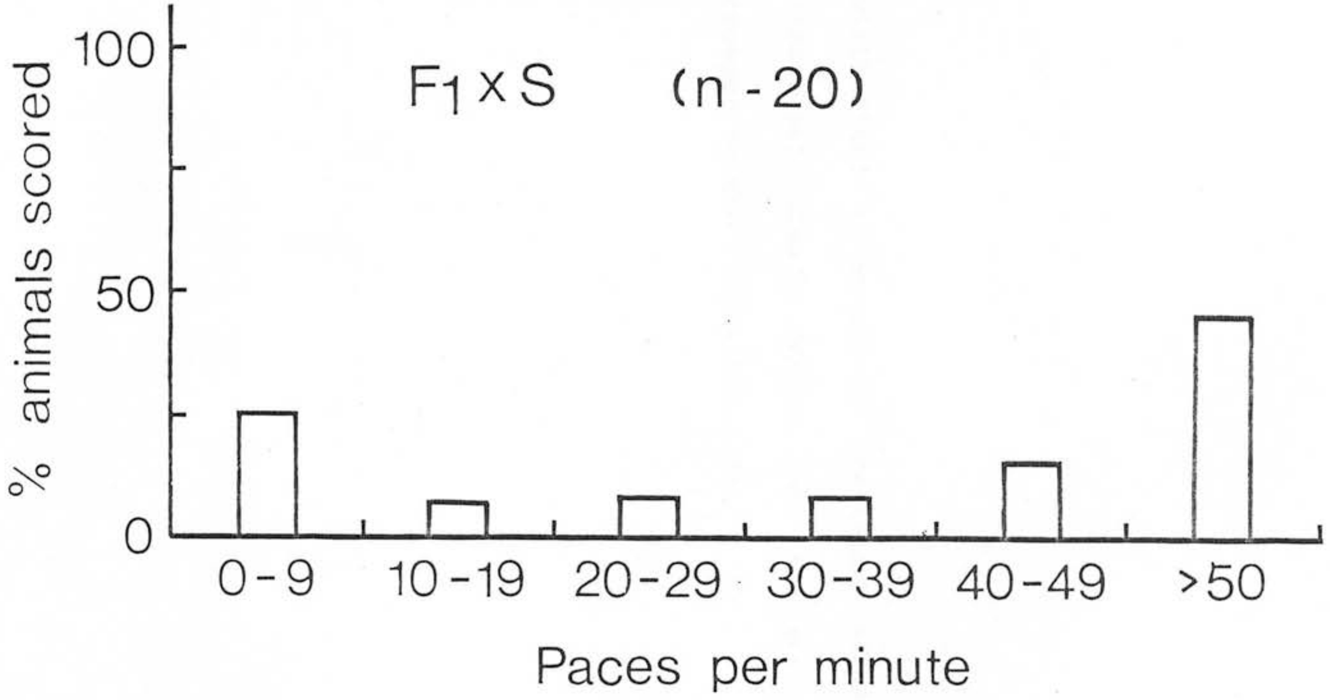

F$_1$ x S (n - 20)
% animals scored
100
50
0
0 - 9
10 - 19
20 - 29
30 - 39
40 - 49
>50
Paces per minute

Figure 7i. Distributions of scores for pre-laying pacing (average number of paces taken per minute during the ten minutes before laying) of backcrosses to the T line (F1 x T).

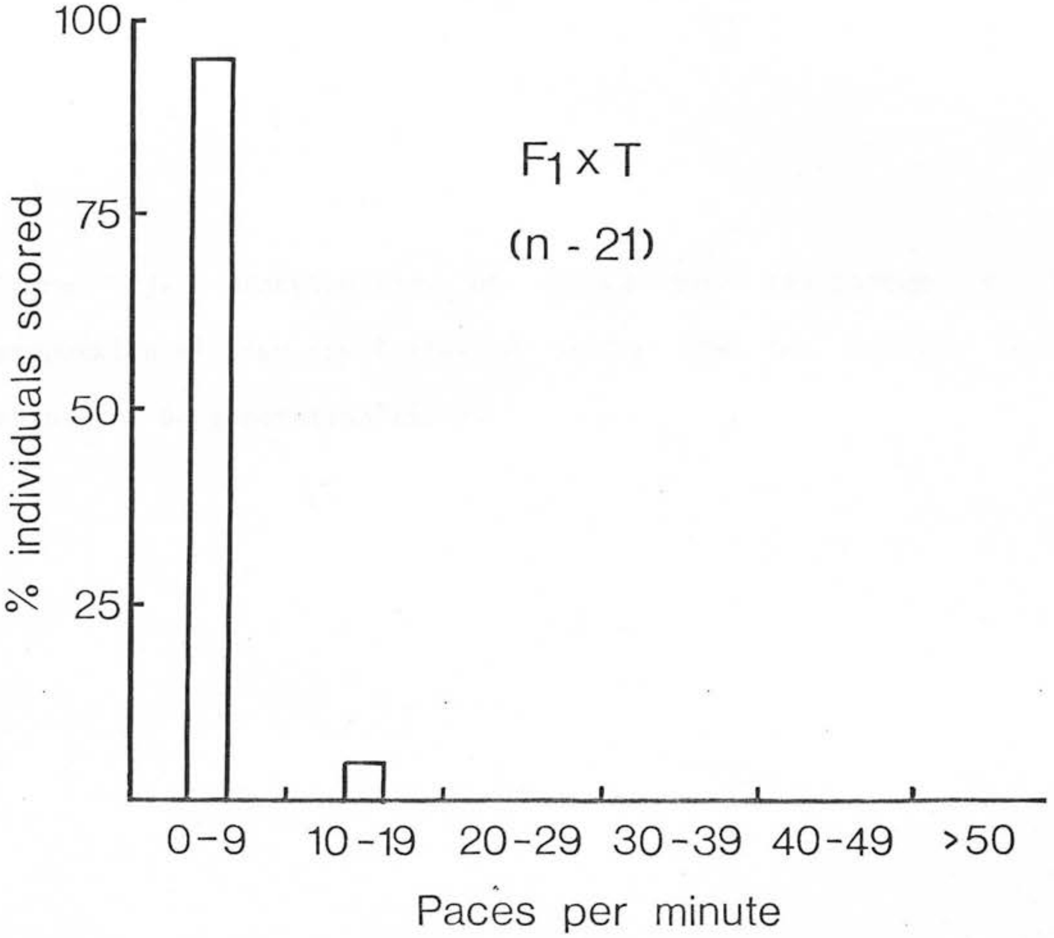

100
75
50
25
% individuals scored
F_1 x T
(n - 21)
0-9
10-19
20-29
30-39
40-49
>50
Paces per minute

Figure 7j. Distributions of scores for pre-laying sitting (proportion of time spent sitting during the ten minutes before laying) of S2 generation birds.

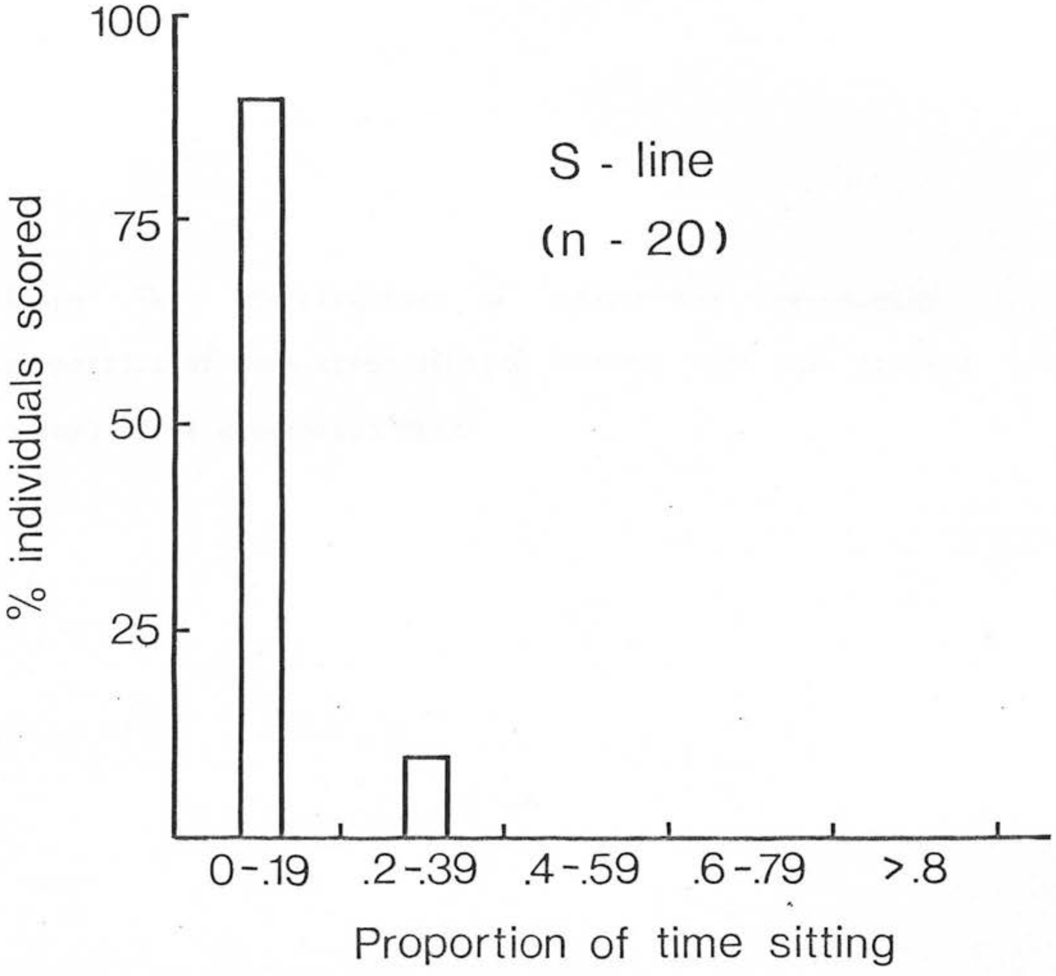

100
75
50
25
% individuals scored
S - line
(n - 20)
0-.19
.2-.39
.4-.59
.6-.79
>.8
Proportion of time sitting

Figure 7k. Distributions of scores for pre-laying sitting (proportion of time spent sitting during the ten minutes before laying) of T2 generation birds.

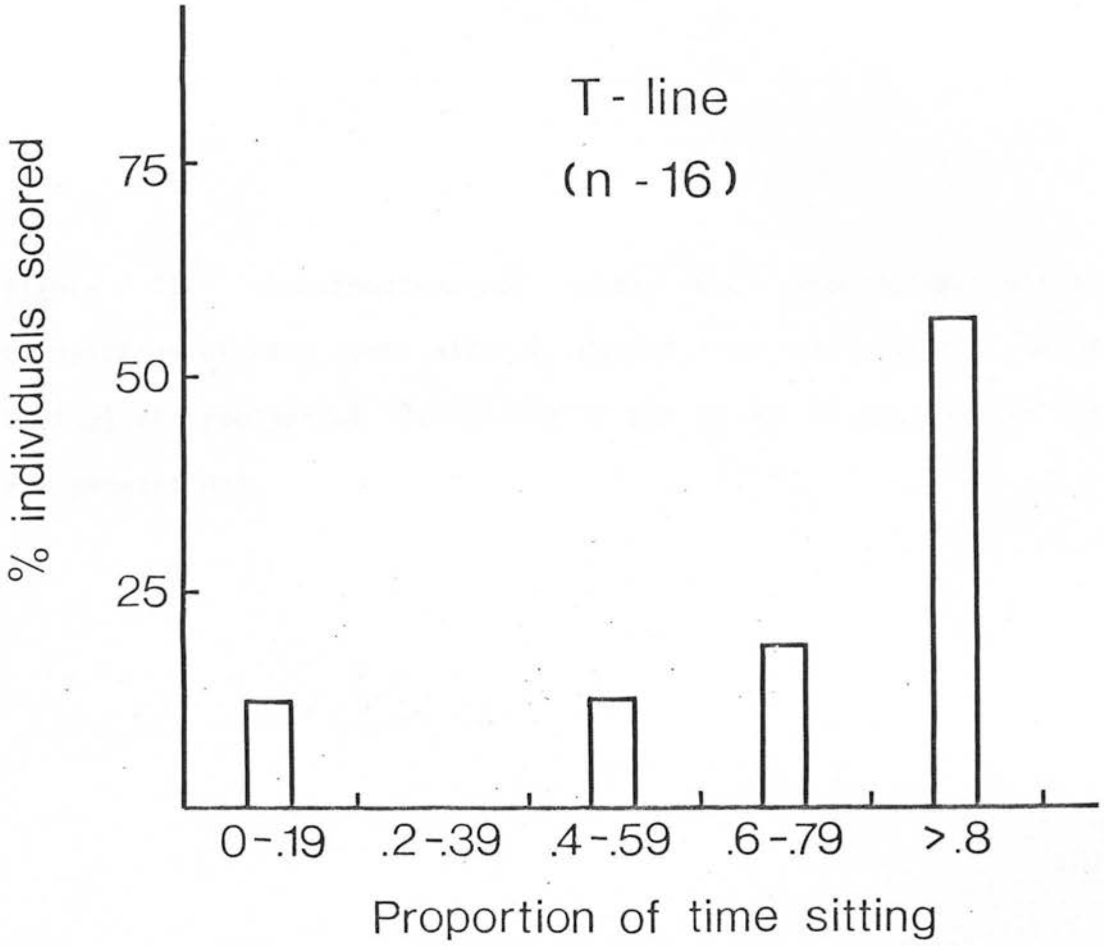

T - line
(n - 16)
% individuals scored
75
50
25
0-.19
.2-.39
.4-.59
.6-.79
>.8
Proportion of time sitting

Figure 71. Distributions of scores for pre-laying sitting (proportion of time spent sitting during the ten minutes before laying) of reciprocal F1 hybrids of the S1 and T1 generations (the F1b generation).

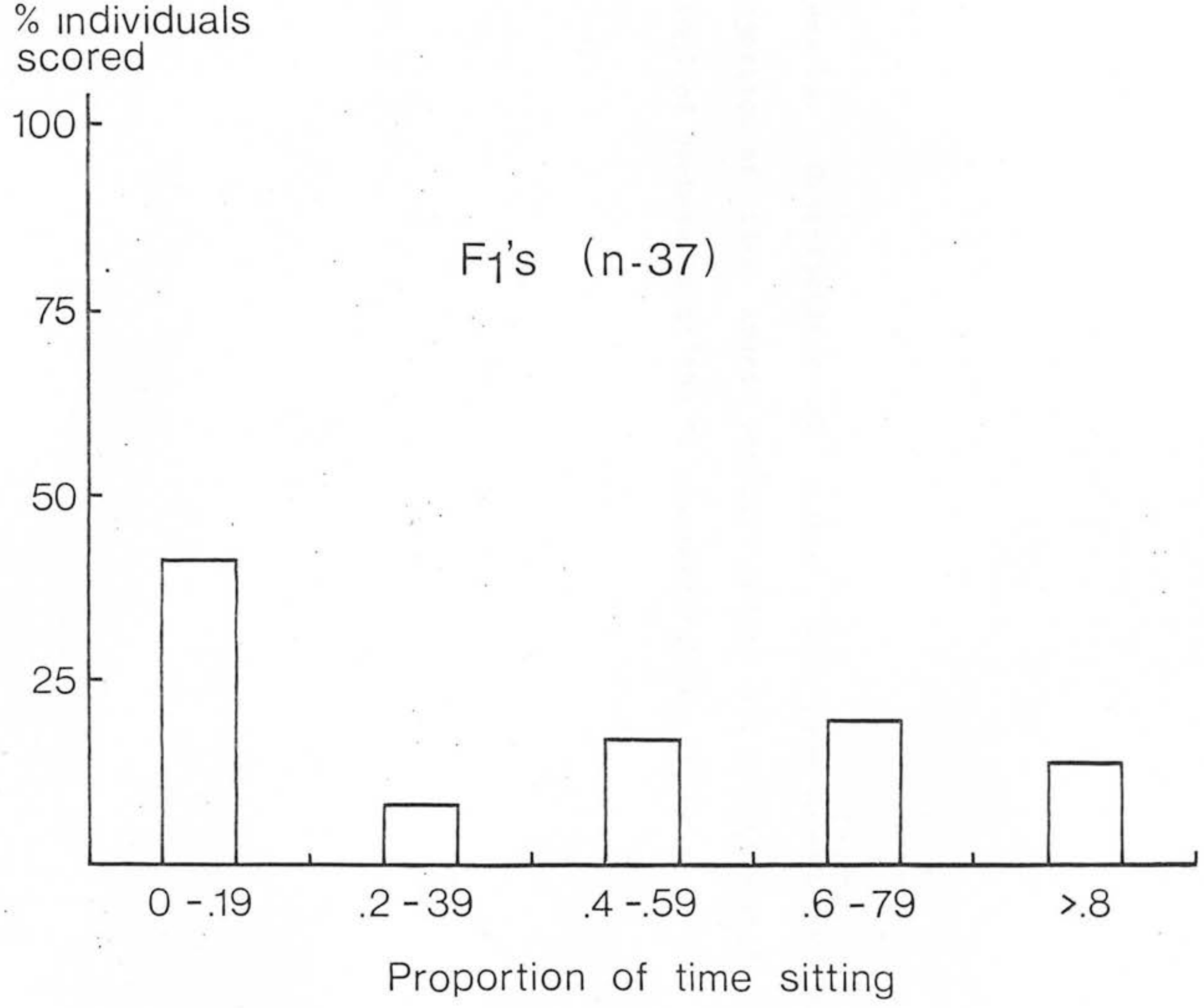
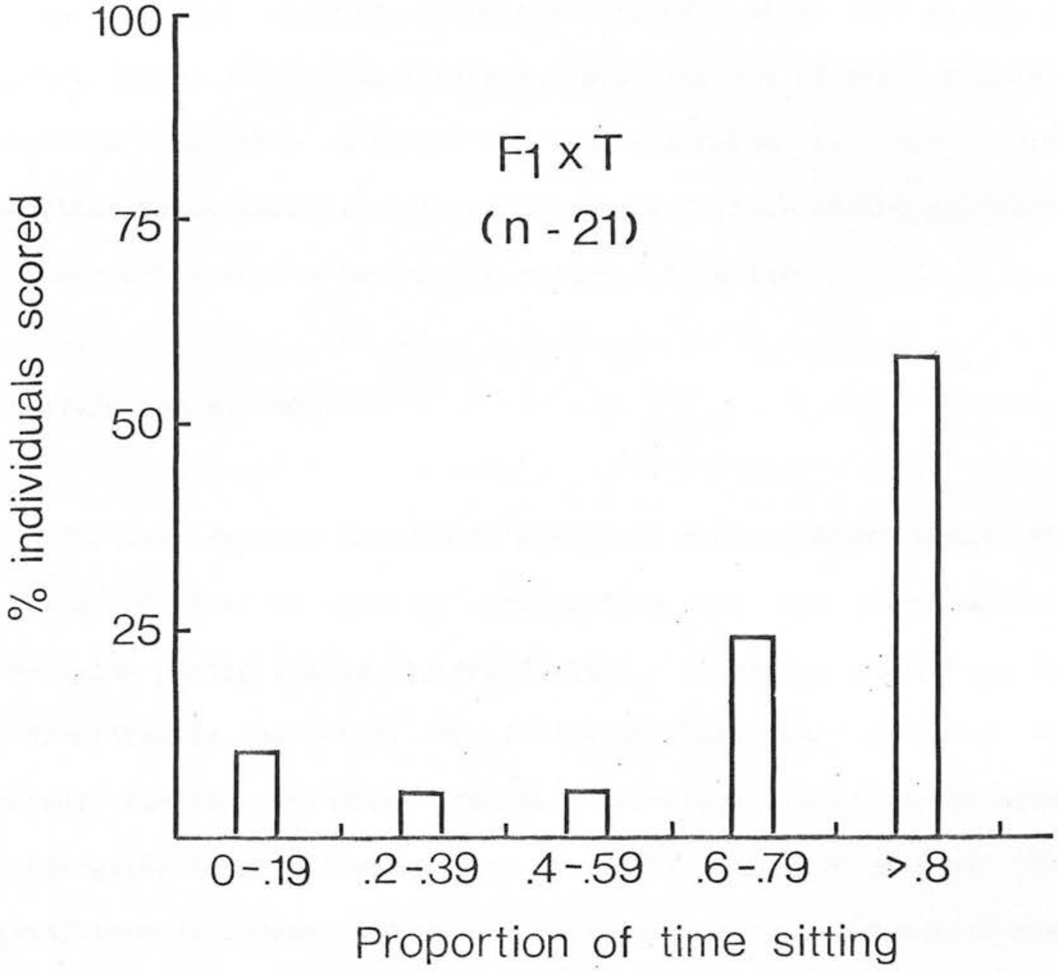

% individuals scored
100
75
50
25
F$_1$'s (n-37)
0 -.19
.2 - 39
.4 -.59
.6 - 79
>.8
Proportion of time sitting

Figure 7m. Distributions of scores for pre-laying sitting (proportion of time spent sitting during the ten minutes before laying) of backcosses to the S1 generation (F1 x S1).

Figure 7n. Distributions of scores for pre-laying sitting (proportion of time spent sitting during the ten minutes before laying) of backcrosses to the T1 generation (F1 x T1).


100
75
50
25
% individuals scored
F1 x T
(n - 21)
0-.19
.2-.39
.4-.59
.6-.79
>.8
Proportion of time sitting

Chapter 8. Quantitative analyses of strain differences in pre-laying behaviour patterns other than pre-laying pacing and pre-laying sitting.

Introduction.

In chapter 3. it was noted that both S and T line hens may on occasion exhibit behaviour patterns other than pacing and sitting during the period before laying. The aim of the experiment described in this chapter was to determine if there were quantitative differences between the S and T lines in the expression of these other traits during the period before laying.

Materials and methods.

The observations described here were made concomitantly with scoring of the S2 and T2 generations for the expression of pre-laying pacing and pre-laying sitting. Husbandry conditions were as described in chapter 2. The following behaviour patterns were scored; feeding, drinking, grooming (preening), rotation, scraping, litter-gathering, feather-raising, head-flicking, and jumping. Full definitions of these behaviour patterns, and the means of their quantification are given in table 8(a).

Although for the reasons given in chapter 2 observation periods were of variable duration, the data presented here refer only to the ten minutes before laying.

The occurrences of each of the nine behaviour patterns scored were recorded on an Esterline Angus event recorder, model number A620.

The large proportion of animals from each strain not showing the various behaviour patterns - see table 8b - made analyses based on the frequency or duration of behaviour inappropriate. Accordingly differences between the S and T lines in the expression of the nine behaviour patterns were made by comparing the number of animals in the two lines showing - or not showing - each behaviour, using the Fisher exact probability test, as described by Siegel, (1956).

Results.

The numbers of S and T line birds showing - or not showing - each of the behaviour patterns scored are shown in table 8(b).

There were no significant differences between the two lines in the numbers of individuals showing the various behaviour patterns, with the exceptions of drinking, feather-raising, and jumping. Significantly more S line than T line birds drank, and jumped ($p = 0.03$, and 0.05 respectively), and significantly more T line than S line birds exhibited feather raising ($p = 0.01$).

Discussion.

The findings presented in this chapter reveal that there are apparently few differences in the pre-laying behaviour of the S and T lines other than in the expression of pre-laying pacing and pre-laying sitting; and that one or other of these two behaviour patterns tends to dominate the behaviour of most birds during the ten minutes before laying.

There were significant differences between the strains in the expression of only three of the behaviour patterns scored. These were; drinking, feather-raising and jumping. That T line birds should exhibit more feather raising than S line birds, and S line birds more jumping than T line birds is not surprising, since feather raising - as defined here - is dependent on the bird sitting, and jumping is unlikely to occur unless the bird is pacing. Though why T line birds should exhibit waves of localised feather raising, which has no apparent function is not clear. It is also unclear why S line birds should drink more than T line birds. Two explanations are; (i) that because S line birds are moving about the cage from time to time they come into close proximity of the drinker, and that the drinker or the presence of water on the drinker leads to the release or ´´disinhibition`` (van Iersel and Bol, 1958) of drinking; or (ii) that since the birds are showing behaviour symptomatic of stress they may also be suffering from a ´dry mouth` due to inhibition of salivation caused by the release of adrenalin (Morgan, 1965). Both explanations are however purely speculative.

A substantial proportion (approximately fifty percent) of the animals from both strains exhibited grooming behaviour at some time during the ten minutes before laying. Why the birds should preen at this time is unclear. The behaviour could be a displacement activity shown in response to the thwarting of nesting or sitting behaviour. Or, since the belly and vent regions tend to be preened more than is usual, it might be a response to uterine movements or neuro-hormonal changes in the oviduct associated with laying.

Animals from both strains exhibited vacuum nesting behaviour. This has two implications; first, the motivation to perform nesting behaviour is high in both strains and second although they do not show behaviour symptomatic of frustration T line birds are presumbly subject to a conflict arising from the thwarting of nesting behaviour.

Table 8a. Definitions and means of quantification of pre-laying behaviour patterns other than pre-laying pacing and pre-laying sitting, shown by S2 and T2 generation hens during the ten minutes before laying.

BEHAVIOUR	DEFINITION
Feeding	Time spent looking at, pecking at or swallowing food.
Drinking	Time (s) spent fixating the ´nipple´ drinker pecking at the drinker, or swallowing water.
Grooming	Time spent engaged in activities associated with care of the plumage. Namely; preening preening, scratching, and shaking. See Kruijt, (1964) for a full description of these behaviour patterns.
Rotation.	The hen adopts the keel down - tail up posture or half squats, and then rotates. One such movement amounting to a turn of 90 degrees or more was scored as one rotation.
Scraping	The hen adopts the keel down - tail up posture or half squats, and then pushes her feet out backwards and sideways succesively. Each backwards and sideways kicking movement was

	scored as one scrape.
Litter-gathering	The hen sits or half crouches, she then extends her neck so that her head is moved downwards and forwards, she then retracts her neck so that her head is drawn back against her body with her bill just above, or just in contact with the floor of the cage. A series of such movements performed without interruption was scored as one bout of litter-gathering.
Feather-raising	Time spent with the dorsal plumage held in the ruffled posture (as described by Morris, 1956.).
Head-flicking	Rapid and repeated movement of the head from from one side to the other. One series of such movements performed without interruption was defined as one bout of head-flicking.
Jumping	Upwards and forwards movement of the body, involving pushing off with both legs, and simultaneously removing both feet from the floor. One such movement was defined as one jump.

Table 8b. The numbers of S2 and T2 birds exhibiting behaviour patterns other than pre-laying pacing and pre-laying sitting during the ten minutes before laying.

Behaviour pattern	Strain	Number of animals		P
		showing behaviour	not showing behaviour	
Feeding	S	6	14	0.10
	T	1	15	
Drinking	S	10	10	0.03*
	T	2	14	
Grooming	S	9	11	1.00
	T	8	8	
Rotation	S	9	11	0.30
	T	4	12	
Scraping	S	11	9	0.30
	T	5	11	
Litter gathering	S	11	9	1.00
	T	8	8	
Feather raising	S	4	16	0.01**
	T	11	5	

Head	S	5	15	0.17
flicking	T	8	8	
Jumps	S	5	15	0.05*
	T	0	16	

Chapter 9. Ethological analysis of pre-laying pacing and pre-laying sitting 1. Are strain differences in pre-laying behaviour a reflection of strain differences in fearfulness or emotionality?

Introduction

The behavioural differences between the S and T lines are not restricted to pre-laying behaviour in battery cages. Another striking behavioural difference between the two lines lies in the responses shown to human beings, and to novel objects. S line hens typically withdraw from human beings, whereas T line birds stand still or actively approach. T line hens however tend to show more withdrawal from novel objects than S line hens, though this difference is stimulus specific (Murphy, 1975).

The aims of the experiments described here were; (i) to determine whether or not there was a relationship between pre-laying behaviour and behavioural responses to human beings and novel objects, and (ii) to determine if selection for pre-laying pacing and pre-laying sitting had brought about correlated changes in such responses.

Experiment 9 (i). Responses to a novel object.

Materials and methods

Thirteen S0, seventeen S2, seventeen T0 and fourteen T2 generation birds were tested. Each bird was tested in its home cage (see chapter 2.) All tests were carried out between 14.00 and 17.00 hrs. To avoid pre-laying behaviour confounding the responses shown to the novel object no bird was tested unless it had laid before

12.00 hrs. on the day of the test. Husbandry conditions were as described in chapter 2. All birds were tested when between thirty and forty weeks old.

At the start of the test the observer waited until the bird was feeding, or standing with its head through the bars of the cage front, then walked quietly up to the cage and placed the novel object - a nine inch length of 1/4´´ diameter dowelling supported vertically by a two inch square wooden stand - in the bird`s food dish. The observer then retreated one metre from the bird`s cage, and scored its behaviour during the ensuing minute, using the following scoring system. The minute after presentation of the novel object was divided into two thirty second periods. If the bird pecked the object in either thirty second period it was afforded a score of zero for that period. If the bird did not peck at the object within a thirty second period then its behaviour at the end of that period was scored as follows; standing with head through bars of cage front looking at object - score 1, standing looking at object from within the cage - score 2, standing facing the side of the cage - score 3, standing facing the rear of cage - score 4, showing escape behaviour - score 5. The scores for each thirty second period were then summed to give an overall score for fearfulness of between zero and ten.

Between lines, and between generations comparisons of scores were made using the Mann-Whitney test (two tailed). Correlations between scores for responses to the novel object and pre-laying pacing, and pre-laying sitting were calculated using Spearman`s rho correlation coefficient. Both types of test were computed using the ´Omnibus` computer program (Medis, 1980 a; 1980b).

Results

The scores for responses to the novel object of the S0 and S2, and T0 and T2 birds are shown in tables 9(i) and 9(ii) of appendix 1. There were no significant differences between the S0 and S2 generations, the T0 and T2 generations, the S0 and T0 generations, and the S2 and T2 generations in the responses shown to the novel object (table 9a.).

The correlations between scores for responses and pre-laying pacing, and pre-laying sitting are shown in table 9b. Only one correlation approached significance, this was the correlation between pre-laying pacing and response to the novel object in the S0 generation (rho = - 0.545; p = 0.051).

Table 9a. Comparison of the responses of S0, T0, S2 and T2 hens to a novel object. Responses were ranked on a scale from zero to ten; a score of zero implying little or no fear, a score of ten extreme fear. Comparisons were made using the Mann-Whitney U test (2-tailed).

COMPARISON	Z	P
S0 V S2	0.446	0.63
T0 V T2	1.229	0.22
S0 V T0	0.682	0.50
S2 V T2	0.06	0.95

Table 9b. Correlations (Spearman´s rho) between scores for pre-laying pacing and pre-laying sitting, and responses to a novel object of S0, T0, S2 and T2 hens.

CORRELATION BETWEEN RESPONSE TO NOVEL OBJECT AND	GENERATION	rho	P
PACING	S0	- 0.545	0.051
SITTING	S0	0.193	N.S.
PACING	S2	0.102	N.S.
SITTING	S2	0.139	N.S.
PACING	T0	0.359	N.S.
SITTING	T0	0.24	N.S.
PACING	T2	- 0.367	N.S.
SITTING	T2	0.094	N.S.

Experiment 9(ii). Responses to handling.

Materials and methods

Thirteen S0, eighteen S2, fourteen T0, and fifteen T2 generation birds were tested. Each bird was tested in its home cage (see chapter 2). All tests were carried out between 14.00 and 17.00 hrs. No bird was tested unless it had laid before 12.00 hrs. on the day of the test. Husbandry conditions were as described in chapter 2. All birds were tested when between thirty and forty weeks old.

The observer waited until the bird to be tested was feeding, or standing with its head through the bars of the cage front. The observer then moved up to the cage, opened the cage door, and picked up the bird. The bird`s response to being handled was assessed on the following scale; peck or threaten experimenter - score 0, no reaction -score 1, step backwards - score 2, crouch or turn away - score 3, turn away and crouch - score 4, retreat to back of cage - score 5, retreat to back of cage and struggle when picked up - score 6.

Because handling one bird tended to disturb the other birds in the poultry house, tests were separated by an interval of five minutes.

Between lines and between generations comparisons were made using the Mann-Whitney U test (two tailed). Correlations between scores for responses to handling and pre-laying pacing, and pre-laying sitting were calculated using Spearman´s rho correlation coefficient. Both types of test were computed using the ´Omnibus´ computer program (Medis 1980a, 1980b).

Results

The scores for responses to handling of the S0 and S2, and T0 and T2 hens are shown in tables 9.iii. and 9.iv. of appendix 1. There were no significant differences between the S0 and T0 generations in the responses shown to handling, there was however a very highly significant difference between the T2 and S2 generations, the S2 generation showing more fear than the T2 generation hens (table 9c). Across generations comparisons showed that S2 birds were significantly more fearful than S0 birds, and that T2 generations birds were significantly more fearful than the T0 generation birds.

The correlations between scores for responses to handling and pre-laying pacing, and pre-laying sitting are shown in table 9d. Only three significant correlations were found. There were significant negative correlations between responses to handling and pre-laying pacing in the S0 generation and response to handling and pre-laying sitting in the T0 generation; and a significant positive correlation between response to handling and pre-laying sitting in the S0 generation.

Discussion

The results of experiment 9(i) implied that there was no relationship between fear and pre-laying pacing or fear and pre-laying sitting. There being little or no evidence of correlations between responses to the novel object and either pre-laying behaviour, and no changes in responses to the object across generations in either the S or the T line. Experiment 9(ii) however produced contrary but confusing results. First, fear as measured by handling, increased significantly across generations in both the S and T lines,implying that selection for pre-laying pacing in the S line and pre-laying sitting in the T linehad in some way affected fear responses. Second, there were significant negative correlations between pacing and handling responses in the unselected S line, and between handling responses and sitting in the unselected T line which implied that both pre-laying pacing and pre-laying sitting were in some way related to fear responses. No such correlations existed in the selected S and T lines implying exactly the opposite.

The apparent ambiguity in the results of these two experiments is probably attributable to one or a combination of the following factors.

(i). The practical difficulties associated with designing tests for the measurement of fear (see Murphy, 1978 for a review of this subject). For instance the responses shown by the birds to the novel object in experiment 9(i) might have been attributable not to fear of the object - but rather to an interaction of tendencies to withdraw from the observer who presented the novel object and to explore the novel object.

(ii). Differences between the strains in responsiveness to the supposedly fear inducing stimuli. For example, S line birds show more withdrawal from human beings than T line birds (Murphy, 1975).

(iii). In this experiment fear was assessed on the basis of withdrawal responses. Absence of withdrawal responses does not always imply that an animal is not afraid (Jones et al, 1981).

(iv). Concerning the significant correlations found between pre-laying pacing and handling responses in the S0 generation, and between pre-laying sitting and handling responses in the T0 generation. These may well have been statistical anomalies arising from the small sample sizes and skewed distribution of the data. For example the correlation between sitting and handling responses in the T0 generation can be abolished by excluding the scores of two animals from the analysis.

(v). The increases in handling response scores across generations in both the S and T lines may have been batch or environmental effects. Since although the two lines were selected for two independent characters both lines showed increases in handling responses.

The findings of this chapter, although they imply that there is no relationship between fear and pre-laying pacing and pre-laying sitting in the S and T lines, do not prove this conclusively.

Table 9c. Comparisons of the responses of S0, T0, S2, and T2 hens to handling. Responses were ranked on a scale from zero to six, a score of zero implying little or no fear, a score of six extreme fear.

COMPARISON	Z	P	
S0 V S2	2.269	0.02*	S0 < S2
T0 V T2	2.244	0.02*	T0 < T2
S0 V T0	0.648	0.52	S0 > T0
S2 V T2	3.197	0.001***	S2 > T2

Table 9d. Correlations (Spearman´s rho) between scores for pre-laying pacing or pre-laying sitting and responses to handling of S0, T0, S2 and T2 hens.

CORRELATION BETWEEN RESPONSE TO HANDLING AND:	GENERATION	rho	P
PACING	S0	- 0.584	0.034*
SITTING	S0	0.615	0.024*
PACING	S2	0.034	N.S.
SITTING	S2	- 0.019	N.S.
PACING	T0	0.362	N.S.
SITTING	T0	- 0.603	0.021*
PACING	T2	0.203	N.S.
SITTING	T2	0.190	N.S.

Chapter 10. Ethological analysis of pre-laying pacing and pre-laying sitting II. Are strain differences in pre-laying pacing and pre-laying sitting a reflection of strain differences in behavioural responses to frustration?

Introduction

When domestic hens become frustrated, depending on the severity of the frustration and the stimulus situation, they typically show either displacement preening, increased aggression, or stereotyped pacing (Duncan, 1970). The aims of the experiments described in this chapter were; (i) to determine if there was any relationship between the stereotyped pacing shown during the pre-laying period and the behaviour patterns shown in response to the frustration of feeding behaviour and (ii) to determine if there were any differences between the S and T lines in their responses to frustration which could be related to the differences in their pre-laying behaviour.

Materials and methods.

Fourteen S2 generation and eleven T2 generation birds were tested. Each animal was tested in its home cage (see chapter 2). The animals' histories and their husbandry conditions were as described in chapter 2. All the animals were tested when between twenty six and thirty nine weeks of age. All tests were carried out between 14.00 and 16.00hrs.

On each of the three days prior to testing each bird was deprived of food at a fixed time between 08.00 and 10.00hr., after six hours of food deprivation the bird was presented with a food hopper containing 300g of food. After ten minutes the hopper was removed, and the bird deprived of food for a further thirty minutes.

After this three day training period each animal was tested in two situations, these were;

(i). FRUSTRATED:- the bird was deprived of food for six hours. The period of deprivation being the same as in the bird`s training period. After deprivation the bird was presented with food contained in a hopper covered with a transparent perspex lid. The bird could therefore see the food but could not obtain it. After ten minutes the food hopper was removed and the bird deprived for a further thirty minutes, after which its food hopper was replaced.

(ii). CONTROL:- The bird was allowed free access to food during the six hours in which during the days of the training period and the frustrated test it had been deprived of food. At the end this six hour period the bird′s food hopper was removed and immediately replaced with one covered with a perspex cover for ten minutes. After this period the perspex covered food hopper was removed and replaced with an uncovered hopper.

In both the frustrated and control tests, during the period which the birds were presented with covered food dishes the expression of the following behaviour patterns was recorded:

(i). The number of steps taken.

(ii). The number of thwarted pecks, i.e. the number of pecks directed at the perspex cover of the food dish.

(iii). The number of re-directed pecks, i.e. the number of pecks directed at objects other than the cover of the food dish.

(iv). The time (s) spent drinking.

(v). The time (s) spent sitting.

(vi). The time spent preening

The expression of each of these behaviour patterns was recorded on a twenty channel Ester-line Angus event recorder, model number

A620, run at a chart speed of 0.75`` per minute.

Between lines comparisons of each of the behaviour patterns scored in both the frustrated and the control situations, were made using the Mann-Whitney U test (two tailed). Within line comparisons between the control and test situations were made using the ´sign test` (two tailed) within lines correlations between scores for pre-laying pacing and the number of steps taken in the frustrated test situation were calculated using the Spearman ´rho` correlation coefficient. All calculations were made using the ´Omnibus` computer programme (Meddis, 1980a; 1980b).

Results.

The scores of the S2 and T2 birds for each of the behaviour patterns scored , in the frustrated and control tests, are shown in table 10a. Within strains comparisons of the expression of the various behaviour patterns are shown in table 10b. S2 birds made more thwarted pecks and took more steps in the frustrated test than in the control test, there were no significant differences between the frustrated and control situation in the expression of any of the other behaviour patterns scored. T2 birds made more thwarted pecks during the frustrated test than in the control test, and spent more time drinking in the control test than in the frustrated test. There were no significant differences between the frustrated and control situations in the expression of any of the other behaviour patterns scored.

There were no significant differences between the two lines in the expression of any of the behaviour patterns scored in the frustrated or control situations (table 10c).

The correlations between the number of steps taken in the pre-laying period and the number of steps taken in the frustrated test are shown in table 10d.

Discussion

The absence of differences in the behaviour patterns shown by S and T line hens in the frustrated test implies that S and T line birds respond to the thwarting of feeding behaviour in similar ways, and therefore that the differences in their pre-laying behaviour are unlikely to stem from general differences in behavioural responses to frustration. A conclusion supported by the findings of Wood-Gush, (1972), who - in an experiment essentially similar to this one - deprived birds of food for twenty-four hours and then presented them with visible but inaccessible food, and found that under such conditions birds from both strains exhibited stereotyped pacing behaviour, although S line birds paced more than T line birds. Similarly in this experiment, although both strains paced more in the frustrated situation than in the control situation, only in the S line was the difference significant. All of which may imply either that S line birds are more easily frustrated than T line birds, or that S line birds respond more intensely to frustration than T line birds.

Only two other significant differences in behaviour between the frustrated and the control situation were found these being an increase in thwarted pecking in the frustrated test in both lines, and an increase in time spent drinking in the frustrated test in the T line. The increase in thwarted pecking is hardly surprising since in the frustrated situation the birds would have a greater motivation to feed than in the control situation, where attention to food was probably more due to its removal and representation than to hunger (Bayer, 1929). Why T line birds should drink more than S line birds when frustrated is however unclear.

The absence of a correlation between the number of paces taken in the ten minutes before laying is, in the case of the T line birds, is not surprising since the majority of locomotion shown by T line birds during the pre-laying period takes place during the course of nesting behaviour, and there is no reason why nesting behaviour and behavioural responses to the thwarting of feeding behaviour should be in any way related. The absence of such a correlation in the case of the S line birds, where in both situations pacing appears to be a response to frustration, is more interesting. Since it implies that either there is individual variation in the degree of frustration engendered by the thwarting of particular behavioural drives, or that the expression of pre-laying pacing is only loosely dependent on the degree of frustration, and may be influenced by factors associated with the frustrating situation.

Table 10a The mean (+/- S.E.) scores for the expression of six behaviour patterns in a ten minute period of fourteen S2 and eleven T2 generation hens when tested in two situations: a). FRUSTRATED:- deprived of food for six hours, and then presented with visible but inaccessible food and b). CONTROL:- allowed free access to food, and then presented with visible but inaccessible food.

BEHAVIOUR PATTERN	TEST	GENERATION	MEAN (+/- S.E.) SCORE
NO. OF THWARTED PECKS	FRUSTRATED	S2	99.14 +/- 21.66
	CONTROL	S2	39.57 +/- 13.64
	FRUSTRATED	T2	67.00 +/- 10.21
	CONTROL	T2	8.73 +/- 4.18
NO. REDIRECTED PECKS	FRUSTRATED	S2	45.71 +/- 12.73
	CONTROL	S2	22.50 +/- 6.49
	FRUSTRATED	T2	25.00 +/- 3.92
	CONTROL	T2	9.36 +/- 3.42
TIME (S) SPENT DRINKING	FRUSTRATED	S2	2.90 +/- 9.65
	CONTROL	S2	31.71 +/- 15.85
	FRUSTRATED	T2	4.36 +/- 2.93
	CONTROL	T2	76.00 +/- 32.81
TIME (S) SPENT PREENING	FRUSTRATED	S2	14.86 +/- 4.97
	CONTROL	S2	137.71 +/- 33.84
	FRUSTRATED	T2	33.82 +/- 17.14
	CONTROL	T2	106.18 +/- 40.83

TIME (S) SPENT SITTING	FRUSTRATED	S2	-
	CONTROL	S2	-
	FRUSTRATED	T2	-
	CONTROL	T2	-
NUMBER OF STEPS TAKEN	FRUSTRATED	S2	168.07 +/- 44.92
	CONTROL	S2	88.00 +/- 16.70
	FRUSTRATED	T2	139.46 +/- 33.29
	CONTROL	T2	83.27 +/- 28.39

Table 10b. Within lines comparisons of the expression of the various behaviours scored in the frustrated and control tests.

COMPARISON	LINE	Z	P
Number of thwarted pecks.	S	2.14	0.030*
	T	3.16	0.002**
Number of redirected pecks.	S	1.60	0.100
	T	1.51	0.128
Time spent drinking (s).	S	1.63	0.098
	T	2.12	0.032*
Time spent preening (s).	S	0.83	0.203
	T	1.67	0.092
Time spent sitting (s).	S	-	-
	T	-	-
Number of paces taken.	S	2.67	0.008 **
	T	1.51	0.0128

Table 10b. Between lines comparisons of the various behaviours scored in the control and the frustrated tests.

COMPARISON	TEST	Z	P
Number of thwarted pecks.	Frustrated	0.931	0.352
	Control	1.744	0.078
Number of redirected pecks.	Frustrated	0.446	0.653
	Control	0.992	0.322
Time spent drinking (s).	Frustrated	0.057	0.952
	Control	0.469	0.638
Time spent preening (s).	Frustrated	1.244	0.215
	Control	1.302	0.190
Time spent sitting (s).	Frustrated	-	-
	Control	-	-
Number of steps taken.	Frustrated	0.986	0.322
	Control	0.849	0.395

Table 10d. Correlations (Spearman´s rho) between scores for pre-laying pacing (average number of steps taken per minute in the ten minutes before laying) and scores for the number of steps taken in ten minutes when frustrated by being presented with visible but inaccessible food after six hours of food deprivation, of fourteen S line and ten T line birds.

STRAIN	rho	P
S	- 0.054	> 0.05 NS.
T	0.02	> 0.05 NS.

Chapter 11. Ethological analysis of pre-laying pacing and pre-laying sitting. III. Are strain differences in in the expression of pre-laying pacing and pre-laying sitting a reflection of strain differences in stimulus generalisation mechanisms?

Introduction.

Wood-Gush (1972) suggested that the differences in the pre-laying behaviour of S and T line hens might arise because the battery cage fails to provide the apropriate environmental stimuli for the release of sitting behaviour. S line hens unable to find a suitable site for nesting become frustrated, and as a consequence exhibit stereotyped pacing behaviour. T line hens however generalise to sub-optimal stimuli within the cage and show a more normal sequence of sitting and nesting behaviour patterns (see Chapter 12 for a fuller discussion of this point).

If this hypothesis is correct and T line hens are better able, than S line hens, to generalise to environmental stimuli releasing sitting behaviour in the period before laying then the question arises is this ability to generalise to sub-optimal stimuli specific to the environmental stimuli releasing nesting behaviour, or is it a non-specific phenomenon? That is to say are T line hens less specific than S line hens in their responses to all environmental stimuli?

The aim of the experiment described in this chapter was to determine if hungry T line hens would more readily accept - generalise to - novel food stuffs than would hungry S line hens.

Materials and methods.

Six S line hens and six T line hens were tested. These twelve birds were drawn at random from the Poultry Research Centre`s stocks and were the only animals used in this study which were not members of, or descendents of the original population of thirty one S line and forty T line birds described in chapter 2. Husbandry of these birds from one day old to completion of this experiment was as described in chapter 2. All birds were tested when between twenty-six and thirty-nine weeks of age. All birds were tested in their home cages.

For thirteen days each bird was deprived of food at a fixed time between 09.00 and 10.00 hrs. After six hours deprivation each bird was presented with, and allowed free access for twenty minutes, to a trough containing 300g of its usual food (the Poultry Research Centre`s layers mash). After this twenty minute period the trough was removed and the bird deprived of food for a further thirty minutes . The trough was then replaced and the bird allowed to feed at will until it was deprived again on the morning of the following day, when the trough of food was removed and the weight of food it contained made up to 300g. During this thirteen day period a record was kept of the amount of food consumed by each bird on each day, its latency to feed at the start of the twenty minute feeding period - latency to feed being defined as the time, in seconds, between presentation of the bird with food and its first peck at the food - and the amount of food the bird consumed in the twenty minute feeding period.

On the fourteenth day of deprivation each bird`s food trough was removed at the usual time, and six hours later replaced with one containing a novel food stuff (layers mash dyed green with a commercial food colouring). The bird was then allowed free access to the novel food for twenty minutes, a record being kept of its latency to feed and the amount of the novel food it consumed in the twenty minute period. After the twenty minutes had elapsed the novel food was removed, and replaced thirty minutes later with the bird`s normal food

After a further three days of deprivation and presentation with ´´normal`` layers mash each bird was presented with a second novel food (whole wheat grains), and after a further three days of deprivation and presentation with ´´normal`` food with a third novel food (rolled porridge oats). A record was kept of the latency to feed and the amount of food consumed in the twenty minute feeding period by each bird for each novel food.

In order to correct for possible intra-individual variability in latencies to feed, or amounts of food consumed in the twenty minute feeding period; each bird`s latency to feed when presented with a novel food was expressed as a proportion of its mean latency to feed when presented with its usual food, and the amount of the novel food it consumed as a proportion of the mean amount of ´´normal`` food consumed in twenty minutes after six hours of food deprivation. Between lines comparisons of all the parameters measured were made using the Mann-Whitney U test (two-tailed). All calculations were made using the ´´Omnibus`` computer programme (Meddis, 1980a and 1980b).

Results.

The mean (+/- S.E.) weight of food consumed per day, latency to feed when presented with food after six hours of food deprivation, and the weight of food consumed by each bird during the thirteen day training period are shown in in table 11a. There were no significant differences between the S and T lines in respect of any of these three parameters (table 11b.).

The latencies of the birds to feed when presented with each of the three novel foods are shown in table 11c. There was no significant difference between the S and T lines in the latency to feed when presented with layers mash dyed green or rolled porridge oats, T line birds however had a significantly greater latency to feed than S line birds when presented with wheat (table 11d.)

The amounts of each of the novel foods consumed by each of the birds tested is shown in table 11e. There was no significant difference between the S and T lines in the amount of green mash and rolled oats eaten, but S birds ate significantly more wheat than T line birds (table 11f.).

Discussion

The hypothesis tested in this experiment - that T line hens generalise more readily to sub-optimal stimuli than S line hens - predicts that T line hens would be more likely to accept slightly novel food stuffs than S line hens. The two strains did not differ significantly in their latencies to feed when presented with their usual food after six hours of food deprivation, nor in the amount of food consumed in the twenty minutes after its presentation. However when the two strains were presented with the three novel foods after six hours deprivation, there was again either no difference between the strains in the latency to feed and the amount of novel food consumed (two of the novel foods - green mash and rolled oats), or the S line had a shorter latency to feed and consumed more (one novel food - whole wheat grains). These findings are not in accord with those predicted by the hypothesis, and imply that it should be rejected. However before drawing such a conclusion it is necessary to make the following points:

i). Firstly concerning latencies to feed: In general T line birds are more neophobic than S line birds, and S line birds are more likely to actively explore novel objects or environments (Murphy, 1975). All three of the novel foods presented differed in colour from the birds usual food, but only the whole wheat grains differed markedly in shape and form. Thus since the birds latencies to feed differed significantly only with the most unusual of the three foods, these findings could be interpreted in terms of differences in neophobia.

Second; concerning the amounts of the novel foods consumed: Birds from both strains consumed very little of the green mash and rolled oats, and this could simply be a reflection of the fact that the foods were unpalatable. Further, although S line birds did consume significantly more grain than T line birds, they also started feeding significantly earlier and therefore had more time available for feeding.

Thus although the findings are not consistent with T line birds being more generally more able to generalise to sub-optimal stimuli, they cannot be regarded as proof that this is the case.

Table 11a. The mean (+/- S.E.) weight of food consumed in twenty four hours, latency to feed when presented with food after six hours of food deprivation, and weight of food consumed in twenty minutes following six hours of food deprivation by six S line and six T line hens.

BIRD	MEAN (+/-S.E.) WEIGHT (g) OF FOOD CONSUMED IN 24HR.	MEAN (+/-S.E.) WEIGHT (g) OF FOOD CONSUMED IN 20M.	LATENCY (S) TO FEED
S5	90.39 +/- 5.59	9.46 +/- 1.25	3.15 +/- 5.16
S8	88.85 +/- 2.67	9.31 +/- 1.33	10.62 +/- 2.08
S1983	87.31 +/- 8.14	16.62 +/- 2.38	3.80 +/- 7.96
S4	93.46 +/- 4.98	9.92 +/- 1.02	3.39 +/- 1.02
S1976	91.69 +/- 6.19	13.39 +/- 1.11	3.88 +/- 0.71
S1964	106.92 +/- 4.82	11.77 +/- 1.03	3.54 +/- 1.45
T8428	103.46 +/- 7.46	12.80 +/- 3.12	18.48 +/- 3.78
T8420	81.15 +/- 6.98	11.23 +/- 1.15	4.77 +/- 1.34
T8859	95.00 +/- 6.07	7.58 +/- 1.12	3.73 +/- 0.67
T8861	53.08 +/- 4.99	5.15 +/- 0.70	3.54 +/- 0.84
T8422	65.77 +/- 3.20	6.85 +/- 0.90	3.77 +/- 0.86
T8421	96.92 +/- 6. 39	9.00 +/- 1.20	3.23 +/- 0.61

Table 11b. Between lines comparisons of the mean (+/- S.E.) weight of food consumed in twenty four hours, latency to feed when presented with food after six hours of food deprivation, and weight of food consumed in twenty minutes following six hours of food deprivation by six S line and six T line hens.

COMPARISON	Z	P
WEIGHT OF FOOD (g) CONSUMED IN 24HR.	0.48	0.63
WEIGHT OF FOOD (g) CONSUMED IN 20M.	0.40	0.69
LATENCY (s) TO FEED.	0.40	0.07

Table 11c. Latencies to feed (s) of six S line and six T line hens when presented with various novel foods after six hours of food deprivation. Unbracketed figures are actual latencies, bracketed figures are the actual latencies expressed as a fraction of the birds` latency to feed when presented with its normal food after six hours of food deprivation, (see Table 11a.).

BIRD	LATENCY TO FEED (S)		
	GREEN MASH	WHOLE WHEAT GRAINS	ROLLED OATS
S5	1	1	4
	(0.32)	(0.32)	(1.27)
S8	2	1	-
	(0.18)	(0.09)	-
S1983	2	3	9
	(0.52)	(0.79)	(2.37)
S4	5	1	19
	(1.48)	(0.30)	(5.61)
S1976	2	3	17
	(0.52)	(0.77)	(4.38)
S1964	8	1	10
	(2.26)	(0.28)	(2.28)
T8424	3	1200	1200
	(0.16)	(64.94)	(64.94)
T8420	1	1200	1200
	(0.21)	(251.57)	(251.57)
T8859	5	1200	7

	(1.34)	(321.72)	(1.88)
T8861	2	1200	1200
	(0.57)	(338.98)	(338.98)
T8422	11	1200	1200
	(2.92)	(318.30)	(318.30)
T8421	1	4	4
	(0.31)	(1.24)	(1.24)

Table 11d. Between lines comparisons of latencies to feed, corrected for inter-individual variation, of six S line and six T line hens when presented with various novel foods after six hours of food deprivation.

NOVEL FOOD	Z.	P	
GREEN MASH	0.321	0.750	
WHOLE WHEAT GRAINS	2.882	0.004*	S < T
ROLLED OATS	1.095	0.270	

Table 11e. Weight of food (g) consumed by each of six S line and six T line hens when presented with various novel foods after six hours of food deprivation. Unbracketed figures are actual amounts consumed, bracketed figures are the actual amounts consumed expressed as a proportion of the amount consumed by each bird when presented with its normal food after six hours of food deprivation, (see table 11a.).

BIRD	WEIGHT OF FOOD CONSUMED (g).		
	GREEN MASH	WHOLE WHEAT GRAINS	ROLLED OATS
S5	20	6	5
	(2.11)	(0.63)	(0.53)
S8	5	3	-
	(0.54)	(0.32)	-
S1983	1	6	5
	(0.06)	(0.37)	(0.30)
S4	10	1	1
	(1.01)	(0.01)	(0.01)
S1976	10	10	1
	(0.75)	(0.75)	(0.08)
S1964	8	1	5
	(0.68)	(0.09)	(0.43)
T8424	1	1	0
	(0.08)	(0.08)	-
T8420	1	0	0
	(0.09)	-	-

T8859	1	0	5
	(0.13)	-	(0.66)
T8861	10	0	0
	(1.94)	-	-
T8422	1	0	0
	(0.15)	-	-
T8421	6	2	5
	(0.67)	(0.20)	(0.50)

Table 11f. Between lines comparisons of the amounts of food (g) consumed, corrected for intra-individual variation, of six S line and six T line hens when presented with various novel foods after sixhours of food deprivation.

NOVEL FOOD	Z	P	
GREEN MASH	1.210	0.130	
WHEAT GRAINS	2.608	0.008**	S > T
ROLLED OATS	1.121	0.130	

Chapter 12. Conclusions and general discussion. I. The pre-laying behaviour of domestic fowl housed in battery cages. A model and its implications.

Introduction.

In previous chapters it has been argued that the differences in the pre-laying behaviour of S and T line hens housed in battery cages are a consequence of differences in responses to the disruption of pre-laying and nesting behaviour, and are probably not a reflection of general differences in responses to aversive situations, frustration, or the ability to generalise to environmental releasers. It has also been argued that there is genetic variation in the behavioural responses shown by S and T line hens to this disruption of pre-laying and nesting behaviour - stereotyped pacing in the S line and sitting in the T line - and that these traits are inherited independently. The expression of pre-laying pacing being controlled by a single gene or a polygenic threshold effect, and the expression of pre-laying sitting being under the control of genes with additive effects. In this chapter I attempt to bring at least some of these findings together. First, by constructing a model of the pre-laying behaviour of S and T line hens in battery cages. Second, by briefly discussing some of their theoretical implications.

A model of the pre-laying behaviour of domestic hens confined in battery cages.

As mentioned in chapter 1 in environments less restricted than the battery cage the pre-laying and nesting behaviour of the hen can be divided into three sequential phases. These are;

i). A phase of general restlessness which marks the onset of pre-laying behaviour (Wood-Gush and Gilbert, 1969a).

ii). A phase of nest examination which culminates in nest site selection (Wood-Gush, 1963).

iii). A phase of nest-building and sitting behaviour (Wood-Gush, 1975a).

In battery cages both S and T line hens show elements of the behaviour patterns characteristic of restlessness, and of nest-examination (see chapter 3), and it is apparently at the transition between the nest examination and nest building and sitting phases that the behavioural divergence between the S and T lines occurs.

On the basis of the findings presented here and those presented by Wood-Gush, (1972 and 1975a and 1975b) the following model is put forward to explain the causation of this divergence.

As the nest examination phase comes to an end, the tendencies to exhibit nest-building and sitting increase and become prevalent to the tendencies to show nest examination. In response to this T line birds generalise to sub-optimal stimuli from the cage associated with the the release of sitting behaviour (Wood-Gush, 1972 and 1975), and pass into the nest-building and sitting phase, thus allowing expression of the genes controlling sitting behaviour. S line birds however are unable to generalise to the sub-optimal stimuli which release sitting in the T line birds, and as a consequence suffer thwarting of the tendencies to show nesting and sitting behaviour. As the point of lay approaches these tendencies become increasingly strong, and the conflict which arises because they cannot be expressed results in the bird becoming frustrated. This frustration is expressed in stereotyped pacing, which becomes more and more intense as the point of lay approaches, and the degree of frustration increases (see figures 12a, 12b, and 12c).

This model can also be used to explain the behaviour of birds which show neither pacing nor sitting, and birds which show both. Birds which show neither behaviour will either, like T line birds enter the nest-building and sitting phase, but having entered the phase lack the genetic pre-disposition to sit; or alternatively, like S line birds be unable to generalise to the suboptimal stimuli releasing nesting and sitting and become frustrated, but as a consequence of the single gene or polygenic threshold effect controlling the expression of pre-laying pacing lack the pre-disposition to express this frustration in stereotyped pacing. Such animals typically spend much of the pre-laying period standing in the hunched posture facing the rear of the cage, from time to time giving the pre-laying call. Animals which show both behaviour patterns will be essentially S line like, becoming frustrated and expressing this frustration in stereotyped pacing, but will also have a strong genetic predisposition to sit, and as the point of lay approaches and the motivation to sit increases, show sitting as a vacuum activity alternated with periods of pacing.

The model in its present form does not however explain the extreme consistency shown in pre-laying behaviour by both S and T line hens. It is suggested here that this individual consistency in the expression of pacing and sitting is the result of a conditioned or learnt response associated with a relief from stress which accompanies laying of the egg. Considerable evidence exists that laying the egg is physiologically stressful for the hen. During the pre-laying period there are marked increases in the plasma concentration of the stress hormone corticosterone (Beuving, 1980, Beuving and Vonder, 1977)), core temperature (Bobr and Sheldon, 1977: Winget et al, 1965) and heart rate (pers. ob.). The elevation of all three of these variables peaks at the time of lay and tends to decline rapidly thereafter. These findings suggest the stress associated with laying is terminated suddenly in the few moments taken to actually lay the egg. Given this, it is possible that the behaviours shown by the hen in the period before laying, particularly those shown very shortly before laying, might become associated with the relief from stress, and thus become reinforced in a manner analagous to the way in which the ´´superstitious`` behaviour patterns sometimes shown by animals in Skinner boxes are reinforced (Skinnner, 1948). Thereby becoming fixed in the bird`s behavioural repertoire as a type of pre-laying ´´ritual``. Thus a S line bird which had just come into lay would tend to exhibit a particular level of pre-laying pacing, and with succesive ovipositions this level of pacing would become stabilised and consistent. Similarly a T line hen would have a tendency to sit for a particular period of time before laying, and with successive ovipositions would become conditioned to sit consistently for this period.

The question of how this behaviour difference between the S and T lines arose during domestication is an interesting one. Wood-Gush, (1972) suggested that: Either the threshold for the release of pre-laying sitting had risen in the S line, with the result that the birds had lost the ability to respond to the relevant stimuli for sitting. Or that the thresholds for sitting in the T line had been lowered, allowing the birds to generalise to sub-optimal stimuli from the cage. It is not possible to distinguish between thes two hypothesis on the basis of the findings presented here. However, evidence from other studies indicates that the latter hypothesis is the more likely. First, when kept in pens with nest boxes both strains show sitting and nesting behaviour which indicates that both retain the ability to respond to appropriate stimuli for the release of sitting (Wood-Gush, 1972). Second, brown leghorns, which are regarded to be a primitive strain, exhibit stereotyped pacing (Duncan,1970) which implies that pacing is the more primitive behaviour. Third, S line hens appear to be more specific in their choice of nest site (Appleby et al, In press), and are widely held to be less prone to floor laying when housed in pens with trap nests. All of which indicates that it is the behaviour of the T line rather than the S line which has changed during domestication.

The pre-laying behaviour of domestic hens in battery cages: Some implications.

The major findings of this study - that there is genetic variation in the expression of both pre-laying pacing and sitting - has two important but very diverse implications. The first of these implications relates to Tinbergen`s (1952) ´´derived`` activities hypothesis, the second implication to the possibility of improving the welfare of animals kept under intensive husbandry conditions by selecting for behavioural traits relevant to adaption to life under such conditions.

i). Implications for the ´´derived`` activities hypothesis.

As mentioned in chapter 1 Tinbergen´s ´´derived`` activities hypothesis postulates that many visual displays have been derived, through the processes of emancipation and ritualisation, from the behaviour patterns shown in response to conflict situations. This hypothesis demands that there be genetic variation in the performance of such behaviour patterns. Since in the absence of such variation the evolutionary changes in these behaviour patterns envisaged in the ``derived`` activities hypothesis could not have occurred. Until this study there was no evidence which showed directly that such variation existed. Thus the finding that there is heritable variation in the behaviour patterns shown by domestic hens in response to the conflict engendered by the thwarting of their pre-laying and nesting behaviour, which occurs when they are confined in battery cages, goes someway to substantiate the derived activities hypothesis. It is not, of course argued here that these findings imply that there is genetic variation in the expression of all conflict behaviours in all species, or that pre-laying pacing and pre-laying sitting in domestic hens are necessarily nascent displays, only that variation in the expression of these two traits is inaccord with the predictions of the ``derived activities`` hypothesis.

Implications for the improvement of animal welfare.

The potential value of behavioural genetics in the improvement of the welfare of domestic animals kept under intensive husbandry conditions is discussed at length in chapter 13 and is mentioned here only in relation to the expression of pre-laying pacing and sitting.

The finding s presented in this thesis show that there is genetic variation in the expression of both pre-laying pacing and pre-laying sitting in battery cages and that both traits respond to selection. There is therefore no reason in theory why it should not be possible to select for or against the expression of either trait on a commercial scale. Further, and perhaps more importantly, since pre-laying pacing appears to be inherited in a dichotomous fashion - i.e. a bird paces or it does not - exactly how many steps the hen takes in the period prior to laying is of little importance . Selection against this particular trait could therefore be operated on the basis of does the bird pace or not. An assesement which can be made from short term casual observations rather than from detailed long term observations. Therby making it possible to score large numbers of animals in a relatively short period of time (see chapter 13 for a further discussion of this point).

Figure 12a. The number of paces taken per minute by a S line hen during the thirty minutes before laying plotted against minutes before laying, showing how the intensity of pacing increases as the point of lay approaches.

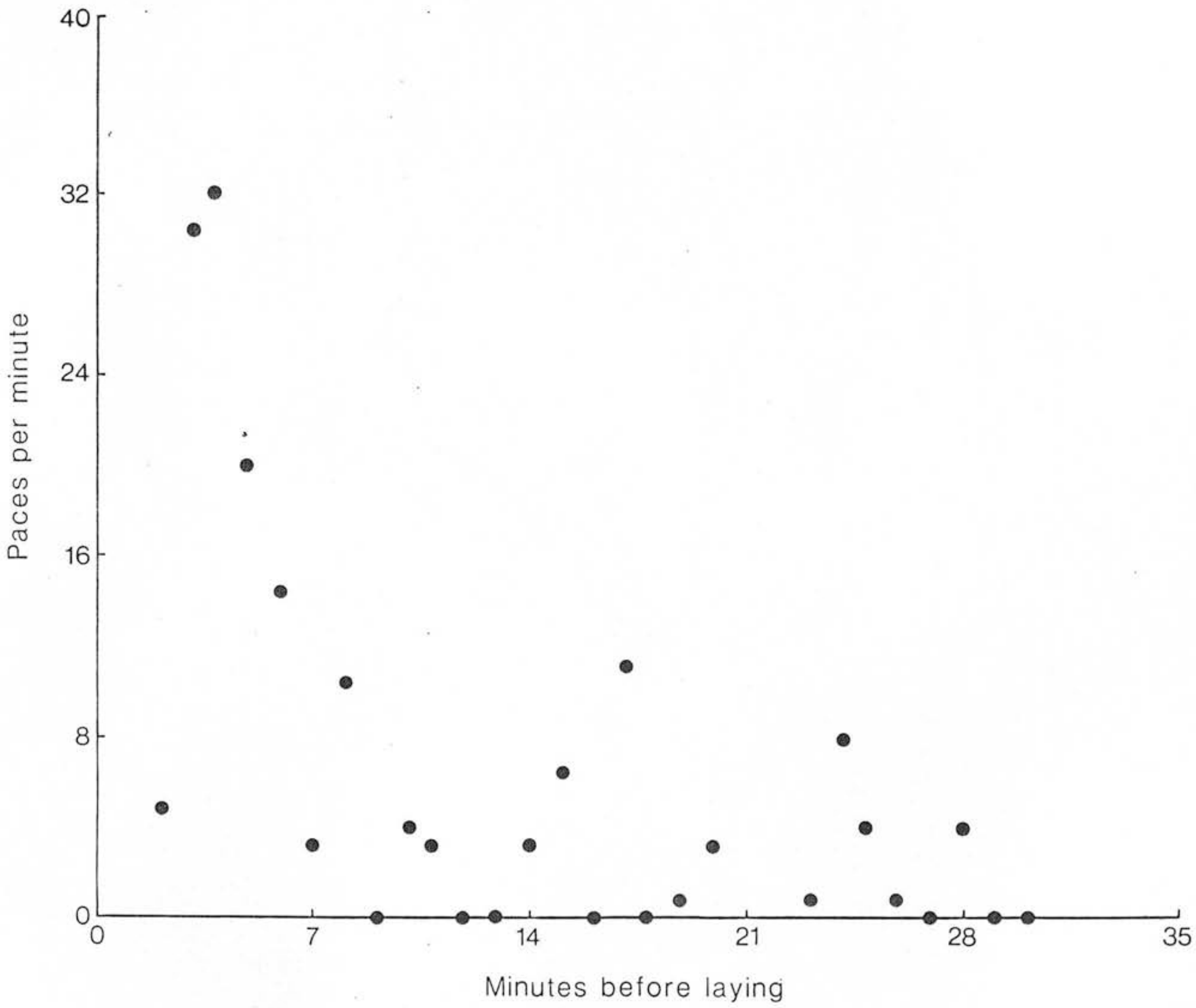

Paces per minute
40
32
24
16
8
0
0
7
14
21
28
35
Minutes before laying

Figure 12b. The number of paces taken per minute by a S line hen during the thirty minutes before laying plotted against minutes before laying, showing how the intensity of pacing increases as the point of lay approaches.

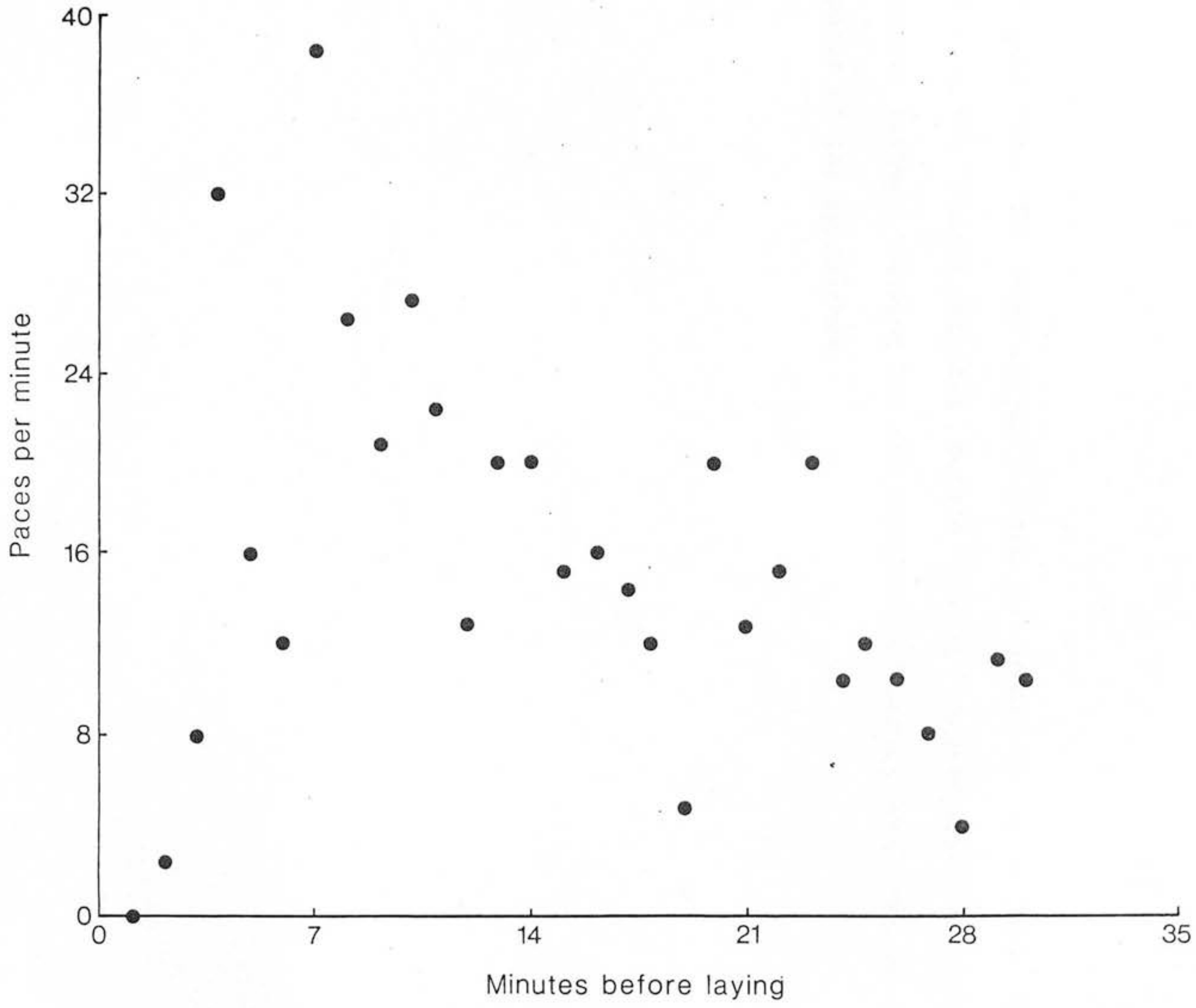
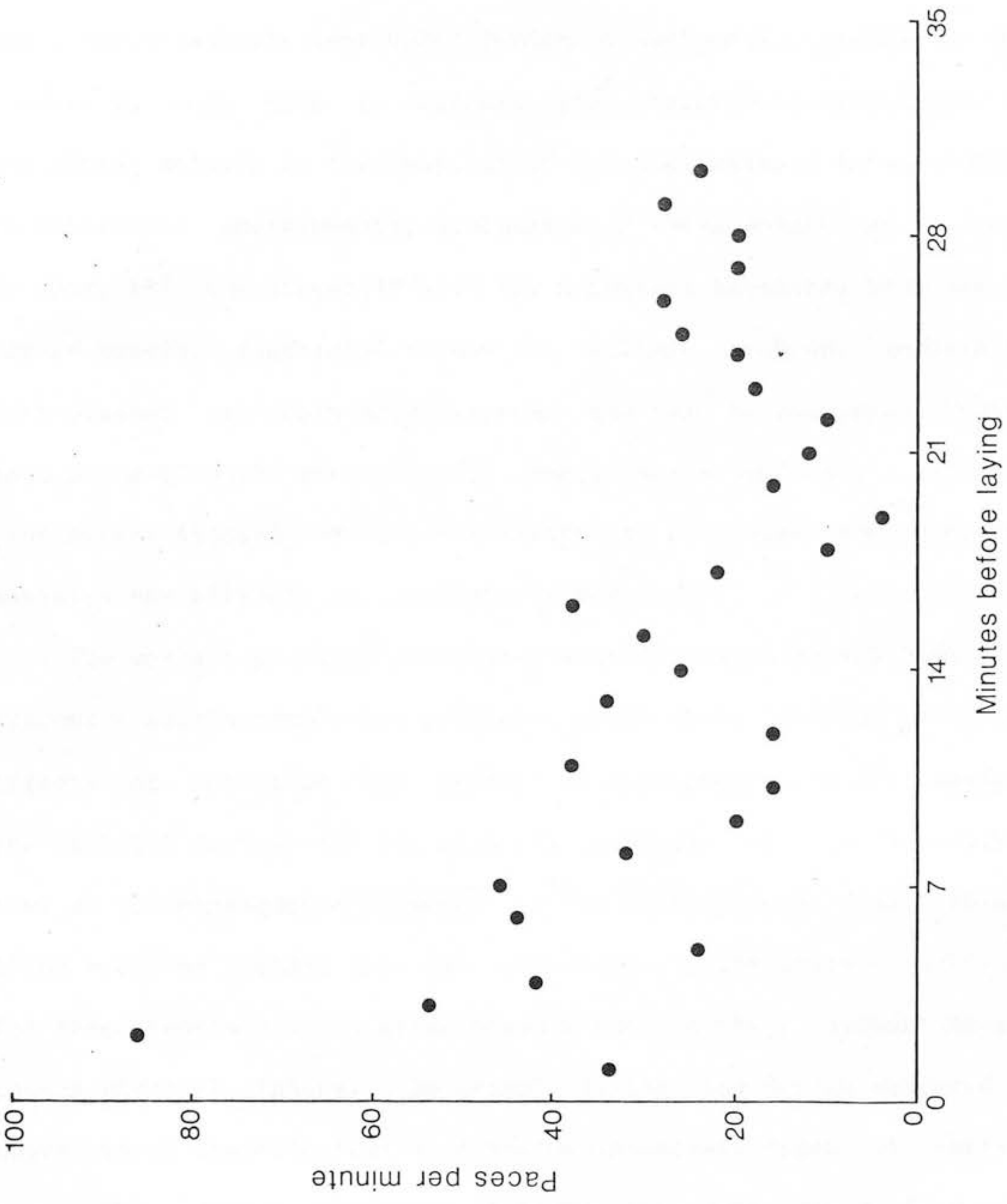

Paces per minute
40
32
24
16
8
0
0
7
14
21
28
35
Minutes before laying

Figure 12c. The nmber of paces taken per minute by a S line hen during the thirty minutes before laying plotted against minutes before laying , showing how the intensity of pacing increases as the point of lay approaches.


Paces per minute
100
80
60
40
20
0
0
7
14
21
28
35
Minutes before laying

Chapter 13. Conclusions and general discussion II. The potential role of behavioural genetics in the improvement of animal welfare.

In this chapter I review the potential value of behavioural genetics in the improvement of the welfare of domesticated animals kept under intensive husbandry conditions. No attempt is made here to discuss the ethical acceptability of exploiting animals in this way, or of breeding animals for **adaptati**on to artificial environments, discussion of these points can be found in (Fox, 1978 and Singer,1975). The arguments presented here are as far as possible restricted to how the welfare problems associated with present day husbandry systems can best be resolved. Taking into account both the animals` requirements and the economic limitations imposed by the necessity to minimise the cost, and maximise the effiency of animal husbandry.

The welfare problems associated with intensive animal husbandry systems - setting aside the problems which have arisen as ´side effects` of selection for production characteristics (for example the skeletal lesions and leg weakness suffered by modern broiler fowl as a consequence of selection for rapid growth, Poulos et al, 1978) - can be divided into two categories. These are:-

(i) Those problems which arise because the husbandry system itself causes physical injury. An example is the foot damage suffered by heavy hybrid domestic fowl when housed in certain types of battery cage. This damage occurring because the cage floor is poorly designed, in that excessive pressure is applied to a limited number of points on the birds` feet (Hughes and Lee, 1977).

(ii) Those problems which arise because the animals cannot express, in an appropriate manner, certain of their innate behavioural drives. Examples are, the stereotyped pacing shown by some strains of domestic hens during the pre-laying period when confined in battery cages because they cannot express their normal repertoire of nesting behaviour patterns; and feather pecking, which appears to arise from redirected exploratory pecking or food pecking (Anon., 1976).

The first of these two categories of welfare problem called by Duncan, (1980c) ´wear-and-tear injuries`, can best be resolved by environmental change, that is, by improving the design of husbandry systems. This point is illustrated by the findings of Tausen (1978) which show that the incidence of ´wear-and-tear` injuries in battery housed domestic fowl can be reduced substantially by modification of various aspects of cage design.

The second category of welfare problems, - those which arise as a consequence of the thwarting of innate behavioural drives - could also be resolved by environmental change (though in some cases, the environmental change required would be radical), or alternatively they might be resolved by genetic change, that is, by selecting against the expression of those behaviour patterns which lead to welfare problems.

Several authors have pointed out the advantages that would acrue from selection for behavioural traits relevant to welfare, (eg; Wood-Gush, 1981 and Beilharz, 1982), and there is no reason in theory why such selection should not be possible. Substantial evidence exists which demonstrates that it is possible to select for a wide variety of behaviour patterns in taxonomically diverse species, and there is no reason to assume that behavioural traits relevant to the welfare of domesticated species could not also be selected for. Indeed, it has already been demonstrated that in the domestic chicken there is heritable variation in the expression of several behaviour traits relevant to welfare. These are:

fearfulness (Faure and Folmer 1975, Faure 1980), feather pecking (Dickerson et al 1961, Cuthbertson 1980) and stereotyped pacing in the period before laying (this study).

However, as Faure (1980) points out, it does not necessarily follow that because it is possible to select for behavioural traits relevant to welfare under laboratory conditions it will also be possible to select for such traits on a commercial scale. The major objections to selection for behavioural traits on a commercial scale are :- (I) It would take an unacceptably long time to bring about significant improvements in welfare. Selection for behavioural traits is therefore not worthwhile.

(II) Behaviour is difficult to quantify, and takes a long time to measure. The effectiveness of commercial selection is dependant on the use of very large numbers of animals and it would be impossible to score very large numbers of animals for behavioural traits.

(III) Present day husbandry systems are not standardised. Even apparently uniform environments such as the battery cage vary in respect of features such as stocking density, space available for feeder, type of feeder, etc. Different husbandry conditions bring with them different welfare problems and it is very unlikely that it would be possible to breed domestic animals behaviourly adapted to all types of husbandry systems.

(IV) Selection for behavioural traits would be difficult to incorporate into the already complex selection programmes employed by animal breeders and further selection for such traits might conflict with selection for production characteristics.

I will discuss each of these objections by turns.

<u>Objection I.</u> The time required to effect change.

Under conditions of artificial selection, the rate at which genetic change can be brought about at the population level is determined by four factors. These are: (i) the generation time, (ii) the number of offspring per dam per generation, (iii) the ease with which the breeding population can be manipulated and (iv) the intensity of selection and the heritability of the traits concerned. Factors (i), (ii) and (iii) are species limitations. In species such as cattle where the generation time is high, the number of offspring is low and the population geographically scattered - which makes the measurement of behaviour and the manipulation of breeding stock difficult - these factors are major obstacles in the use of genetic change in the improvement of welfare. In such species it is unlikely that it will be possible to improve welfare through genetic change. For these species, therefore, we must concentrate on environmental change in order to improve welfare. However, in species such as the domestic fowl, in which the generation interval is short, the number of offspring per individual potentially great, and in which breeding stock is concentrated at particular sites, genetic change can be effected rapidly and must certainly be considered as a potential tool in the improvement of welfare.

The heritability of most behavioural traits relevant to welfare is an unknown quantity; it is of course likely that some traits will be of high heritability, and some of low heritability. However, under conditions of artificial selection, pressures can be (and already are, with respect to production characters) very intense, and given this, even traits of low heritability may show a significant response to selection within a relatively short period of time.

<u>Objection II</u>. The difficulties associated with scoring animals for

behavioural traits make it impossible to score enough animals for selection of behavioural traits to be operated on a commercial scale.

This objection stems from the premise that behaviour is difficult to quantify and can only be accurately measured on the basis of multiple measurements. Faure (1980, 1981) has reviewed the feasibility of defining measures of behaviour suitable for use on a commercial scale on domestic fowl, and makes the following points ;

(a) selection for behavioural traits can be effected on the basis of single short term observations (Faure and Folmer, 1975) - a point substantiated by the findings of this study.

(b) some behaviour patterns leave permanent ´traces` and therefore can be measured without actual observation of the behaviour pattern itself. An example of such a behaviour is feather pecking in the chicken. Hens can be classified as ´peckers` and ´non-pacers` on the basis of feather loss, the best feathered birds being the ´peckers` (Cutherbertson,1980; Hughes and Duncan, 1972).

(c) it is possible to devise automatic devices for the monitoring of behaviour, which eliminate the necessity for continuous observation. - see Bessei (1981) for a review of some of the automated systems available for the monitoring of behaviour patterns, and Faure (1980) and Savory and Duncan (1982) for examples of the use of automatic recording systems in the monitoring of behaviour.

(d) when a behaviour pattern is expressed over long periods of time (eg: brooding, and perching) large numbers of animals can be scored using scanning techniques.

Faure´s arguments - which can be applied to other domestic species - show that selection for behavioural traits can be carried out on a commercial scale, and to reinforce this the following point is made. Detailed studies of behaviour are usually designed to detect subtle quantitative differences in behaviour between individuals. However in attempting to select for at least some behaviour traits relevant to welfare, such distinctions are probably irrelevant since the question is not ´how often did the animal show the behaviour` or ´how intense was its expression of the behaviour` but rather - ´does the animal show the behaviour pattern or does it not` . For example, it is demonstrated here that a bird may be designated as a ´pacer` or a ´non-pacer` in the period before laying, and Cuthbertson (1980) suggests that (with respect to feather pecking) hens can be classified as ´peckers` and ´non-peckers`. In those cases where such ´yes and no` classifications are possible, very large numbers of animals can be scored by scanning techniques. It would be possible for example to classify in the region of eighty percent of the laying hens in a battery house system as ´pre- laying pacers` or ´non pacers` on a single day.

Objection (III). The problems of environmental diversity.

In discussing environmental diversity in relation to selection for behavioural traits relevant to welfare it is important to distinguish between the problems which arise because particular animals are kept under a range of husbandry conditions at various times in their lives, and those which arise because a given species is kept under a variety of husbandry systems although individual animals experience only one. As Beilharz and Zeeb (1981) point out, if dairy cattle are to spend six months on pasture ´´performing all the typical outdoor behaviour patterns`` - since (as argued previously) it is unlikely that it will be possible to bring about changes in the behavioural requirements of such species within the foreseeable future - ´´then it is unreasonable to house them in winter under conditions in which they cannot perform their natural behaviour patterns``. For these species we must therefore look to environmental change for the improvement of welfare. However, in species where the animals spend all of their lives under one particular set of husbandry conditions the situation is different. It cannot be denied that before attempting to select such species for behaviour traits it will be desirable to standardise husbandry systems, not only for production stock but also for breeding stock, - unless breeding stock are to be selected on the basis of progeny testing - since selection for behavioural traits will clearly be most effective in the improvement of welfare if the animals are selected for adaption to, and kept under one set of husbandry conditions.

In view of this, the diversity in present husbandry systems and the possibility that husbandry design may change in the future may at first sight appear to be a valid objection to the use of genetic change in the improvement of welfare. However: -

(i) if genetic change is rejected as a means of improving welfare, then welfare must be improved by environmental change. Such change is in itself likely to bring about some degree of standardisation. To argue that genetic change cannot be used to improve welfare because husbandry systems are not uniform, and then to argue that welfare is best improved by optimisation of husbandry design (which will inevitably involve some degree of standardisation) is somewhat illogical.

(ii) not all welfare problems are environment specific. Feather pecking in domestic hens, although its incidence is greatest in battery cages, can and does occur under all intensive husbandry conditions (Anon., 1976). Selection against this trait would therefore improve welfare irrespective of the husbandry system.

(iii) standardisation of husbandry systems would have the advantage of reducing the number of welfare problems to be resolved. For example, if the deep litter system was adopted as the standard environment for laying hens, then stereotyped pacing during the period before laying would no longer be a problem and need not be selected against.

In view of these points, the diversity of present day intensive husbandry systems is not a valid reason for ruling out genetic change as a means of improving welfare. Rather before attempting to improve welfare through genetic changes, we must define what the animals` environmental needs actually are (see Duncan, 1980c, for a discussion of this point), and then within practical and economic limitations design the husbandry system which best meets these needs. Once this has been achieved we can identify those welfare problems which remain and select against the expression of those behaviour patterns which contribute to them.

<u>Objection (IV)</u>. Commercial selection procedures are already so complex that it would be impossible to incorporate selection for behavioural traits relevant to welfare without adversely affecting production.

It cannot be denied that modern selection programmes for production characteristics are very complex, and that it would be difficult to incorporate selection for a wide variety of behavioural traits into these programmes without seriously reducing productivity (see Bowman, 1974, for a discussion of the problems and practicalities of selecting for multiple traits). Beilharz, (1982) has suggested that this problem could be overcome by selecting for behavioural traits in stages - or, as this procedure is usually called, by tandem selection. Unfortunately, attractive as this idea may first seem, tandem selection for behavioural traits relevant to welfare is unlikely to be practical. Firstly, because it takes a very long time before all required traits can be covered, and secondly, (because of random genetic drift or negative genetic correlation between traits) selection for subsequent characters may reverse much of the changed effected during selection for previous ones. The most efficient means of selection for multiple traits is ´selection by means of an index` (Bowman, loc. cit). Computation of such an index however, becomes increasingly difficult, and the progress for each character declines as the number of traits selected increases, particularly if the genetic correlation between characters is negative. Given this, and the existing complexity of selection for metric characters, it will be necessary to reduce the number of behavioural traits to be selected for, to a minimum.

Whether or not behavioural traits relevant to welfare are negatively genetically correlated with production characters is an unknown factor. Admittedly, if the correlations are negative this will hinder the rate of progress in the improvement of welfare. However, if the number of behavioural traits is limited then selection should be possible without unduly affecting production. After all, it has been possible to select domestic fowl for negatively correlated production factors such as egg number and egg size.

Having discussed the problems and practicalities of selecting for behavioural traits problems on a commercial scale, it is now possible to make an assessment of the potential value of genetic change in the improvement of welfare. It is my opinion, for the reasons outlined above, that in species such as cattle (where the generation interval is great, the number of offspring left by each dam low, breeding stock geographically scattered and, one individual may experience a variety of environments) genetic change is unlikely to be effective in improving welfare - not so much because it is impossible but because it would take an unacceptably long time to effect significant changes. In such species we must rely on environmental change for the improvement of welfare. In species such as the chicken which lend themselves to genetic manipulation, selection for behavioural traits could be a very powerful tool for the improvement of welfare, but only if used in conjunction with environmental change. If genetic change is to be exploited in the improvement of welfare we must first define what the animals` behavioural needs actually are, and then decide which husbandry system is to be used, and within economic practical limitations design this system so that as far as possible it meets these needs. Once this has been achieved we can then identify the welfare problems which remain, and attempt to resolve them by selecting against those behavioural patterns which contribute to them. Given this, the requirements of both man and animal should be met.

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* Erratum. For Wright, (1934). See page 146.

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Appendix 1.

Tables of results not included in the text.

Table 4.i. Scores of twelve S line hens for pre - laying pacing (average no of paces taken per minute in the ten minutes prior to laying) on two occasions.

ANIMAL	PACES PER MINUTE	
	SCORE 1	SCORE 2
1	5.3	13.6
2	45.0	56.5
3	27.1	25.8
4	8.0	6.8
5	8.6	10.9
6	53.7	47.5
7	7.4	6.0
8	15.9	36.4
9	21.8	35.1
10	32.7	33.8
11	83.2	74.5
12	19.1	14.7

Table 4.ii. Scores of thirteen T line birds for pre - laying pacing (average number of paces taken per minute in the ten minutes prior to laying) on two occasions.

ANIMAL	PACES PER MINUTE	
	SCORE 1	SCORE 2
1	0.3	0.1
2	2.0	0.5
3	0.0	0.0
4	2.3	0.0
5	5.6	1.4
6	0.0	0.1
7	2.0	0.3
8	0.1	0.0
9	22.8	11.1
10	36.6	31.9
11	2.1	7.3
12	2.9	1.9
13	1.1	0.0

Table 4.iii. Scores of twelve S line birds for pre - laying sitting (proportion of time spent sitting during the ten minutes prior to laying) on two occasions.

ANIMAL	PROPORTION OF TIME SPENT SITTING	
	SCORE 1	SCORE 2
1	0.6381	0.4980
2	0.0000	0.0000
3	0.0000	0.0000
4	0.4724	0.7146
5	0.1299	0.1201
6	0.0807	0.0000
7	0.2913	0.5984
8	0.0000	0.0000
9	0.0059	0.0000
10	0.0000	0.0000
11	0.2264	0.2717
12	0.0000	0.0551

Table 4.iv. Scores of thirteen T line birds for pre - laying sitting (proportion of time spent sitting during the ten minutes prior to laying) on two occasions.

ANIMAL	PROPORTION OF TIME SPENT SITTING	
	SCORE 1	SCORE 2
1	0.3976	0.3071
2	0.3583	0.4528
3	0.9626	0.9921
4	0.6280	0.9547
5	0.7657	0.9311
6	0.9488	0.9528
7	0.8543	0.9094
8	0.9449	0.9606
9	0.0394	0.0039
10	0.0000	0.0000
11	0.7967	0.7382
12	0.3563	0.4665
13	0.3484	0.3051

Table 4.v. Scores for pre - laying pacing (average number of paces taken per minute in the ten minutes prior to laying) by five S line birds on five occasions.

(PACES PER (MINUTE) SCORE NO.	BIRD 1	2	3	4	5
1	25.0	18.5	27.1	8.6	21.1
2	32.7	7.0	25.8	10.9	17.9
3	33.8	11.7	28.9	7.8	21.7
4	39.6	18.5	22.7	8.8	9.5
5	21.1	17.9	21.7	17.9	15.8

TABLE 4.vi. Scores for pre - laying pacing (average number of paces taken per minute in the ten minutes prior to laying) by five T line birds on five occasions.

(PACES PER MINUTE) SCORE NO.	BIRD				
	1	2	3	4	5
1	2.0	0.3	36.6	2.9	1.1
2	0.3	0.1	31.9	1.9	0.0
3	8.3	1.7	29.7	2.6	16.7
4	4.1	0.6	27.9	4.0	17.2
5	11.1	4.1	34.4	4.3	29.0

TABLE 4.vii. Scores for pre - laying sitting (proportion of time spent sitting in the ten minutes prior to laying) by five S line birds on five occasions.

PROPORTION OF TIME SPENT SITTING SCORE NO.			BIRD		
	1	2	3	4	5
1	0.0059	0.1890	0.0000	0.1299	0.2644
2	0.0000	0.1634	0.0000	0.1201	0.2717
3	0.0000	0.1614	0.0000	0.4429	0.3976
4	0.0000	0.2933	0.0000	0.1378	0.2853
5	0.0000	0.2854	0.0000	0.1811	0.1457

Table 4.viii. Scores for pre - laying sitting (proportion of time spent sitting during the ten minutes prior to laying) by five T line birds on five occasions.

PROPORTION OF TIME SPENT SITTING SCORE NO.	BIRD 1	2	3	4	5
1	0.8543	0.3976	0.0000	0.7967	0.3563
2	0.9094	0.3071	0.0000	0.7382	0.4665
3	0.6059	0.3425	0.0000	0.5433	0.4001
4	0.5321	0.4094	0.0000	0.4094	0.2973
5	0.5703	0.2874	0.0000	0.4461	0.4918

Table 9.i. Responses of S0 and S2 generation hens to a novel object. Responses were ranked on a scale from zero to ten. A score of zero implying little fear of the object, a score of ten extreme fear.

GENERATION			
S0		S2	
BIRD	RESPONSE	BIRD	RESPONSE
S5609	4	S877	10
S5667	6	S719	7
S5657	4	S721	4
S5674	8	S3194	10
S5598	6	S2984	0
S5589	7	SNB1	8
S5681	6	S3872	5
S5578	6	S2981	2
S5669	4	S3362	2
S5591	6	S2973	5
S5610	5	S3892	8
S5672	5	S3896	6
S5628	3	SNB2	4
		SNB3	6
		S3911	4
		S3921	7
		S3915	9

Table 9.ii. Responses of T0 and T hens to a novel object Responses were ranked on a scale from zero to ten. A score of zero implying little or no fear of the object, a score of ten extreme fear.

GENERATION

T0		T2	
BIRD	RESPONSE	BIRD	RESPONSE
T5659	7	T855	8
T5593	4	T857	7
T5636	4	T845	7
T5660	4	T2999	8
T5585	4	T2997	8
T5634	4	T2998	4
T5583	4	T3829	5
T7483	6	T3835	4
T5584	6	TNB1	6
T5713	7	TNB2	7
T5661	4	TNB3	4
T5594	4	TNB4	4
T7484	5	T3906	4
T5645	4	T3828	5
T5643	4		
T5603	8		
T5624	8		

Table 9.iii. Responses of S0 and S2 generation hens to handling. Responses were ranked on a scale from zero to six. A score of six implying extreme fear, a score a score of zero little or no fear.

GENERATION			
S0		S2	
BIRD	RESPONSE	BIRD	RESPONSE
S5987	5	S877	6
S5620	6	S719	5
S5591	5	S721	5
S5674	3	S3194	6
S5609	5	S2984	6
S5589	2	SNB1	4
S5672	6	S3872	5
S5999	6	S2981	6
S5610	2	S3362	5
S5681	0	S2973	5
S5667	0	S3892	5
S5598	3	S3896	6
S5628	2	S3898	5
		SNB2	6
		SNB3	4
		S3911	5
		S3921	6
		S3915	5

Table 9.iv. Responses of T0 and T2 hens to handling . Responses were ranked on a scale from zero to six. A score of zero indicating little or no fear of the object, a score of six extreme fear.

GENERATION			
BIRD	RESPONSE	BIRD	RESPONSE
T0		T2	
T5613	3	T855	5
T5979	3	T857	3
T7483	1	T845	6
T5584	2	T2999	3
T5960	2	T2996	5
T5661	3	T2998	5
T5971	3	T3829	2
T5959	2	T3835	3
T5928	6	T3906	3
T5594	2	T3828	5
T7484	2	TNB1	5
T5603	5	TNB2	4
T5970	5	TNB3	4
T5624	3	TNB4	4
		TNB5	4

Appendix 2.

The ´´agar flake staining`` technique for determining the fertility of domestic fowl eggs.

This technique was developed by Mrs. C. Mather of the A.R.C.`s Poultry Research Centre, from a proceedure originally described by Hamburger, (1942), and is reprinted here by kind permission of Dr. S. Tullet.

A). Preparation of neutral red agar flakes.

Make up 3% Agar-agar (as per the manufacturer`s recommendations), and pour it out to a depth of 5mm in a large flat dish. When set, dry the agar in a warm (60`C) oven for several hours. Then cool the agar and cover with 1 - 2 in the stain, in a cool place for five days. Then pour off the supernatant and rinse the agar under running water to remove excess stain. Remove the wet agar from the dish and dry completely in a warm oven. When dried, cut the agar into small flakes (1cm), and store the flakes in an air-tight container.

B). Staining the blastoderm.

Crack the egg out into a petri-dish. Push an agar flake into the thin albumen and allow it to soften a little. Carefully strip the albumen away from the vitelline membrane over the blastoderm (look for the matt surface of the vitelline membrane appearing), and a lay softened flake of agar over the blastoderm for about three minutes.

The stain should leave the agar flake and colour the blastoderm. If the albumen is not removed the stain will colour only the albumen and will run off when the flake is removed. If the staining is not deep enough after three minutes replace the flake for a further period of time.

The fertile blastoderm is an intact sheet of cells whereas the infertile blastodisc has vacuoles through which the yellow yolk can be seen. This technique was developed for use on fresh eggs but it can be used up to about five days after the start of incubation.

Appendix 3.

Pedigrees

This appendix shows, as far as they can be traced, the genetic lineages of all the animals - with the exception of the twelve animal which were the subject of the experiments described in chapter 11 - used in this study; together with the scores for pre-laying pacing, and pre-laying sitting of each female. The data are grouped according to family and generation e.g. unselected T line, T line selected over one generation for the expression of pre-laying sitting, and so forth. Using these tables the pedigree of any animal, with the exception of those which lost their wing tags during rearing and are refered to as SNB1, SNB2, TNB1, and so forth in the tables, can be traced back to a particular female parent of either the unselected S line or the unselected T line generations.

Table 3.i. Pedigrees of the unselected S line, the S0 generation.

SIRE	DAM	MALE PROGENY	FEMALE PROGENY	PACES PER MINUTE	PROPORTION OF TIME SPENT SITTING
?	S235	S5663	S5667	27.6	0.3189
		S5665			
?	S236	-	S5657	53.3	0.0059
?	S231	-	S5640	45.0	0.0000
?	S245	-	S5672	18.9	0.5728
			S5997	32.7	0.0059
			S5669	53.7	0.0807
?	S2410	-	S5674	8.0	0.4724
?	S2411	S5682	S6040	21.8	0.0000
			S6044	83.2	0.0000
			S5681	27.1	0.0000
?	S2511	S5608	S5609	8.6	0.1299
			S5610	26.1	0.0000
?	S265	S5582	S5999	19.1	0.2264
		S5998	S5578	24.4	0.0000

?	S267	-	S5994	7.0	0.1890
			S5591	7.4	0.2913
			S5598	32.4	0.2008
			S5602	54.6	0.0000
?	S268	S5618	S5620	5.3	0.6381
			S5987	1.3	0.8091
?	S2612	S6046	S5589	15.9	0.0000
?	S277	S5629	S5628	37.3	0.0000

Table 3.ii. Pedigrees of the S line birds selected over one generation for the expression of pre-laying pacing, the S1 generation.

SIRE	DAM	MALE PROGENY	FEMALE PROGENY	PACES PER MINUTE	PROPORTION OF TIME SPENT SITTING
S5582	S5640	S711	S710	47.5	0.0000
		S745	S3495	10.4	0.0000
		S746			
S5608	S6044	-	S742	28.4	0.1102
			S744	28.4	0.0000
S5998	S5602	-	S734	30.7	0.2598
S6046	S5669	S3498	S714	15.3	0.0000
			S740	14.1	0.2874
			S741	48.4	0.0000
?	?	-	SNB1	50.5	0.0000
?	?	-	SNB2	51.3	0.0118

Table 3.iii. Pedigrees of the S line birds selected for the expression of pre-laying pacing over two generations, the S2 generation.

SIRE	DAM	MALE PROGENY	FEMALE PROGENY	PACES PER MINUTE	PROPORTION OF TIME SPENT SITTING
S745	SNB2	-	S3911	33.5	0.1733
			S2984	23.4	0.2417
			S3915	51.2	0.0000
			S2981	55.0	0.0000
			S3194	44.7	0.0800
			S3892	66.3	0.0600
			S3921	44.6	0.0133
			S877	76.2	0.0133
S711	S741	-	S3472	17.3	0.1467
			S3362	88.7	0.0000
			S719	23.9	0.3000
S746	S744	-	S881	90.3	0.0000
			S721	64.8	0.0000
			S3896	51.4	0.0400
			S3390	41.5	0.0133
			S3898	53.4	0.0000
			S2973	57.4	0.1200

?	?	-	SNB1	50.0	0.0000
			SNB2	45.1	0.0933
			SNB3	39.0	0.1467

Table 3.iv. Pedigrees of the unselected T line, the TO generation.

SIRE	DAM	MALE PROGENY	FEMALE PROGENY	PACES PER MINUTE	PROPORTION OF TIME SPENT SITTING
?	T398	T5954	-		
?	T399	-	T5970	33.6	0.0000
?	T407	T5605	T5603	26.9	0.0000
		T5967	T5965	0.1	0.9449
		T5966			
?	T408	T5983	T5643	7.8	0.0000
			T7484	5.6	0.7657
			T5645	7.0	0.7776
?	T4010	T5956	T5624	49.2	0.0098
?	T415	-	T5613	0.6	0.7953
			T7483	2.0	0.8543
?	T418	-	T5661	2.7	0.0413
			T5979	1.1	0.3563
			T5660	0.0	0.9331
			T5659	0.0	0.9528

?	T4111	T5958	T5959	2.9	0.6201
			T5960	2.1	0.3484
			T5584	2.1	0.8898
			T5585	0.1	0.8976
			T5583	1.7	0.9173
?	T426	T5712	T5961	22.8	0.0394
			T5713	2.3	0.6280
?	T428	–	T5928	3.1	0.2520
?	T436	T5633	T5634	0.3	0.3976
		T5637	T5971	2.9	0.7967
		T5973	T5636	0.0	0.9567
?	T4312	–	T5594	4.0	0.1772
			T5593	0.0	0.9488
?	?	–	TWLB	2.0	0.3583
			TBLB	0.0	0.9626

Table 3.v. Pedigrees of the T line birds selected for the expression of pre-laying sitting over one generation, the T1 generation.

SIRE	DAM	MALE PROGENY	FEMALE PROGENY	PACES PER MINUTE	PROPORTION OF TIME SPENT SITTING
T5633	T5659	-	T705	10.7	0.3740
			T3468	3.6	0.5472
T5605	T5636	-	T747	1.5	0.8071
T5973	T5593	-	T965	1.1	0.6457
			T3471	6.0	0.0000
			T3472	3.5	0.0630
T5967	T5660	T970	T3475	0.6	0.8584
		T974	T971	2.6	0.7874
		T708	T3473	9.8	0.4291
		T726	T3474	0.0	0.8740
			T724	3.7	0.7264
T5637	T5965	-	T3477	1.0	0.8740
			T720	2.4	0.8740
			T722	9.2	0.0000
T5966	TBLB	T3480	T706	0.0	0.9567
		T3485	T3482	0.1	0.9488

			T3484	0.0	0.9252
			T3486	0.2	0.8583
			T730	5.3	0.7165
?	?	-	TNB1	0.0	0.9803
			TNB2	27.1	0.0000

Table 3.vi. Pedigrees of the T line birds selected for the expression of pre-laying sitting over two generations, the T2 generation.

SIRE	DAM	MALE PROGENY	FEMALE PROGENY	PACES PER MINUTE	PROPORTION OF TIME SPENT SITTING
T726	T3484	-	T855	0.0	0.9800
			T3906	0.0	0.9200
			T2998	0.5	0.9200
			T3829	0.0	0.9333
			T2999	2.3	0.0000
			T2996	8.7	0.6933
			T3828	15.1	0.9467
T974	T3477	-	T857	0.0	0.8167
			T3835	1.1	0.7467
T3480	T3474	-	T3382	7.8	0.4933
			T845	0.0	0.9133
?	?	-	TNB1	1.6	0.7067
			TNB2	0.0	0.8733
			TNB3	7.2	0.4667
			TNB4	15.1	0.0933
			TNB5	2.3	0.8750

Table 3.vii. Pedigrees of the initial (Fla) Fl hybrids derived from matings between S line males and T females drawn at random from the unselected S and T line populations.

SIRE	DAM	MALE PROGENY	FEMALE PROGENY	PACES PER MINUTE	PROPORTION OF TIME SPENT SITTING
S5629	T5583	ST4121	ST4122	29.7	0.0000
S5655	T5713	-	ST763	1.3	0.9646
			ST4125	6.5	0.3937
S5682	T5645	ST752	ST755	4.2	0.0000
			ST756	0.0	0.8543
			ST758	6.0	0.0000
S5618	T5634	ST3674	ST3677	7.8	0.0000

Table 3.viii. Pedigrees of the initial (Fla) hybrids derived from matings between T line males and S line females drawn at random from the unselected S and T lines.

SIRE	DAM	MALE PROGENY	FEMALE PROGENY	PACES PER MINUTE	PROPORTION OF TIME SPENT SITTING
T5958	S5994	TS783	TS782	0.2	0.8543
			TS784	17.8	0.0315
			TS4134	9.0	0.2382
			TS4136	25.7	0.0000
			TS4137	17.8	0.0000
T5959	S5997	-	TS786	17.1	0.0000
		-	TS4138	57.6	0.0000
T5712	S5578	-	TS772	2.5	0.7579
T5954	S5667	TS787	TS788	1.4	0.4900
		TS790	TS791	1.1	0.6693
			TS795	0.7	0.4449
			TS796	4.8	0.0591
T5983	S6040	TS3659	TS3663	25.6	0.0000
			TS3665	15.0	0.4063

Table 3.ix. Pedigrees of the F1b hybrids derived from matings between S1 generation males and T2 generation females.

SIRE	DAM	MALE PROGENY	FEMALE PROGENY	PACES PER MINUTE	PROPORTION OF TIME SPENT SITTING
S711	T3484	-	ST1372	6.9	0.3733
			ST1373	22.9	0.1700
			ST976	13.9	0.0000
S711	T3482	-	ST1503	23.2	0.0267
			ST1590	17.3	0.0000
			ST943	18.7	0.0800
S745	TBLB	-	ST962	6.4	0.5717
S746	T3477	-	ST911	0.0	0.9607
			ST910	0.5	0.8667
			ST975	14.8	0.1867
S746	T3474	-	ST1384	23.4	0.0000
			ST1572	9.1	0.4667
			ST1574	0.6	0.9200
			ST1573	4.5	0.0000
			ST958	3.4	0.6000
			ST1381	17.8	0.0000

Table 3.x. Pedigrees of the Flb hybrids derived from matings between Tl males and Sl females.

SIRE	DAM	MALE PROGENY	FEMALE PROGENY	PACES PER MINUTE	PROPORTION OF TIME SPENT SITTING
T970	SNB2	-	TS3373	35.2	0.0133
			TS1969	1.0	0.1333
			TS1414	50.4	0.0000
			TS1413	8.1	0.5633
			TS1998	12.1	0.0000
T974	S741	-	TS1433	3.5	0.6133
			TS6933	7.8	0.3733
T708	S710	-	TS967	6.7	0.4383
			TS1585	13.5	0.3467
T726	S6044	-	TS1404	8.1	0.5200
			TS1408	5.9	0.7333
			TS1585	13.5	0.3667
			TS1510	3.5	0.7467
			TS1995	4.5	0.7467
T726	SNB1	-	TS1513	0.0	0.9000
			TS1369	6.8	0.7467
			TS966	8.9	0.0267

			TS1576	5.2	0.8133
			TS1563	2.0	0.7183
T726	S744	-	TS1586	1.0	0.4267
			TS1509	25.5	0.1867

Table 3.xi. Pedigees of backcrosses to the S line (S x Fl).

SIRE	DAM	MALE PROGENY	FEMALE PROGENY	PACES PER MINUTE	PROPORTION OF TIME SPENT SITTING
S3498	TS4134	-	BCS1905	39.8	0.1600
S711	ST788	-	BCS184	48.9	0.0000
S745	ST758	-	BCS1925	97.0	0.0000
			BCS926	23.9	0.0917
			BCS1924	30.0	0.0000
S746	ST3677	-	BCS1918	99.5	0.0000
			BCS1919	86.2	0.0000
			BCS1920	0.8	0.8633
			BCS167	99.1	0.0000
			BCS1922	12.8	0.4000
ST3674	S710	-	BCS1968	43.0	0.3200
			BCS129	7.3	0.2000
ST752	S744	-	BCS1955	76.0	0.0000
TS790	SNB1	-	BCS1948	65.0	0.3867
			BCS1946	0.0	0.9867
			BCS1966	64.9	0.0000

TS787	SNB2	-	BCS1959	58.4	0.1333
			BCS1960	71.0	0.1200
TS4144	S741	-	BCS124	1.2	0.6800
			BCS1901	0.0	0.9999

Table 3.xii. Pedigrees of backcrosses to the T line (T x F1).

SIRE	DAM	MALE PROGENY	FEMALE PROGENY	PACES PER MINUTE	PROPORTION OF TIME SPENT SITTING
T970	TS795	-	BCT1912	0.2	0.8000
			BCT1911	7.5	0.1267
			BCT1910	0.0	0.7200
			BCT1914	0.0	0.8133
T974	TS772	-	BCT1907	1.3	0.9100
			BCT1909	0.7	0.9033
T726	ST4125	-	BCT131	0.4	0.9200
			BCT132	1.3	0.8533
			BCT1941	13.2	0.2850
T3485	ST755	-	BCT154	3.7	0.7867
			BCT1939	0.0	0.9067
			BCT194	3.9	0.0000
			BCT154	3.4	0.8000
			BCT186	5.5	0.6133
			BCT144	2.1	0.7000
T708	ST763	-	BCT146	4.7	0.8400
TS3659	TBLB	-	BCT125	3.0	0.9067
			BCT126	0.0	0.9067

TS783	T3484	-	BCT1932	0.0	0.5000
ST4121	T3477	-	BCT1933	1.5	0.7867
			BCT169	5.4	0.8333