

BEHAVIOUR AND THERMOGENESIS OF RACING PIGEONS HOUSED UNDER TRANSPORT CONDITIONS

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Abstract

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During homing contests, racing pigeons (Columba livia) are transported to their release site under crowded conditions. Behaviour and thermogenesis under these conditions were studied in two experiments. In the first experiment, temperature (26 °C or 36 °C) and water availability (access or deprived) had no significant effect on either behaviour or heat production of old male pigeons. However, the frequency of threatening behaviour and the proportion of activity-related heat production in total heat production increased during the 23-hour experimental period, whereas no decrease in aggressive behaviour was found. In the second experiment the effect of testing age (young or old) and sex (male or female) were considered in relation to behaviour and thermogenesis. Young pigeons were more immobile than old pigeons, but heat production was lower in old pigeons. Male groups had a higher activity-related heat production and had more head injuries resulting from pecking than females. Again, no decrease in aggressive behaviour or changes in behaviour patterns over time were found. Body-weight at the start of the experiment was predictive of subsequent behaviour in the crate. A higher body-weight was related to more threatening behaviour, less displacement and less head injuries. The consistent level of aggressive behaviour over time, causing predictable head injuries, indicates that a 'ceiling effect' in adaptation is reached under crowded transport conditions. To improve pigeon welfare, serious considerations must be given to transporting racing pigeons under less crowded conditions.

Keywords: aggression, animal welfare, behaviour, pigeon, transport

Introduction

Racing pigeons (*Columba livia*) participating in homing contests are transported from the home loft to the release site at a high stocking density. Dutch transport guidelines suggest transporting pigeons at a space allowance of 225 to 300cm² per bird. The conditions within a transport crate may be comparable to over-crowded roosting perches, where serious fights between pigeons can take place (Goodwin 1983). At present, no quantitative data are available on the general behaviour of pigeons housed under transport conditions.

Transport conditions are not only affected by high stocking densities. Since the Dutch racing season ranges from April to September, inadequate climatic control of the transport

vehicle may put the pigeons at risk of heat exposure during summer. In addition, water deprivation for a period of 12 to 24 hours may occur (Gorssen *et al* 1993). Marder (1983) noted increased aggression in heat-exposed pigeons. A combination of heat exposure and water deprivation results in dehydration of pigeons (Arad *et al* 1987). Additional locomotor activity in heat-exposed pigeons, due to an increased amount of social interactions, increases total heat production. For thermoregulatory purposes, the birds are forced to increase heat loss through water evaporation, resulting in a higher degree of dehydration (Blaxter 1989). It remains unclear as to what extent dehydration affects the behaviour of pigeons transported in restricted space.

Apart from the physiological variation caused by transport conditions, the social environment of the pigeons within a crate varies between crates. Each crate is homogeneous with respect to both age and sex. Male and female pigeons are separated into two age groups, young pigeons between 6- and 10-months-old in their first racing season and old pigeons, older than one year and having experienced at least one racing season. Among pigeon fanciers it is generally believed that aggressive behaviour only occurs in old male groups. Murton *et al* (1972a) however, adopted six months as the cut off point where a non-breeding juvenile pigeon become a potentially-breeding adult pigeon. This suggests that differences in behaviour between young and old male pigeons are smaller than those assumed by pigeon fanciers.

During transport, the pigeon's behaviour might be affected by the motion, noise and vibration associated with a driving vehicle. However, during racing pigeon contests the time pigeons spend in a stationary truck with the engine off is considerable and this may also affect their behaviour. These stationary periods include the waiting time before departure of the vehicle and especially the time between arrival at the release site and final release of the birds. Adverse weather conditions at the release site or between the release site and the home site often delay the moment of release by several hours or even days.

In this paper, two experiments are presented. In the first experiment, old male pigeons were used to test the hypothesis that a combination of heat exposure and water deprivation may increase the level of behavioural activity in pigeons. In the second experiment, we compared 'young' and 'old' groups of pigeons consisting of either males or females to investigate whether the occurrence of aggressive behaviour is limited to old male groups only. In both experiments differences in thermogenesis were studied in relation to differences in behaviour.

Materials and methods

Design, animals and pre-experimental housing

Prior to the experiments, pigeons were housed in an outdoor half-open aviary under natural photoperiod, humidity and temperature. The aviary was divided into compartments of 2x4x2m. Each compartment contained four or five groups of 10 pigeons. Male and female pigeons were separated, with no visual contact between male and female groups. Each morning at 0800h, the pigeons were fed a commercial diet of whole grains (mainly peas, corn, beans and barley) in a daily ration of 40g per bird with water supplied *ad libitum*.

In each experiment, 80 pigeons were allotted to eight groups of 10 birds. Both experiments were designed on a two-way factorial basis.

In Experiment 1, the effect of water availability (access to water versus deprived of water) and ambient temperature (26°C versus 36°C) on pigeon behaviour and thermogenesis was examined. Adult male pigeons were used and these had already been at the University's facilities for one year before the start of the experiment.

In Experiment 2, the effect of age and sex of the pigeons on behaviour and thermogenesis was examined. The crates were kept at a constant temperature of 36°C to mimic the high temperatures within crates which can occur during transport on warm summer days. All groups had continuous access to water. At the end of the racing season, three weeks before the start of the experiment, 40 pigeons of about six-months-old (young) and 40 pigeons older than one year of age (old) arrived at the University's facilities. Both age groups consisted of 20 males and 20 females.

Procedure

Both experiments consisted of four replications comprising two groups of 10 pigeons. Each experimental period started at 0800h of day 0, when the diet composition was changed to wholegrain corn only. At 1100h of the same day, two groups of pigeons were transferred to the laboratory. A description of each bird was made (plumage, colour and spots). If the appearance of birds within a group was similar, ink marks were sprayed on the back of the birds to assure correct visual identification of the individuals. Pigeons were also checked for pecking lesions at the bill base and around the eyes. Each group was confined to a transport crate (50x56x25cm) with aluminium sides, open wire-top and hard plastic-grid floor. No feed was available. For groups with access to water in Experiment 1 and for all groups in Experiment 2, a drinking trough was attached to the outside of the crate.

At 1300h the experimental period in which climate respiration was measured (referred to as the 'exposure period') started. Until 1210h of day 1 each crate was placed on a platform in one of two climate-respiration chambers of 1.8m³ each, as described by Verstegen *et al* (1987). Throughout the entire experimental period, lights were off between 1930 and 0700h. Relative humidity level was kept at 70 per cent at 26°C and at 44 per cent at 36°C.

Data collection and parameters

The individual body-weight (BW \pm 1g) of the pigeons was recorded at the start and end of the exposure period. During the exposure period, heat production was measured by indirect calorimetry in successive 9-minute intervals on the basis of the exchange of CO₂ and O₂, as described by Verstegen *et al* (1987). A Hartmann and Braun Uras 3G infrared absorption CO₂ analyser (Elsag, Baily, Hartmann & Braun, Delft, The Netherlands) and a Servomex 1100 H paramagnetic O₂ analyser (Servomex B V, Zoetermeer, The Netherlands) were used. Analysers were calibrated every 24 hours and all gas volumes were converted to standard temperature and pressure, dry. Airflow through the chambers was 10l min⁻¹. Total heat production (HP_{tot}) was calculated according to Romijn and Lokhorst (1961). Using BW at the start of the exposure period, HP_{tot} was expressed in W kg⁻¹. Behavioural activity was measured using Doppler-radar activity meters (Radar MD5, Vierpool, Amsterdam, The Netherlands) which were placed about 1m above the crate. Each movement of the pigeons was interpreted as a frequency change in the reflected ultrasound waves emitted by the meters. These frequency changes were counted over the 9-minute measurement interval for HP_{tot}, resulting in a 9-minute activity score (counts per interval). Activity-related HP (HP_{ac}) was estimated per group by linear regression of 9-minute HP data on 9-minute activity

counts. From HP_{tot} and HP_{ac} , activity-free HP (HP_{af}) was calculated. This procedure was previously adopted for veal calves housed in identical climate-respiration chambers (Schrama *et al* 1995). However, in our experiments the combination of a $1.8m^3$ air-volume with only 10 birds present at a $10l\ min^{-1}$ airflow will affect the relationship between heat production and activity counts measured on the same 9-minute interval. Periods with low activity-related heat production following periods with high activity-related heat production may result in an overestimation of the actual HP_{af} by means of the estimated HP_{af} .

Inside both climate-respiration chambers a video camera was installed about 1m above the pigeons' crate. The cameras were connected with a monitor and a real-time recorder placed next to the chambers. During six periods of 30 minutes each (starting at 1500, 1700, 1845, 0715, 0930 and 1115h) video-recordings of behavioural measures were made on each of the eight groups. The resulting 48 periods of recorded behavioural measures, covering the whole experiment, were analysed in random order using focal sampling. This involved dividing each 30-minute period into 10 non-overlapping sampling intervals of 150s. During each interval, the behaviour of one pigeon was recorded and the data was stored on a personal computer using a software package designed for event recording ie The Observer[®] (Noldus 1991).

The ethogram which was used included drinking, preening, stretching, shaking, roosting (lying with feathers fluffed and rump-patch visible), pecking (with or without contact), wing-beating, wing-twitching, and the bowing display (head-nodding, crop-twisting, small steps and often vocalizing), all according to Goodwin (1983). The bowing display was further specified as fixed or as rotating. Additionally, immobility (standing still, feathers tight, rump-patch covered), retreat (displacement as a consequence of aggressive behaviour of another bird), hiding (lowering the head and hiding it under tail or breast of another pigeon), looking around (with head movements in both the horizontal and vertical plane) and walking (displacement not due to aggressive behaviour from another bird) were added to the ethogram.

Furthermore, videotapes were used to record changes in the location of each bird within the crate. At the start of each 30-minute interval the position of the head was noted as being in one of four quadrants marked on screen, whereafter this procedure was repeated at 5-minute intervals. As a measure of mobility, the total frequency of position changes between consecutive 5-minute intervals was used.

After the exposure period, lesions around the base of the bill and around the eyes were scored. These areas are the focal points of attack during pecking (Goodwin 1983). Four areas were examined per pigeon; two ceres (white protuberances) at the base of the bill and two eye surroundings. Each area was given a score of 0, 1 or 2. If no lesions were visible, the score for that area was 0. Minor, point-like lesions were scored 1 and major, dispersed lesions were scored 2. For each bird, the scores for each of the four areas were added together to give an overall lesion score, ranging from 0 (no damage) to 8 (severely damaged). Lesions were scored independently by three observers and the individual lesion score was calculated as the mean of these three observations.

Data preparation and analysis

The group was treated as the experimental unit and this was used in statistical analysis. For both experiments results were analysed using a two-way analysis of variance (ANOVA)

model. The data were checked for normal distribution and were transformed if appropriate. Heat production data were analysed for 'lights on' and 'lights off' separately. Prior to analysis, some behavioural elements were combined to form behavioural categories. 'Avoidance' included both retreating and hiding; 'threatening' consisted of wing-twitching and the bowing display; 'autonomous' covered roosting, looking around and walking and 'grooming' included preening, shaking and stretching. For analysis of time effects, observations were split up into measurements 'before the dark period' and 'after the dark period'. For all three 30-minute intervals before and after the dark period, the behavioural observations (frequencies or durations) were summed. Paired differences between individual means in the periods before and after darkness were averaged at group level and these group means were analysed by ANOVA.

Measurements on individual animals (behavioural and non-behavioural) were ranked within groups. Ranked data for all groups were pooled and Spearman rank correlations between measurements were calculated for both experiments separately.

For each experiment, sequences of behavioural data were analysed separately for the observations made before and after lights off. The sequences were pooled for the three pigeons with the highest lesion score (pecked) and for the three pigeons with the lowest lesion score (non-pecked) in each group. Based on the combination of these two observation periods (before and after lights off) and two lesion score classes (pecked and non-pecked), observed behavioural transitions are put in four preceding-following transition matrices with a zero-off diagonal. Expected frequencies are calculated using the iterative method and analysis of residuals provided by MatMan (De Vries *et al* 1993). Dependence of following behaviour upon the preceding behaviour is calculated by the standardized residual (q) indicating to which degree and in which direction an observed (o) transition frequency deviates from the expected (e) frequency:

$$q = \frac{(o-e)}{\sqrt{e}}$$

This reveals significant transitions in the behaviour sequence for values of q larger than three (Fagen & Mankovich 1980). Kinematic path diagrams were made for visualizing behavioural frequencies and significant interactions.

Results

Experiment 1

Behavioural measurements

Neither temperature or water availability affected the pigeons' behaviour (Table 1). All groups spent more than 63 per cent of the observed time immobile (Table 1). An interaction approaching significance was present between temperature and water availability with respect to immobility ($F(1,4) = 7.3, P = 0.054$). The time spent in threatening behaviour ranked second overall with pigeons spending more than 14 per cent of the observed time performing this behaviour. Autonomous behaviour was displayed during 9 to 13 per cent of the observed time. Grooming formed only a minor component of the observed behaviour patterns. Pecking frequencies were not affected by water deprivation or heat exposure. The proportion of the

pecks-with-contact in the total of all observed pecks (with or without contact) was 0.38. This was not affected by water deprivation or heat exposure.

Table 1 Behavioural measurements for Experiment 1. Least square means and standard errors of the untransformed values are presented. ANOVA yielding statistical differences was performed using an $\arcsin(\sqrt{\%})$ transformation for proportions and a $\sqrt{\text{frequency}}$ -transformation for frequencies ($n = 8$ for each measurement).

| Behaviour (per cent of observed time) | 26 °C ^{2,3} | | 36 °C | | SE |
|---------------------------------------|----------------------|------|-------|------|-----|
| | DW | AW | DW | AW | |
| <i>Immobile</i> | 71.8 | 65.7 | 63.1 | 74.3 | 4.2 |
| <i>Threaten</i> | 16.9 | 17.7 | 19.6 | 14.1 | 3.9 |
| <i>Autonomous</i> | 9.4 | 13.0 | 11.4 | 9.0 | 3.3 |
| <i>Avoidance</i> | 0.7 | 1.4 | 2.6 | 1.2 | 0.9 |
| <i>Grooming</i> | 0.6 | 0.9 | 0.3 | 0.0 | 0.4 |
| * <i>Pecks-without-contact</i> | 3.7 | 7.5 | 13.7 | 7.2 | 4.7 |
| * <i>Pecks-with-contact</i> | 2.5 | 4.4 | 9.3 | 3.8 | 3.1 |

DW indicates deprived of water and AW indicates access to water. * Unit of measurement = times per pigeon

Heat production and non-behavioural measurements

Heat production was not affected by ambient temperature ($F = 0.33$, $P = 0.60$) or water availability ($F = 0.01$, $P = 0.93$) (Table 2). The proportion of HP_{ac} in HP_{tot} during lights on was highest at 36 °C ($F = 4.22$, $P = 0.11$).

Table 2 Heat production measurements during lights on and non-behavioural measurements for Experiment 1. Least squares means and standard errors are presented ($n = 8$ for each measurement).

| Parameter | 26 °C | | 36 °C | | SE |
|-------------------------------------|-------|-------|-------|-------|-------|
| | DW | AW | DW | AW | |
| HP_{tot} ($W\ kg^{-1}$) | 4.32 | 4.40 | 4.55 | 4.43 | 0.22 |
| HP_{af} ($W\ kg^{-1}$) | 3.57 | 3.31 | 3.14 | 3.26 | 0.21 |
| HP_{ac}/HP_{tot} ($W\ kg^{-1}$) | 0.17 | 0.25 | 0.31 | 0.26 | 0.04 |
| <i>Number of lesions</i> | 2.5 | 3.1 | 3.6 | 3.2 | 0.5 |
| <i>Body-weight at start (kg)</i> | 0.548 | 0.552 | 0.545 | 0.565 | 0.030 |
| <i>Body-weight loss (%)</i> | 8.5 | 7.7 | 11.8 | 7.9 | 1.61 |

DW indicates deprived of water and AW indicates access to water. HP_{tot} is total heat production. HP_{af} and HP_{ac} are activity-free heat production and activity-related heat production respectively.

Lesion scores were not affected by water deprivation or heat exposure (Table 2). Mean body-weight loss was highest in water-deprived birds ($F = 4.26$, $P = 0.11$). The variation in body-weight loss within groups was measured as the coefficient of variance (CV). The CV was 13.6 per cent for water-deprived groups and 26.2 per cent for groups with access to water ($F = 4.64$, $P = 0.10$).

Time effects

The amount of aggressive behaviour did not decrease over time. The proportion of HP_{ac} in HP_{tot} and proportion of threatening behaviour increased with time (Table 3). Autonomous behaviour and time spent immobile were lower during the last part of the exposure period (Table 3).

Table 3 Comparison between mean (\pm SE) observations made during the first (before lights off (BL)) and last (after lights off (AL)) part of the exposure period in Experiment 1 ($n = 8$ for each observation).

| Observation | BL | AL |
|---|------------------------------|------------------------------|
| HP_{ac}/HP_{tot} ($W\ kg^{-1}$) | 0.21 ^c \pm 0.03 | 0.30 ^d \pm 0.02 |
| Immobile (% of observed time) | 72.1 ^a \pm 2.44 | 65.3 ^b \pm 2.29 |
| Threaten (% of observed time) | 12.1 ^c \pm 1.55 | 22.0 ^d \pm 2.07 |
| Autonomous (% of observed time) | 12.8 \pm 2.29 | 8.6 \pm 1.45 |
| Pecks-without-contact (number per pigeon) | 3.2 \pm 0.96 | 4.6 \pm 1.21 |
| Pecks-with-contact (number per pigeon) | 1.8 \pm 0.51 | 3.3 \pm 0.95 |

HP_{ac} is activity-related heat production and HP_{tot} is total heat production.

^{a,b} and ^{c,d} indicate significant differences at $P \leq 0.05$ and $P \leq 0.01$ respectively

Behavioural sequences during Experiment 1 are presented for non-pecked pigeons (lesion score 1.5 ± 0.7 (mean \pm SD)) and for pecked pigeons (4.8 ± 1.0) (Figure 1). The observed behaviour patterns were predominantly associated with aggressive interactions. The interaction-related behavioural elements are located at the left and upper side of each diagram. The immobile state was the central behavioural element in both pecked and non-pecked groups, before as well as after the dark period. In pecked pigeons, an alternation between immobility and retreat (avoidance) was present. This alternation was absent in non-pecked pigeons, where the retreat frequency was also consistently lower than in pigeons with high lesion scores. No direct transition was found between the left side of each diagram on one hand (bowing, pecking, avoidance) and the autonomous behavioural elements at the right side of each diagram (preening, roosting, looking around).

Again, the difference between the behavioural sequences before and after the dark period was small, not only for the non-pecked pigeons but also for the pecked pigeons.

Individual variation in measurements

Rank correlations were relatively small between behavioural and non-behavioural measurements (Table 4). However, pigeons with a relatively high body-weight at start had a lower mobility score, ie were more stationary in the crate than pigeons with a low body-

weight at start. Also, heavier birds tended to show more threatening and autonomous behaviour and spent less time immobile.

Table 4 Spearman rank correlations on pooled individual measurements ranked within groups, for Experiment 1.

| Parameter | BW _s | BW _l | LS | MS | T | I | A | Peck _{nc} | Peck _c |
|--------------------|-----------------|-----------------|------|-------|-------|--------|--------|--------------------|-------------------|
| BW _s | - | 0.07 | 0.03 | -0.25 | 0.18 | -0.23 | 0.19 | 0.17 | 0.10 |
| BW _l | - | - | 0.16 | -0.06 | -0.25 | 0.16 | 0.02 | -0.30 | -0.21 |
| LS | - | - | - | 0.16 | -0.14 | 0.06 | 0.00 | 0.04 | -0.10 |
| MS | - | - | - | - | -0.32 | 0.27 | -0.25 | -0.22 | -0.06 |
| T | - | - | - | - | - | -0.80* | 0.02 | 0.71* | 0.56* |
| I | - | - | - | - | - | - | -0.44* | -0.62* | -0.40* |
| A | - | - | - | - | - | - | - | 0.01 | -0.05 |
| Peck _{nc} | - | - | - | - | - | - | - | - | 0.75* |
| Peck _c | - | - | - | - | - | - | - | - | - |

BW_s = body-weight at start

BW_l = body-weight loss

LS = lesion score

MS = mobility score

T = time spent threatening

I = time spent immobile

A = time spent on autonomous behaviour

Peck_{nc} = pecks-without-contact

Peck_c = pecks-with-contact

* indicates significant correlations at $P \leq 0.05$ (Krauth 1993)

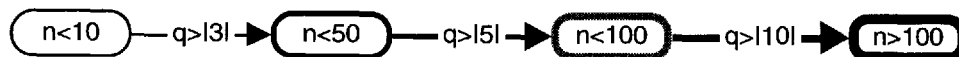


Figure 1a Information for Figure 1b.

Legend for the pooled data of 24 pigeons:

$N < 10$ = number of occurrences of this behavioural element is less than 10; $N < 50$ = number of occurrences of this behavioural element is less than 50 but greater than 10; $N < 100$ = number of occurrences of this behavioural element is less than 100 but greater than 50; $N > 100$ = number of occurrences of this behavioural element is greater than 100.

$q > 3$ = a significant transition from one behavioural element to another element in the direction of the arrow; $q > 5$ = a higher significant transition from one behavioural element to another element in the direction of the arrow; $q > 10$ = a very significant transition from one behavioural element to another element in the direction of the arrow.

For all arrows relating to q if there is no minus sign in the arrow then the first behavioural element is followed significantly more than expected by the second behavioural element and if there is a minus sign in the arrow the first behavioural element is followed significantly less than expected.

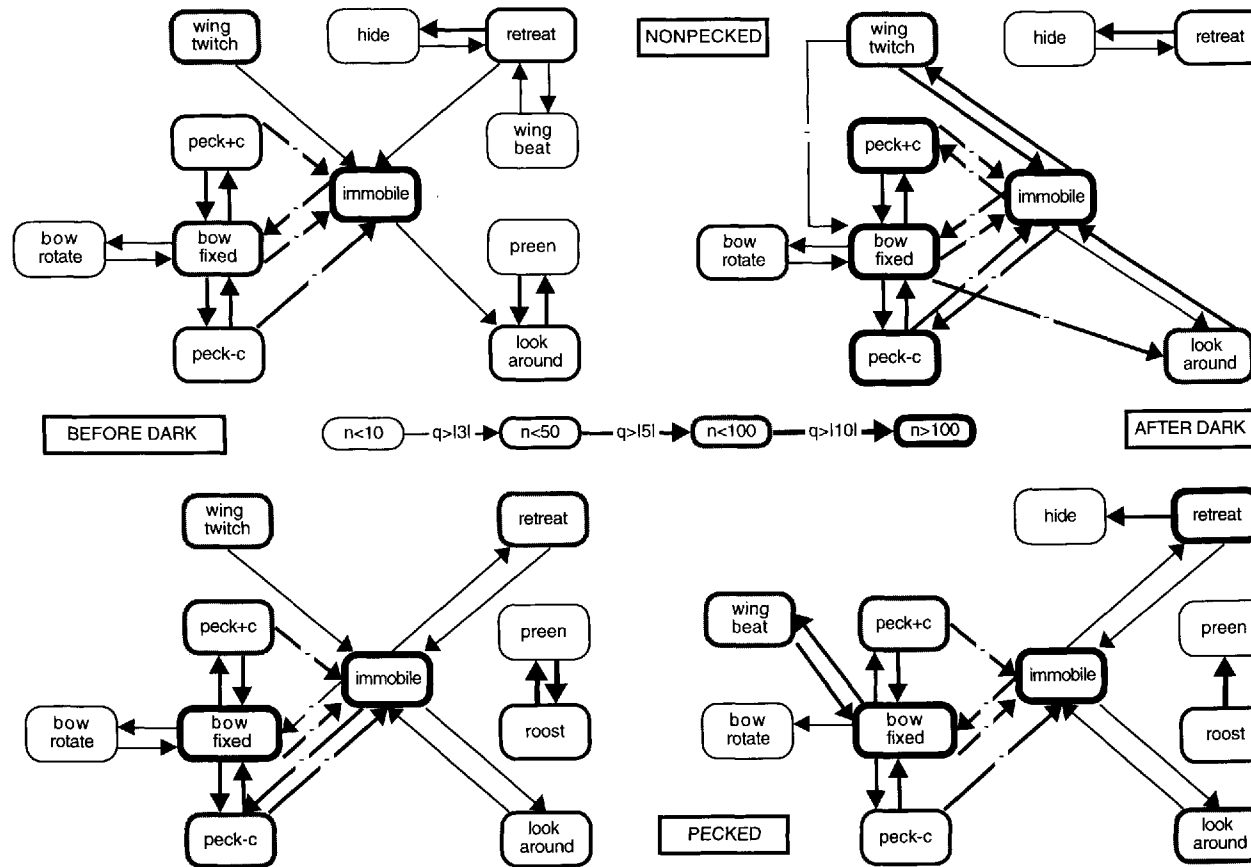


Figure 1b Behaviour sequences during Experiment 1 before and after lights off. Within each of eight groups, behavioural recordings of three birds with the highest lesion score (pecked) and three birds with the lowest lesion score (non-pecked) were selected and pooled (24 birds per diagram) (q = strength of association, n = frequency).

Experiment 2*Behavioural measurements*

In Experiment 2, pigeons were also predominantly immobile (Table 5). Old pigeons were immobile during 57.1 per cent of the time and young pigeons for 70.2 per cent ($F = 16.6$, $P = 0.015$). An interaction, approaching significance, was present between temperature and water availability with respect to immobility ($F = 7.3$, $P = 0.054$).

Old pigeons tended to exhibit more threatening behaviour than young pigeons (18.7% vs 13.5%; $F = 6.05$, $P = 0.07$). A similar trend was observed with respect to avoidance behaviour (10.1% vs 2.3%; $F = 5.45$, $P = 0.08$). With respect to sex, grooming behaviour tended to occur more in females (0.7% vs 1.8%; $F = 6.62$, $P = 0.06$).

As in Experiment 1, pecking frequencies were not affected by water deprivation or heat exposure. In Experiment 2, the proportion of pecks-with-contact in the total number of pecks was 0.35 in male groups and 0.27 in female groups ($F = 13.3$, $P = 0.022$).

Table 5 Behavioural measurements during Experiment 2. Least square means and standard errors of the untransformed values are presented. ANOVA yielding statistical differences was performed using an arsin ($\sqrt{\%}$) transformation for proportions and a $\sqrt{\cdot}$ -transformation for frequencies ($n = 8$ for each measurement).

| Behaviour (per cent of observed time) | Young | | Old | | SE |
|---------------------------------------|-------------------|-------------------|-------------------|-------------------|-----|
| | DW | AW | DW | AW | |
| <i>Immobile</i> | 69.2 ^a | 71.2 ^a | 57.2 ^b | 56.9 ^b | 4.4 |
| <i>Threaten</i> | 14.4 | 12.6 | 21.0 | 16.3 | 3.2 |
| <i>Autonomous</i> | 11.7 | 10.4 | 8.4 | 13.4 | 3.0 |
| <i>Avoidance</i> | 2.0 | 2.5 | 10.8 | 9.4 | 4.7 |
| <i>Grooming</i> | 1.1 | 1.7 | 0.4 | 1.9 | 1.0 |
| * <i>Pecks-without-contact</i> | 7.4 | 8.2 | 9.2 | 11.5 | 1.9 |
| * <i>Pecks-with-contact</i> | 4.4 | 3.4 | 4.6 | 3.7 | 0.8 |

DW indicates deprived of water and AW indicates access to water. * Unit of measurement = times per pigeon

^{a,b} indicate significant differences at $P \leq 0.05$

Heat production and non-behavioural measurements

For young pigeons, HP_{tot} during lights on was $7.35W\ kg^{-1}$, which was $0.32W\ kg^{-1}$ higher than for old pigeons ($F = 4.7$, $P = 0.10$) (Table 6). However, this was not due to a higher activity-related HP, as indicated by the higher HP_{af} (5.88 vs $5.35W\ kg^{-1}$; $F = 9.9$, $P = 0.034$). For male and female groups, HP_{ac} during lights on was 1.90 and $1.25W\ kg^{-1}$ respectively ($F = 32.8$, $P = 0.005$). The higher activity-related HP for males is also reflected in the higher ratio HP_{ac}/HP_{tot} (0.26 vs 0.18 for males and females respectively). There were no interactions in any of the HP_{tot} -related measurements.

Table 6 Heat production measurements during lights on and non-behavioural measurements for Experiment 2. Least squares means and standard errors are presented (n = 8 for each measurement).

| Parameter | Young | | Old | | SE |
|-------------------------------------|--------------------|--------------------|--------------------|--------------------|-------|
| | DW | AW | DW | AW | |
| HP_{tot} ($W\ kg^{-1}$) | 7.51 | 7.18 | 7.26 | 6.79 | 0.15 |
| HP_{af} ($W\ kg^{-1}$) | 5.80 ^a | 5.95 ^a | 5.18 ^b | 5.53 ^b | 0.16 |
| HP_{ac}/HP_{tot} ($W\ kg^{-1}$) | 0.23 ^a | 0.17 ^b | 0.29 ^a | 0.18 ^b | 0.01 |
| Lesions (no) | 1.7 ^a | 1.2 ^b | 2.0 ^a | 1.4 ^b | 0.3 |
| Body-weight at start (kg) | 0.506 ^a | 0.450 ^b | 0.530 ^a | 0.480 ^b | 0.016 |
| Body-weight loss (%) | 8.7 ^a | 8.2 ^a | 6.1 ^b | 5.8 ^b | 0.85 |

DW indicates deprived of water and AW indicates access to water. HP_{tot} is total heat production. HP_{af} and HP_{ac} are activity-free heat production and activity-related heat production respectively.

^{a,b} indicate significant differences at $P \leq 0.05$

Lesion scores for males and females were 1.9 and 1.3, respectively ($F = 8.16$, $P = 0.046$). For young pigeons, lesion scores were 1.5, whereas old pigeons had an average lesion score of 1.7 ($F = 1.7$, $P = 0.26$).

Females had significantly lower body-weight than males (0.465 vs 0.518kg; $F = 20.9$, $P = 0.01$). Start weight of old and young birds was 0.518kg and 0.465kg respectively ($F = 5.41$, $P = 0.08$). The relative body-weight loss of young pigeons was 8.5 per cent, compared with a loss of 6.0 per cent for old pigeons ($F = 17.5$, $P = 0.014$). The weight loss variation within groups was not affected by sex ($P = 0.81$) or age ($P = 0.70$).

Time effects

In Experiment 2, the occurrence of aggressive behaviour did not decrease over time (Table 7). Differences in the occurrence of aggressive behaviour between the first and last part of the exposure period were smaller than in Experiment 1 (Table 3).

Table 7 Comparison between mean (\pm SE) observations made during the first (before lights off (BL)) and last (after lights off (AL)) part of the exposure period (n = 8 for each observation).

| Observation | Experiment 2 | |
|---|-----------------|-----------------|
| | BL | AL |
| HP_{ac}/HP_{tot} ($W\ kg^{-1}$) | 0.21 \pm 0.06 | 0.23 \pm 0.05 |
| Immobile (% of observed time) | 65.3 \pm 3.78 | 62.0 \pm 2.32 |
| Threaten (% of observed time) | 13.6 \pm 2.50 | 18.5 \pm 1.52 |
| Autonomous (% of observed time) | 12.6 \pm 1.67 | 9.2 \pm 0.91 |
| Pecks-without-contact (number per pigeon) | 4.1 \pm 0.78 | 5.0 \pm 0.53 |
| Pecks-with-contact (number per pigeon) | 2.2 \pm 0.39 | 1.8 \pm 0.24 |

HP_{ac} is activity-related heat production and HP_{tot} is total heat production.

The behavioural sequences which were observed during Experiment 1 (Figure 1) are representative of the behavioural sequences observed during Experiment 2.

Individual variation in measurements

Body-weight at the start of the exposure period predicted subsequent behaviour during exposure (Table 8). Pigeons with the highest body-weight at the start were more capable of maintaining their position in the crate, as indicated by a negative correlation between body-weight at start and mobility score during exposure ($r = -0.42$). A high body-weight at the start was also associated with an increase in the time spent in threatening behaviour and with lower lesion scores, although this was not significant.

Table 8 Spearman rank correlations on pooled individual measurements ranked within groups, for Experiment 2.

| Parameter | BW _s | BW _l | LS | MS | T | I | A | Peck _{nc} | Peck _c |
|--------------------|-----------------|-----------------|--------|--------|-------|--------|-------|--------------------|-------------------|
| BW _s | - | - | - | - | - | - | - | - | - |
| BW _l | 0.08 | - | - | - | - | - | - | - | - |
| LS | 0.32 | 0.14 | - | - | - | - | - | - | - |
| MS | -0.42* | 0.26 | 0.44* | - | - | - | - | - | - |
| T | 0.27 | -0.29 | -0.37* | -0.54* | - | - | - | - | - |
| I | 0.23 | 0.20 | 0.40* | -0.56* | - | - | - | - | - |
| A | 0.22 | -0.16 | -0.18 | -0.44* | 0.25 | -0.48* | - | - | - |
| Peck _{nc} | 0.27 | -0.21 | -0.23 | -0.53* | 0.60* | -0.41* | 0.40* | - | - |
| Peck _c | 0.19 | -0.13 | -0.09 | -0.21 | 0.44* | -0.24 | 0.23 | 0.75* | - |

BW_s = body-weight at start

BW_l = body-weight loss

LS = lesion score

MS = mobility score

T = time spent threatening

I = time spent immobile

A = time spent on autonomous behaviour

Peck_{nc} = pecks-without-contact

Peck_c = pecks-with-contact

* indicates significant correlations at $P \leq 0.05$ (Krauth 1993)

Lesion scores provided an indication of the type of behaviour displayed by the pigeons during exposure. Lesion score was positively correlated with mobility score ($r = 0.44$), and negatively correlated with threatening behaviour ($r = -0.37$). Therefore, pigeons with a high mobility score and an unstable position in the crate displayed less threatening behaviour ($r = -0.54$), less autonomous behaviour ($r = -0.44$), and pecked less ($r = -0.53$ in pecking-without-contact).

Body-weight loss was a poor indicator of behaviour during exposure. Pigeons which showed more threatening behaviour tended to have a lower body-weight loss ($r = -0.29$), whereas pigeons with a high mobility score tended to have a higher body-weight loss ($r = 0.26$).

Discussion

In this paper, two experiments on pigeons housed under crowded conditions were presented. The persistence of aggressive behaviour patterns over time and the relationship between observed behaviour patterns and initial body-weight of the pigeons are discussed, as is the relation between heat production, body-weight loss and behaviour patterns.

Behaviour patterns: persistence of aggressive behaviour over time

The persistence of aggressive behaviour patterns over time was demonstrated in both experiments. This fits into the general theory that no fixed hierarchy develops within groups of pigeons in a pigeon loft (Heinroth & Heinroth 1949). Cross and Goodman (1988) found that in paired aggression tests involving male pigeons, the number of aggressive attacks decreased with time once a dominant-subordinate relationship was established. In our 23-hour experiments, with a group size of 10 pigeons, no decrease in aggression levels over time was observed. This suggests that group size is an important determinant for the development of a fixed hierarchy within a group. The dependency of the pigeon's learning capacity on its social environment might explain the absence of a fixed hierarchy in our experiments. Diebschlag (1941) reported that low-ranking pigeons have a learning performance comparable to birds that occupy a higher rank in the loft if those low-ranking pigeons are tested away from conspecifics. However, introduction of higher-ranking pigeons in to the observation chamber resulted in a clear decrease in the test performance of the low-ranking bird. Test performance returned to the previously established levels after removal of the high-ranking individual.

Pigeons with a high mobility score, ie with an unstable position in the crate, were more at risk of having a high lesion score. Pecked pigeons, with an average lesion score of 4.8 did not alter their behavioural strategy over time, even though a lesion score of 3 or higher corresponds with clearly recognisable head injuries resulting from pecking. Hence, the positive correlation between lesion score and mobility score is not a consequence of an increase in avoidance behaviour once the pigeons were injured. This agrees with Cross and Goodman (1988) who found that body movements provoke more aggressive attacks than immobility. This may explain the predominance of immobile-type behaviour, since immobility appears to prevent further aggressive interactions between pigeons. As aggressive encounters have a cost for dominant and submissive pigeons, in terms of energy and injuries (Cross & Goodman 1988), immobility is the most sensible strategy to adopt under the crowded conditions present in both experiments.

Under the crowded conditions occurring during pigeon transport, the on-going nature of aggressive encounters between pigeons has major implications for the injuries that result. An increase in the duration of transport, leading to a longer period of time during which pigeons are group-confined at low space allowance levels, increases the physical cost of transport for the pigeons in terms of an increase in head injuries.

Body-weight at the start: the relationship with subsequent behaviour patterns

The pigeon's rank within a group, as determined by body-weight at the start of exposure, was predictive of the behaviour displayed during exposure (especially in Experiment 2). Pigeons with the highest weight-rank in a group had a more stable position in the crate, spent more time in threatening behaviour and had a higher pecking frequency. This is in agreement

with Diebschlag (1941) who found a higher frequency of aggressive encounters in high-ranking birds observed in a pigeon loft.

Also in free-ranging feral pigeons, the behaviour within a group was associated with relative body-weight. In a feeding flock of feral pigeons central positions in the flock are occupied by pigeons with the highest body-weight, irrespective of age (Murton *et al* 1972b). Centrally-positioned birds had a higher food intake and a lower activity-related energy cost compared with pigeons in the periphery of the feeding flock.

In general, correlations with body-weight at start and other parameters were stronger in Experiment 2. Comparison of start weight of the old males in Experiment 1 with the corresponding group in Experiment 2 showed an average difference of 35g per pigeon. Also, total heat production was clearly lower in Experiment 1. In our opinion, these differences can be attributed to the pre-experimental treatment of the pigeons. Experiment 1 was performed with pigeons that were housed at the University facilities during one year before the start of the experiment. They had limited possibilities for physical exercise since they were housed in a compartment of 2x4x2m and food leftovers indicated that they were fed at or nearly at *ad libitum* level. Experiment 2 used pigeons that had participated in racing contests until about three weeks before start of the experiment. It is possible that the trained pigeons of Experiment 2 can be more easily compared to the very competitive situation which exists among feral pigeons (Murton *et al* 1972b).

The relationship between behaviour patterns, heat production and body-weight loss

Pigeons housed at high stocking densities are not able to decrease activity levels during heat exposure. From a thermoregulatory view-point this would be the most sensible strategy to adopt. In Experiment 1, where temperature and water availability were the experimental factors, a thermoregulatory adaptation in behaviour was expected for water-deprived pigeons exposed to 36°C. The higher body-weight loss in water-deprived birds at 36°C compared to 26°C indicates an increase in evaporative water loss. Therefore, 36°C may be above the upper critical temperature of pigeons housed under crowded conditions (Mount 1974). Since an increase in behavioural activity at 36°C increases not only heat production but also increases pressure on the pigeon's water economy (Arad *et al* 1987), a reduction in activity to save body water reserves would have been expected at 36°C, especially in water-deprived birds. The contrary was observed. Although these results were not statistically significant, the activity-related heat production was highest in water-deprived groups at 36°C.

Our findings of high activity-related heat production related to aggressive behaviour (pecking) is in accordance with the reported findings of Marder (1983). During a heat-acclimation period prior to the actual measurements in the study by Marder (1983) pigeons had to be housed separately, since aggressive behaviour was well-developed at temperature levels exceeding 50°C.

In Experiment 2, young pigeons had a higher activity-free heat production than old pigeons. As indicated by lower body-weight at the start young pigeons were not yet fully grown. This is in accordance with field observations on body-weight in feral pigeons. Measured over 20 monthly observations, the body-weight of captured, fledged, juvenile birds was on average 35g lower than adults captured in the same period (Murton *et al* 1972a). The higher metabolism due to growth may explain the higher heat production levels in young pigeons (Blaxter 1989). Higher metabolism in young pigeons may also be related to the 2.5

per cent higher body-weight loss in young pigeons compared to old pigeons. Under the hypothesis that body temperature was similar between young and old pigeons, a higher heat production at 36°C would involve an increase in evaporative water loss rates. If this water loss is not compensated by a higher water intake more body-weight is lost. Water intake by the pigeons in this experiment was rarely observed, perhaps this was because the total observation time for each pigeon was only 15 minutes and the total observable time during lights on was more than 11 hours. Therefore, the behavioural observations did not permit a quantitative analysis of possible differences in water intake between age groups. However, the time spent immobile was 13 per cent higher in young groups, which may represent a general tendency for young birds to be less active, including less movements to and from the drinking trough.

Males had a higher activity-related heat production than females as indicated by the time spent in threatening behaviour and by the lesion scores. This may be explained by the stronger tendency in males to become involved in aggressive interactions. It also agrees with observations made in a pigeon loft by Diebschlag (1941) and Fabricius and Jansson (1963). When observing paired pigeons in the pre-incubation time, bowing and attacking behaviour was displayed more by males. This may result in an increased activity-related heat production due to increased muscular activity.

Animal welfare implications

We can conclude that neither temperature or water availability had a significant effect on behaviour or heat production. The frequency of threatening behaviour and the proportion of activity-related heat production to total heat production increased over time. Differences in behaviour patterns between pecked and non-pecked birds were present and these differences remained constant during the experiment. In general, no extinction of aggressive behaviour patterns was found. Young pigeons were more immobile than old pigeons, whereas heat production was lower in old pigeons. Male groups had a higher activity-related heat production, more head injuries and showed relatively more pecking-with-contact than females. Again, no extinction of aggressive behaviour or changes in behaviour patterns over time were found. Body-weight at the start of the experiment was predictive of the subsequent behaviour in the crate. A higher-body weight was associated with more threatening behaviour, lower mobility and less head injuries.

The consistent pattern of behaviour of pecked and non-pecked birds without a decrease in aggressive behaviour over time indicates that, under crowded conditions, pecking continues and adaptation in behaviour does not occur. Under these transport conditions the expected effects of water deprivation and heat exposure are overruled.

Further research should elucidate whether an increase in space allowance will improve pigeon welfare during transport. The effects of light intensity and typical transport phenomena, such as vibration and noise, on the behaviour of pigeons housed in transport crates requires further study in order to provide pigeon transporters with guidelines for improving transport procedures.

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