THERMOREGULATORY AND BEHAVIORAL CHARACTERISTICS OF RACING PIGEONS HOUSED UNDER TRANSPORT CONDITIONS

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THERMOREGULATORY AND BEHAVIORAL CHARACTERISTICS OF RACING PIGEONS HOUSED UNDER TRANSPORT CONDITIONS

J. Gorssen

Proefschrift

ter verkrijging van de graad van
doctor in de landbouw- en milieuwetenschappen,
op gezag van de rector magnificus,
Dr. C.M. Karssen,
in het openbaar te verdedigen
op woensdag 1 november 1995
des namiddags te vier uur in de aula
van de Landbouwuniversiteit te Wageningen

**Gorssen, J. Thermoregulatory and behavioral characteristics of racing pigeons
housed under transport conditions.**
Transport is an essential component of racing pigeon contests. Preliminary studies
indicated that adverse transport conditions might contribute to the occurrence of flight
losses. Flight losses consist of pigeons which do not return to their home loft. In this
thesis, physical and social aspects of the transport environment were studied in relation
to the thermoregulation and behavior of racing pigeons. In all experiments, the pigeons
were group confined to a transport crate during at least 23 h. A combination of
continuous heat exposure and water deprivation results in an increased heat production,
body weight loss, and body temperature. The effect of ambient temperature on heat
production varies both between and within photoperiods. Water deprivation affects this
diurnal variation. Temperature fluctuations during heat exposure increase locomotor
activity and body weight loss. At the space allowance levels currently used during
transport, aggression related behavior is predominant within a group of pigeons.
Aggression levels do not decrease with time. Aggressive interactions cause an increased
activity-related heat production, and result in head injuries. Head injuries are less severe
in groups of female pigeons compared to groups of male pigeons. With increasing space
allowance levels, both the risk of having major head injuries and the occurrence of
aggression-related behavior decrease.
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STELLINGEN

1. Het gebruik van genees- en andere middelen in de duivensport, voortvloeiend uit de behandeling van oogonstekingen, kan verminderd worden door de beschikbare mandoppervlakte per duif tijdens transport te vergroten.

   (Dit proefschrift)

2. De schijnbare rust die kan heersen binnen een groep duiven gehuisvest onder transportcondities vertoont veel gelijkenissen met het wegkijkgedrag van mensen in een goedgevulde lift.

   (Dit proefschrift)

3. Normstelling is een bij uitstek politiek proces dat per definitie voorbij gaat aan de natuurlijke variatie aanwezig in het onderwerp van regelgeving.

4. De dichotomie suggererende terminologie "active and passive copers", gebruikt in de ethologie, is inhoudelijk nauw verwant met de term "zwart-wit foto": de naamgeving wordt bepaald door de extremen wit en zwart, het reële beeld door een veelheid aan grijstinten.

5. Gelet op het duidelijke dag-nachtritme in het effect van de omgevingstemperatuur op de warmteproduktie van duiven is het zinvol om bij toekomstig onderzoek naar de endocrinologische achtergronden van dit verschijnsel gericht te zoeken naar de rol van melatonine in thermoregulatoire effectormechanismen.

   (Dit proefschrift)

6. Het gegeven dat donkere kleurvarianten van de rotsduif, met een langer broedseizoen, een gering aandeel uitmaken van populaties in natuurlijke habitats maar de meerderheid vormen in stadspopulaties (Murton et al. 1973. J. Repr. Fert. Supp. 19:563-577) kan via het "prudent parent" principe (Drent & Daan. 1980. Ardea 68:225-252) verklaard worden door seizoensgebonden beperkingen in energiebeschikbaarheid in natuurlijke habitats.

7. Bedwateren heeft het imago van onschuldige jeugdkwaal. Als adolescent valt een positief zelfbeeld echter grotendeels samen met een positieve appreciatie van het eigen lichaam. Vanuit psychisch oogpunt is het dus essentieel dat de behandelende arts bedwateren zo vroeg mogelijk ernstig neemt, en dienovereenkomstig handelt.

8. Democratisering van de besluitvorming in de overheidssector, met het referendum als triest hoogtepunt, is meestal een populistische schaamlap gericht op de anonimisering van aanvechtbare beslissingen. Onder het motto "wel de lusten, niet de lasten" ontlopen bestuurders aldus hun individuele verantwoordelijkheid die nochtans onlosmakelijk samenhangt met het forse salaris verbonden aan een leidinggevende functie.

9. De aanstelling van beleidsmedewerkers is een indicator voor het slecht functioneren van het hogere kader binnen een organisatie.

10. Kortdurende aanstellingen staan het vormen van informele netwerken binnen de universiteit in de weg. Gecombineerd met de lange inwerkperiode nodig voor het vertrouwd raken met de universitaire besluitvormingsprocedures leidt de huidige aanstellingspolitiek dan ook tot een de facto discriminatie van tijdelijke medewerkers in de democratische beheersstructuren van de universiteit.

11. Wanneer de Nederlandse samenleving in een internationaal perspectief wordt geplaatst, dan lijkt het zelf toegekende epitheton ornans "Nederland-gidsland" vooral gebaseerd op het ruime aanbod van omroepbladen.

12. Motiverend bedoelde opmerkingen van de wetenschappelijke omgeving geven een promotie een bijna middeleeuws-religieus karakter, waarbij de promovendus wordt voorgespiegeld dat de beproevingen doorstaan in de voorbereiding uiteindelijk zullen oplossen in de staat van genade die met "Doctor" wordt benoemd.

13. In Nederland en België is natuurbeheer alleen maar een vorm van gesubsidieerd boeren.

J. Gorssen
Thermoregulatory and behavioral characteristics of racing pigeons housed under transport conditions
Wageningen, 1 november 1995

Es is nicht gut, daß die Tiere so billig sind.

Elias Canetti, 1943
Die Provinz des Menschen

Voorwoord

Ik begin omdat ik geen kracht heb om te denken;
ik voltooi omdat mijn ziel de kracht mist om eerder op te houden.
Dit boek is mijn lafheid.

<div align="right">Fernando Pessoa, "Het boek der rusteloosheid"</div>

Dit proefschrift is de papieren resultante - en het rituele sluitstuk - van ruim 4 jaar volgehouden overspronggedrag.

Dankzij de toevalsgestuurde aanwezigheid van twee oudere, afgestudeerde broers bleef deze promovendus-in-spe gevrijwaard van de dienstplicht voor het Belgische vaderland. Een buitenLeuvens uitstapje in de tot dusver onbekende wereld van het experimentele onderzoek aan landbouwhuisdieren leek een geschikt alternatief voor deze tijd vol pseudo-militaire ledigheid. Via de contacten van Ronny Geers met "Wageningen" resulteerde dit in de mogelijkheid om een jaar lang gastmedewerker te spelen in en rond de klimaat-respiratiecellen van de vakgroep Veehouderij.

Begin 1990 viel de beslissing om deze mogelijkheid ook daadwerkelijk te benutten. Tijdens het gastmedewerkersjaar voorafgaand aan het duiventijdperk bestond het leeuwedeel van mijn bezigheden uit "data-collectie". De visuele en organoleptische min-punten van dit werk, wel bekend voor wie vertrouwd is met de primaire stap bij het opstellen van energie- en stikstofbalansen, werden echter ruimschoots gecompenseerd door de personele omkadering. Peter, Marcel, Hans, Edward, Piet, Eric en Yde: het was een plezier om met jullie samen te werken. Mijn speciale dank aan Koos en Mary-Ann: zij toonden aan dat niet alleen Ella's legkippen hun ei kwijt mogen binnen de geborgenheid van een grote klimaat-respiratiecel.

Na de zeugen, biggen, mestvarkens, kippen en kalveren volgde dan het <u>magnum opus</u>: het duivenproject. Prins, bedankt voor de mogelijkheid om ruim 3 jaar te mogen werken met een fascinerende vogelsoort, die me steeds met bewondering doet toekijken, zelfs in zijn groezelige verschoppelingengedaante van stads- of stationsduif.

De term "creatief spanningsveld" beschrijft beeldend maar accuraat mijn relatie met de Nederlandse Postduivenhouders Organisatie, de opdrachtgever en mede-financier van het project "Klimaatbehoeften van postduiven tijdens transport". Via Ad van Heijst, mijn direct en prettig aanspreekpunt binnen de NPO-geledingen, mijn dank voor de voorbije samenwerking. Een dankbetuiging die zich ook richt tot de firma Leppers in Veenendaal, leverancier van aanzienlijke aantallen proefduiven, eigen aan dit type transportonderzoek. Henny, als onze eigenste "miss Efficiency" tijdelijk gedetacheerd vanuit een HAS in het oost'n des lands, kan er over meepraten.

Hoewel ik als verantwoordelijk onderzoeker op het project werd gezet met de opdracht om nu maar verder "de kar te trekken", moet een kar ook een richting uit worden getrokken. En daarbij is een duw wel eens welkom. Jos, als promotor was je er op de ogenblikken dat het nodig was. En meer moet dat niet zijn. Van harte bedankt voor

het prettige "nabuurschap". Martin, sabbaticals aan de andere kant van de aardkloot en de druk-druk-drukke tijden daaraan voorafgaand zijn weinig bevorderlijk voor een intensieve promotor-promovendus relatie. Maar je soms onconventionele invalshoeken en je opbouwende commentaar hebben meer dan eens de kar rollende gehouden in het bij wijlen erg rulle zand.

Inhoudelijk bewandelt dit proefschrift wegen die zich hooguit in de periferie van het gangbare Wageningse klimaat-respiratiewerk bevinden. Wat buiten de deur shoppen noodzakelijk maakte. Voor Maurine, mijn thermoregulatoire praatpaal, was dit nogal wat kilometers buiten de deur. De ethologische ondersteuning door Paul daarentegen lag om de hoek, beter nog, in een ZODIAC-uithoek. Albino-merels, sperwers, appelvinken en aangewaaide grasparkieten maakten de interne excursies echter steeds de moeite waard. En dan laat ik Feite z'n koffie zelfs nog buiten beschouwing.

Johan, jij kwam pas echt in de kijker toen de herinnering aan het aroma van je kalverproef al bedolven was onder het duivestof. Bedankt voor je kritische steun, niet alleen in de opstartfase, maar ook gedurende de rest van het traject. Tot één van m'n aangenamere Wageningse erfenissen reken ik de vaststelling dat een aanvankelijk stroeve professionele samenwerking kan uitmonden in een prettig contact dat een andere werkkring en een landsgrens overleeft.

Harm, als kamergenoot was je een constante factor doorheen mijn verblijf in ZODIAC. Hoewel er weinig overlap te bespeuren was tussen onze verblijfstijden in de kamer noch tussen onze onderzoeksgebieden, heb ik de babbel tussendoor altijd zeer op prijs gesteld. Hopelijk heb je je niet teveel gestoord aan het cynisme van het Veehouderij-broekie.

Dankbaarheid betuigen voor inhoudelijke ondersteuning is makkelijk: je maakt de betreffende luitjes gewoon co-auteur. Het tot stand komen van dit boekje vloeit echter ook voort uit de steun van mensen die formeel niets met het hele duivengedoe te maken hadden. En die zijn moeilijker in een formele dankzegging te betrekken. Carla, secretaresse van de LU-ontspanningscommissie, en Lisette: Leonidas-import helpt een beetje, maar zelfs een kilo van die witte met een nootje bovenop vormt maar een mager bedankje voor jullie aanwezigheid binnen en buiten de ZODIAC-muren gedurende de afgelopen jaren.

En wat mijn heimat betreft: er wordt wel eens beweerd dat er slechts twee soorten gezag bestaan. De één is gebaseerd op rang, de andere op bekwaamheid. In en om Kloterstraat 12 in Kaulille kon en kan slechts deze laatste gezagsvariant op instemming rekenen. Voor zover dit werk, en mijn hele tijd op ZODIAC, getuigen van een kritische instelling, dan vloeit deze grotendeels voort uit de geest waarin ik thuis ben grootgebracht.
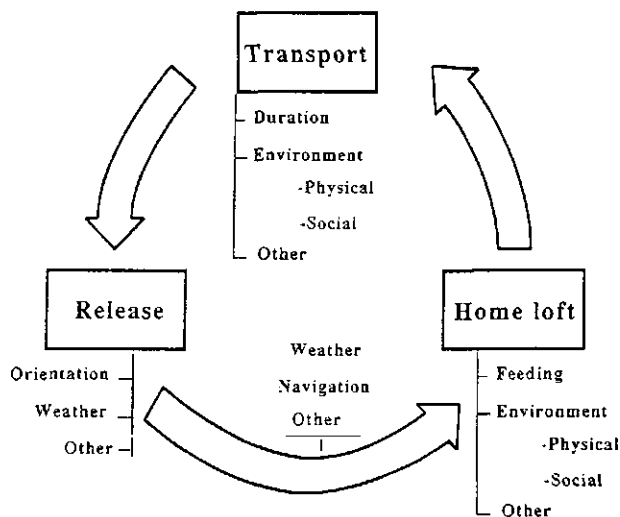
CONTENTS

GENERAL INTRODUCTION:

General Introduction

TRANSPORT OF RACING PIGEONS: AN OUTLINE

"To be first in pigeon homing: championship or luck?"

In the avalanche of scientific papers waiting to be read, this is a striking and provocative title used by Wallraff (1994) in a paper on the navigational capacities of racing pigeons. And, at the same time, it is a question of major concern for all participants (or rather, their owners) in racing pigeon contests. The paper, however, also illustrates nicely the gap between the scientific quest for the mechanisms underlying pigeon homing, i.e., the backgrounds of pigeon orientation and navigation, and the basic practical concern of a racing pigeon owner for the safe and sound return of his (or her) pigeons in a homing contest.

As illustrated in Figure 1, a prosperous journey home may not only depend on the pigeon fancier's craftmanship at the home loft and on the pigeon's navigational abilities after release from the transport crate. Also transport, the cycle step between capture and release, may affect the pigeon's flight success through the bird's capacity to cope with the transport procedure. A procedure that is beyond the pigeon's control.

Figure 1. Dynamic cycle in racing pigeon contests with the three main factors and contributory elements which have potential effect on pigeon performance.

As depicted in Figure 1, the transport procedure has three main elements: the transport duration, the bird's physical environment during transport, and the social environment of the transported pigeons. Although parallels in transport procedures between racing pigeons and poultry can be demonstrated for all three transport elements, one basic difference in the perception of transport by the individual bird has to be stressed. For poultry, transport is incidental, and at fixed stages of development or age: immediately after hatching, at start and end of the laying period, or at the end of the growing period. Due to the very limited possibilities to get acquainted to the transport procedure, this implies that the predictability of a transport procedure is low for poultry. Racing pigeons, however, are enrolled in transport procedures each week or each fortnight during the racing season, and this from an age of about 6 months onwards. Hence, pigeons probably are better adapted to the transport procedure as such than poultry. However, this does not mean that each transport element is constant and, consequently, predictable for the bird. This is illustrated by the three main transport features, presented in Figure 1.

Duration

The transport duration, defined as the time between enclosure in the transport crate and release from the crate, is highly variable, ranging from 12 h or even less, to 72 h or more. These durations are considerably higher than those reported for broiler chickens between capture at the farm and slaughter at the processing plant. Extreme values reported by Bayliss and Hinton (1990) on poultry transport did not exceed 8 h. Duration of pigeon transport has two main determinants: the transport distance and the waiting time after arrival at the release site, set aside the waiting periods during the journey itself due to the driver's rest periods. The latter may be prolongated by several hours if adverse flight conditions are present or foreseen at the release site or between the release site and the home loft.

The physical environment

The physical environment during transport is determined by the climate (e.g., temperature, air humidity, air velocity), light duration and intensity, air composition and, in a broader sense, also husbandry practice (water and feed availability).

In general, pigeons are transported in trucks with a capacity of about 200 transport crates, each of which contains about 30 pigeons. At present, transport trucks have no additional cooling facilities. The fans for forced ventilation, if present, have not enough capacity to cover the ventilation requirements of a fully loaded truck. Hence, heat transfer from the truck to the outside depends mainly on air cooling through natural ventilation while driving. From field studies in comparable broiler transport vehicles, it became evident that the temperature in the truck does not only depend on the outside temperature, but also on temperature control measures taken by the driver during transport stops. Kettlewell and Mitchell (1993) demonstrated that a stop without additional temperature control, such as opening truck doors, resulted in a temperature increase at bird level of about 12°C within in

a time span of 30 min, and this at a constant outside temperature. As a result, the temperature difference between the outside temperature and the inside temperature at bird level increased from 6 to 18°C. The increase in temperature was accompanied by an increase in air humidity, another indication for the dependence of the air quality inside the truck on the ventilation rate.

Exploratory measurements during pigeon transport gave patterns similar to those reported for broilers (Gorssen and van der Hel, 1993). However, since the Dutch racing season starts in April and is generally finished by the end of September, it covers the late part of spring and the entire summer, so the warmest part of the year. The combination of inadequate climatic control and warm outside conditions supported the perception by drivers and caretakers involved in pigeon transport of "heat exposure" as the most prominent parameter of the physical environment. In addition, body weight data collected during the exploratory transport measurements revealed weight losses of on average 9.2%, with a maximum of 14% (Gorssen and van der Hel, 1993). This pointed at a crucial flaw in the internal transport guidelines. The role of water availability was not investigated. It is, however, well established that heat loss through water evaporation is the main thermoregulatory mechanism in heat exposed homeotherms (Blaxter, 1989).

With respect to the light conditions within the transport truck, little is known. Depending on the type of vehicle, exterior light may penetrate into the truck during transport. This means that the time of transport (day or night) can affect the light conditions at bird level while driving. At the release site, the sides of the truck are usually at least partially opened. Hence, prior to release the pigeons are subjected to the natural light regimen.

The social environment

The main feature of the social environment of pigeons during transport is the high stocking density. Transport guidelines prescribe a space allowance of 225 cm^2 per bird for transport durations between 24 and 48 h, 250 cm^2 for transports between 48 and 72 h, and 300 cm^2 space allowance per pigeon for transports of more than 72 h. The total crate surface ranges from 6000 to 9000 cm^2. For a short transport, this results in 40 pigeons per 9000 cm^2-crate.

Furthermore, groups within a crate are homogeneous with respect to age class. Young pigeons, less than one year old and in their first racing season are separated from pigeons older than one year. Furthermore, all old pigeons are separated with regard to sex: male and female groups are housed separately. Generally, this procedure is also followed for young pigeons, although difficulties in sex discrimination at a young age and the belief that aggressive behavior is limited to old male pigeons may lead to mixed groups of young pigeons during some transports. The origin (the owner) of the pigeons within a group is not necessarily identical.

BACKGROUNDS FOR RESEARCH

The primary reason for the present research was the growing concern for the occurrence of flight losses, not only among pigeon fanciers, but also in Dutch society. Flight losses, defined as the number of racing pigeons which does not return to the home loft, are hard to quantify due to a lack of data. As illustrated in Figure 1, the reason for these losses is also difficult to pinpoint: factors before and after release may all come into play. However, the pigeon fancier's awareness of transport conditions as a possible explanation for sudden peaks in bird losses is a clear break with earlier views. Until recently, problems with orientation and navigation combined with adverse weather conditions after release usually were invoked to explain for the empty nests and roosting perches after a racing contest. Findings in poultry support this possible effect of transport conditions. The incidence of Death On Arrival in broilers delivered at the processing plant is higher during summer (Bayliss and Hinton, 1990), and is further increased by a longer transport duration (Warriss et al., 1992). Other research, performed on newly hatched chicks, showed that heat exposure does not only increase mortality during exposure, but also during a following 2-wk period under normal conditions. In this 2-wk period, also decreased growth rates were observed in comparison with non-exposed groups (Van der Hel et al., 1992). Other circumstantial evidence for the possible adverse effects of heat exposure during transport on pigeon performance was found in horses, whose performance abilities decrease following dehydration (Hodgson et al., 1994).

A second and more general reason for research was grounded in the growing awareness of possible animal welfare problems during transport. In contrast with transport of farm animals such as chickens, facts and figures concerning transport and transport conditions of racing pigeons (Columba livia) are lacking in both journals on applied farm animal research and in government statistics concerning agriculture. For the Netherlands, the yearly number of pigeon transports (i.e., each time one pigeon is subjected to the transport procedure) is estimated at about 10.000.000. About 47.000 pigeon fanciers, organized in the NPO (Dutch Racing Pigeon Fanciers Organisation), register approximately 2.000.000 young pigeons yearly for participation in racing contests. These figures indicate that even a marginal change in problems such as flight losses involves a considerable number of birds.

In 1990, the research project was started, funded by the NPO, and financially supported by the Dutch Veterinary Service (Ministry of Agriculture, Nature Conservation and Fisheries). The project was aimed to provide answers to basic questions concerning thermoregulation and behavior of racing pigeons housed under transport conditions. For NPO, these answers should provide the necessary background for experimentally justifiable modifications in the transport guidelines.

In the course of this research project, ended in February 1995, the methodological framework gradually shifted from an initial emphasis on thermal physiology to, finally, pigeon behavior studies. For each study, energy metabolism measurements played a key role, thus forming the core for this thesis. The structure of the thesis reflects this (chrono)logical change

in disciplinary approach. This, however, is the subject of the next paragraph.

THESIS OUTLINE

Temperature and water availability were the main factors of interest at the start of the investigations. Insight in the effect of temperature and water availability on thermoregulation of pigeons housed under transport conditions was needed. Surprisingly, this information could not be retrieved from literature, although the pigeon is one of the most investigated species with respect to thermoregulation (Graf et al., 1989). As illustrated by a selected list of papers in Table 1, the encountered experimental conditions were fundamentally different from those during transport.

Table 1. Experimental conditions during reported thermoregulatory studies on heat production of individually confined pigeons.

N[1]	T_a-range[2] (°C)	Duration (h)	L.R.[3]	R[4]	Source
7	− 10 to 25 (10)	2	D	N	Flynn & Gessaman, 1979
13	27 to 47 (2)	2	D	N	Marder & Gavrieli-Levin, 1986
5	30 to 45 (2)	2-3	D	N	Arad et al., 1987
?	0 to 45 (8)	1-6	D	N	Calder & Schmidt-Nielsen, 1967
23	5 to 40 (8)	± 1	D	Y	Saarela & Vakkuri, 1982
8	− 20 to 35 (12)	2	D	Y	Rautenberg, 1969
6	10 to 25 (2)	3	D	Y	Graf et al., 1987
10	0 to 40 (6)	3-5	D	Y	Webster et al., 1985
8	20 to 35 (2)	≤ 12	12L:12D	Y	Heller et al., 1983
5	5 to 35 (11)	24	12L:12D	Y	Graf, 1980
5	20	120	12L:12D	Y	Graf et al., 1989

[1] N: Number of pigeons used in the experiment.
[2] T_a: Minimum and maximum ambient temperature levels for measuring heat production (number of T_a-levels).
[3] L.R.:   Light regimen during the measurement period (L=light, D=dark).
[4] R: Pigeons restrained to prevent activity or measurement disturbance (Y= yes, N= no).

First, all papers report on research performed with individually confined birds. Thus, the thermoregulatory consequences of social behavior are eliminated. In addition, the pigeons were physically constrained in the majority of the cited studies. This gives a further reduction

in activity patterns compared to those normally observed in a transport crate.

Second, the duration of exposure to a given temperature level was generally short, and not relevant for transport conditions.

Third, a powerful tool for assessing the thermoregulatory effect of temperature on homeotherms is the estimation of the relation between heat production and temperature, focussing on the lower and upper bounds of the zone of thermal neutrality (Mount, 1974). For this purpose, measurements of metabolic heat production at a considerable number of temperature levels is required, preferably with a small interval between temperatures (< 5°C). None of the cited papers meets both these requirements and the transport imposed demand for an extended duration of exposure.

As a result, Chapters 1 to 4 of this thesis focus on the thermoregulation of pigeons housed under transport conditions, with emphasis on the role of water availability at temperature levels at or above thermoneutrality. In Chapter 1, the effect of water availibility and age on the optimal temperature levels is studied. Measurements of heat production, body weight loss and body composition during a 23-h exposure to one of 10 constant temperature levels were used to estimate the upper critical temperature, the upper boundary of the zone of thermal neutrality. The diurnal variation in the relation between heat production and temperature is presented in Chapter 2. The possible effect of water deprivation and locomotor activity levels on this diurnal variation is discussed, based on the heat production measurements collected during the experiment described in Chapter 1. In Chapter 3, individual body temperature data were linked with group measurement of heat production and evaporative heat loss in order to assess the pigeon's capacity to recover from dehydration at three different temperature levels. Also, the effect of water deprivation and T_a on dry thermal conductance was studied.

Chapters 1 to 3 deal with exposure to constant temperature levels, which is, from a transport perspective, a highly artificial situation. Chapter 4, however, concentrates on locomotor activity patterns, heat production and body weight loss during exposure to fluctuating temperature levels both in a cold (15°C) and warm (35°C) reference situation. Chapter 4 also constitutes a bridge between Chapters 1 to 3, where emphasis was placed on the physical environment during transport, and Chapters 5 and 6, where the social environment within a crate and its effect on the behavior of the pigeons are the main points of interest.

With respect to the literature available on behavior and behavioral processes of pigeons, a remarkable parallel with the thermoregulatory studies mentioned above can be observed. Also in ethology and psychology, the pigeon is one of the most widely used animal models. As in thermoregulation, however, the relevance of the experimental work for the improvement of transport guidelines is highly doubtful. In Chapter 5, the behavior of pigeons and the resulting heat production and injuries were studied at a high stocking density in the crate. The sensitivity of pigeon behavior to temperature and water availability was studied. Behavioral differences between young and old pigeons were examined using homogeneous male or female

groups. Chapter 6 concentrated on the effect of stocking density, or space allowance, as such. Groups of male or female pigeons were observed at space allowance levels at and above those applied during transport to date.

The main findings of Chapter 1 to 6 are discussed and interrelatedly considered in the General Discussion. The discussion will focus on the role of time regarding two important characteristics of racing pigeons housed under transport conditions: Thermoregulation and behavior.

CHAPTER 1:

Optimal Temperature Levels for Racing Pigeons (Columba livia) Housed under Transport Conditions: The Role of Water Availability and Age

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ABSTRACT

The effect of water availability and age on the optimal temperature zone of racing pigeons (<u>Columba livia</u>) housed under transport conditions was studied. The upper critical temperature of this zone was estimated based on heat production, body weight alterations and body composition measurements. During 23 h, 40 groups of 15 "First Year" pigeons and 40 groups of 15 or 18 "Old" pigeons were exposed to one of 10 ambient temperature levels between 15 and 39°C, with or without access to water. Age did not affect the optimal temperature zone, whereas water availability had a strong impact. In birds with access to water, no upper critical temperature was found for heat production, body weight loss and dry matter content. Variation in weight loss within groups increased above 32.1°C. Water deprivation caused dehydration, and resulted in mortality at 39°C. Heat production increased by 0.16 $W \cdot kg^{-1} \cdot °C^{-1}$ above the upper critical temperature of 32.7°C. Above 32.1°C, body weight loss and dry matter content increased by respectively $1.3\% \cdot °C^{-1}$ and $0.83\% \cdot °C^{-1}$. The dehydrated state as a result from water deprivation and heat exposure during transport for racing contests may increase bird loss rates.

INTRODUCTION

Racing pigeon contests in The Netherlands chronically cause bird losses. These losses, defined as the number of pigeons that does not return to the home loft, tend to be higher in young pigeons than in older, more experienced birds. Usually, losses are attributed to events occurring at the release site or during the flight home, such as lack of motivation to home, problems with orientation and navigation (Walraff, 1994) and adverse weather conditions. However, findings in poultry suggest that pigeon losses may also be due to heat exposure during transport from the home loft to the release site. Transport conditions of racing pigeons are comparable to those for poultry. Group confinement, and chronical or periodical exposure to high temperature levels are the main similarities. In addition, duration of pigeon transport may vary from 12 to 72 h, with periods of feed and water deprivation extending to 24 h

(Gorssen and Van der Hel, 1993). Water deprivation under heat exposure results in dehydration and impaired thermoregulation (Arad et al., 1987). In broilers, the incidence of Dead On Arrival after transport is higher during summer (Bayliss and Hinton, 1990) and increases with duration of transport (Warriss et al., 1992). Furthermore, heat exposure of neonatal chicks increases mortality and decreases growth rates in the following 2-wk period under normal conditions (Van der Hel et al., 1992). With respect to pigeon transports, no data on mortality are available, and no information is present regarding possible adverse effects of dehydration on pigeon performance. However, horse performance is known to suffer from dehydration (Hodgson et al., 1994). In summary, improvement of thermal conditions and caretaking during pigeon transport seems helpful to reduce bird losses.

In the present paper, we report on studies into the effect of water availability and age on the optimal temperature zone of pigeons housed under transport conditions. Estimates of the upper temperature boundary of this zone, the so-called "upper critical temperature", were based on heat production, body weight and body composition measurements over a 23-h exposure period to a constant ambient temperature.

MATERIAL AND METHODS

Design and animals

In total, 80 groups of racing pigeons were allotted to a factorial design, with water availability, age, and temperature as factors. Water was available at two levels: access to water (AW) or deprivation of water (DW). Two age classes were used, one including pigeons not older than 10 months ("First Year"), the other including birds older than 10 months ("Old"). Ambient temperature (T_a) was set at one of 10 constant levels: 15, 19, 23, 27, 29, 31, 33, 35, 37, or 39°C. Per treatment combination, two groups were used. Each group contained 15 pigeons, except for "Old" groups at 23, 31 and 37°C, where the number of birds was 18. Each group consisted of experimentally naive pigeons of both sexes. All pigeons had racing contest experience, and were obtained 7 to 10 d before start of the exposure period. Upon arrival at the university, they were randomly allotted to experimental groups.

Housing and feeding

After arrival, the birds were housed under natural photoperiod, humidity and temperature in a half-open outdoor loft. They were fed twice daily on a commercial diet of whole grains (corn, barley, sorghum and peas). Water was available ad libitum. On the day before start of the exposure period (Day 0), diet was changed to whole grain corn in order to avoid food selection (Moon and Zeigler, 1979). This prevented variation in individual dietary composition, and thus food composition related water intake due to variable protein contents of the selected diets (McNabb et al., 1972). Immediately after the afternoon feeding (16.00 h) on the same day, animals were grouped. Afterwards, they were transferred from

the loft to a quiet laboratory room for an adaptation period of 16 h. Each group was confined to a metal transport crate with free access to water, but with no food available. For 40 "First Year" groups and 28 "Old" groups of 15 pigeons, the inner dimensions of the crate were 0.60 m width × 0.70 m length × 0.25 m height. For 12 "Old" groups of 18 birds, the inner dimensions of the crate were 0.72 × 0.70 × 0.25 m. For each group size, a mean of 280 cm^2 available surface area per animal resulted. Water was supplied by means of two removable drinking-troughs attached to the outside of the crate. Before start of the following exposure period, the drinking troughs were removed from the crate for groups deprived of water.

At about 10.00 h of Day 1, the exposure period started. The crate was placed on a platform in one of two climate-respiration chambers of 1.8 m^3 each (Verstegen et al., 1987). Ambient temperature was measured by means of a thermocouple placed 0.05 m above the top of the crate. As during pigeon transport, air humidity was maintained at a high level. Relative humidity was kept constant at about 70% up to 35°C. At 37°C and 39°C, it decreased to respectively 64 and 56%. The absolute humidity was thus maintained at the 35°C-level. The thermoregulatory consequences of this minor change in relative humidity in the T_a-range of 35 to 39°C are small (Smith, 1972). During the adaptation and the exposure period, lights were off between 20.30 and 07.30 h.

Measurements

Heat production measurements started about 45 min after closing the chambers, and lasted until 09.45 h of Day 2. Heat production data for each group were collected by indirect calorimetry in 9-min intervals on the basis of the exchange of CO_2 and O_2 (Romijn and Lokhorst, 1961; Verstegen et al., 1987). Oxygen consumption was measured with a Servomex 1100 H paramagnetic analyzer, CO_2 production was analyzed using a Hartmann and Braun Uras 3G infrared absorption analyzer. Analyzers were calibrated every 24 h, and all gas volumes were converted to standard temperature and pressure, dry. Ventilation rate was approximately 17 dm^3·min^{-1}. Heat production was expressed as W·kg^{-1}, using body weight at start of the exposure period. The respiratory quotient was calculated as CO_2 produced over O_2 consumed.

Body weight (BW) of all animals was recorded individually ($\pm$ 1 g) at start of the adaptation period, at start of the exposure period and immediately after exposure (Mettler PM6100). Body weight loss over the exposure period was expressed relatively to body weight at start:

$$BW\ loss\% = 100 \times (BW_{start} - BW_{end})/BW_{start} \qquad [1]$$

Hematocrit values (Hct) were measured at 19, 29, 33, 35 and 39°C in four birds per group immediately after exposure, following weighing of the bird. Blood samples collected from the posterial tibial vein were used.

After weighing, four randomly selected birds per group were killed (T61 i.v., Hoechst AG), and stored in air-tight bags at -18°C until further analysis on the water content of the breast part. This breast part consisted of the sternum, humeri and scapulae with appending muscles. After mechanical homogenization, three samples per pigeon were air dried at 103°C. Finally, the dry matter (DM) content of the breast part was calculated for each pigeon separately as a percentage of total fresh weight based on the mean of the three samples.

Calculations and statistics

For statistical analysis, group was used as the experimental unit. For heat production (HP_{tot}) and Hct, group means were subjected to a 3-way analysis of variance, including water availability, age and temperature as main factors in the model. Results were considered statistically non-significant if $p > 0.05$. Non-significant 2- and 3-way interaction effects were removed from the model. For body weight loss, both group means and group coefficient of variance (CV) were subjected to ANOVA (Procedure GLM: SAS Institute Inc., 1989).

To estimate the upper critical temperature (T_{uc}), a continuous two-phase regression method for the estimation of physiological thresholds was adopted (Nickerson et al., 1989). Since ANOVA revealed no significant 2- or 3-way interactions with respect to "Age", regression estimates were based on pooled data within each water availability level. Estimates for both water treatments were compared using a general linear test statistic (Nickerson et al., 1989). The actually measured T_a was used as independent variable.

In "Old" pigeons, one DW group at 19°C and two DW groups at 39°C were removed from analyses due to technical problems. At 39°C, some animals of the "First Year" DW groups could not cope. One bird was lost in the first group, and 12 birds were lost in the second group. This second replicate was removed from the analyses. Because no data for the "39°C-DW-Old" treatment combination were available, ANOVA was performed on T_a-classes 15 to 37°C only.

RESULTS

Heat production was significantly affected by T_a $(p \leq 0.001)$ and age $(p \leq 0.001)$ (Figure 1). For "First Year" pigeons, HP_{tot} was 6.53 $W\cdot kg^{-1}$, being 0.36 $W\cdot kg^{-1}$ higher than for "Old" birds. Water availability had no effect. No significant interactions were found. However, regression estimates for the two water availability treatments tended to differ $(0.10 > p > 0.05)$. For pigeons with access to water, no upper critical temperature was found. Heat production decreased $(p \leq 0.05)$ with 0.21 $W\cdot kg^{-1}\cdot°C^{-1}$ until 20.0°C, but remained T_a-independent above this T_a at a level of 6.26 $W\cdot kg^{-1}$ (Figure 1.b). Heat production of water deprived pigeons decreased by 0.069 $W\cdot kg^{-1}\cdot°C^{-1}$ $(p \leq 0.01)$ up to 32.7°C, the upper critical temperature for HP_{tot}. Above T_{uc}, HP_{tot} increased by 0.16 $W\cdot kg^{-1}\cdot°C^{-1}$ $(p \leq 0.01)$. The respiratory quotient was 0.74, and was unaffected by the treatments.
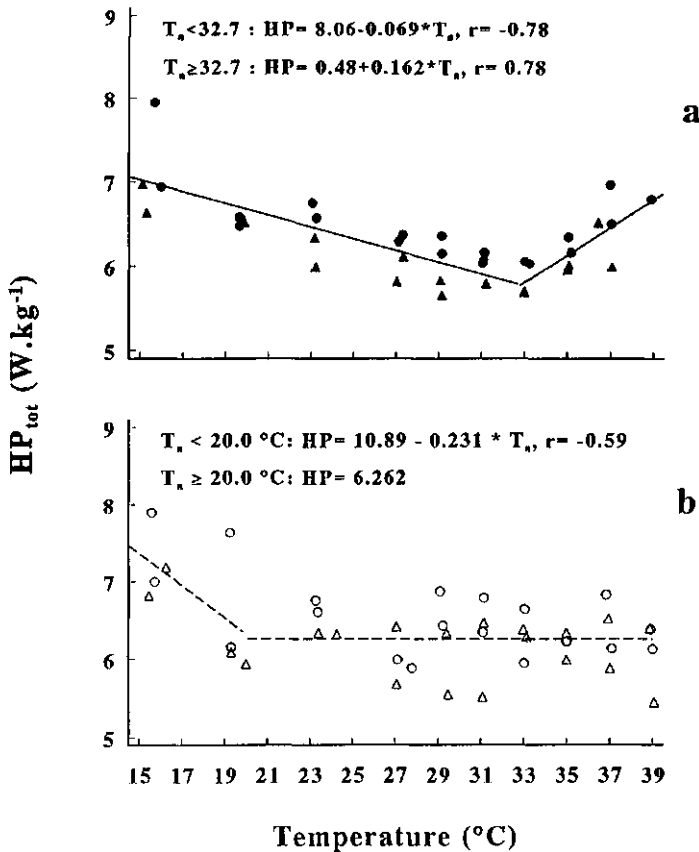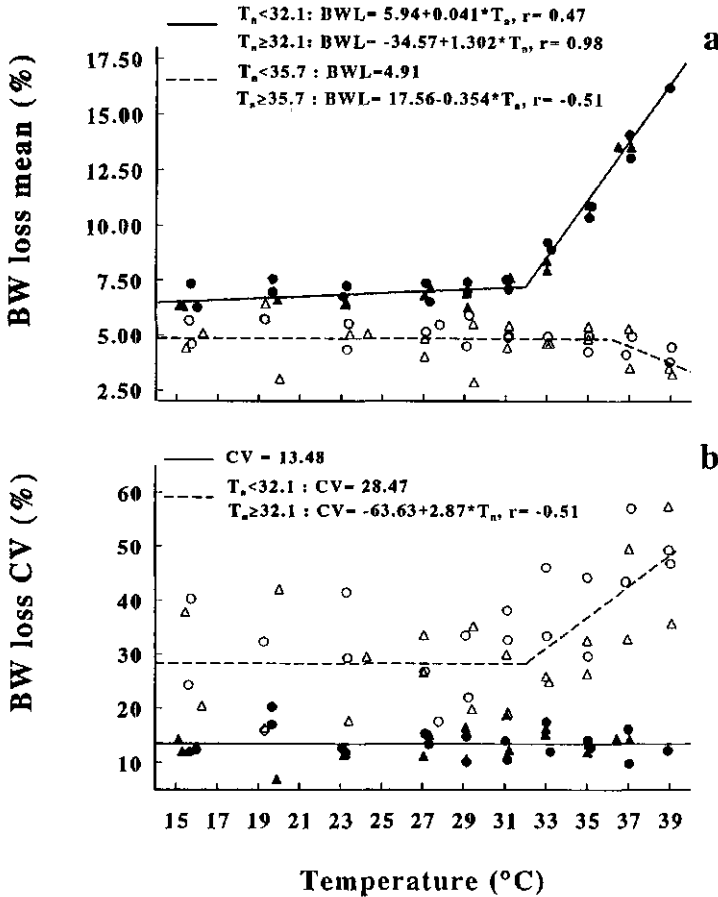
Figure 1. Heat production (HP$_{tot}$); group means of water deprived pigeons (part (a) and pigeons with access to water (part b). Two-phase regression estimates are drawn in overlay. "First Year" pigeons (●,○); "Old" pigeons (▲,△).

Mean body weight at start of the adaptation period was 478 ± 2 g (mean ± SEM, n = 76). Sixteen hours later, mean body weight at start of exposure was 446 ± 2 g. Body weight loss during exposure was significantly (p ≤ 0.001) affected by T_a, water availability and the interaction between T_a and water availability (p ≤ 0.001) (Figure 2). Also with respect to mean BW loss, no T_{uc} was found for pigeons with access to water. Up to 35.7°C, mean BW loss of AW-pigeons remained constant at about 4.91% (Figure 2.a). At higher temperature levels, body weight loss decreased by 0.35%·°C^{-1} (p ≤ 0.05). Regarding BW loss, T_{uc} was estimated at 32.1°C for pigeons deprived of water (Figure 2.a). Above T_{uc}, a sharp increase in BW loss by 1.3%·°C^{-1} occurred (p ≤ 0.001). However, also below T_{uc} a small but

significant ($p \leq 0.05$) temperature-related increase in BW loss was observed. The difference in regression estimates between water treatments was highly significant ($p \leq 0.001$).

Figure 2. Body weight (BW) loss during exposure relative to body weight at start presented as means per group (part **a**) and coefficient of variation per group (CV; part **b**). Two-phase regression estimates are drawn in overlay. Water deprived pigeons ($\bullet$------$\bullet$ and $\blacktriangle$------$\blacktriangle$); pigeons with access to water ($\bigcirc$----$\bigcirc$ and $\triangle$----$\triangle$); "First Year" pigeons ($\bullet$,$\bigcirc$); "Old" pigeons ($\blacktriangle$,$\triangle$).

The coefficient of variation (CV) of BW loss (Figure 2.b) was significantly higher in groups with access to water ($p \leq 0.001$). Variation tended to be higher in "First Year"-birds ($P=0.11$), where the mean CV was 23.8%, compared to 21.2% in "Old" birds. In contrast with HP_{tot} and mean BW loss, no T_{uc} could be estimated for the CV of body weight loss for

water deprived pigeons. In birds with access to water T_{uc} was estimated at 32.1°C. Above T_{uc}, CV increased by 2.87%·°C^{-1} (p≤0.01) (Figure 2.b). The difference in regression estimates was highly significant (p≤0.001).
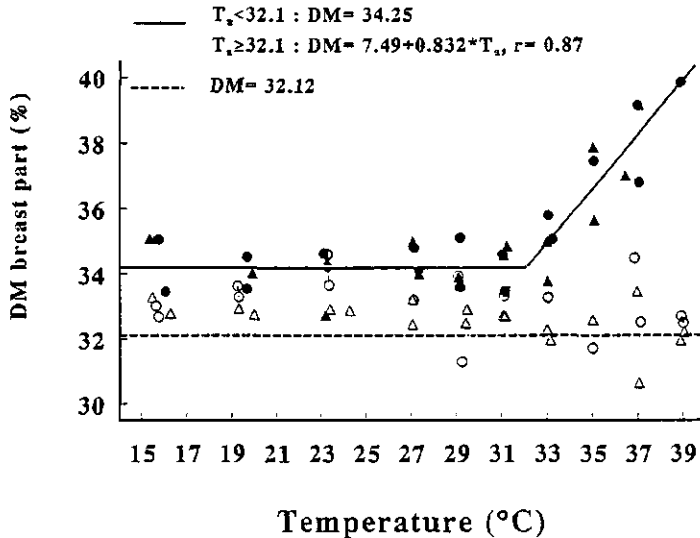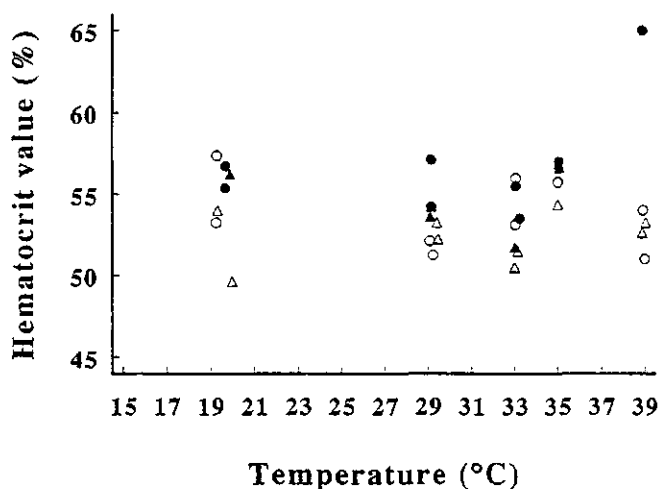

Figure 3. Group means of dry matter (DM) content of the breast part after exposure. Water deprived pigeons (●——● and ▲——▲); pigeons with access to water (○----○ and △---△); "First Year" pigeons (●,○); "Old" pigeons (▲,△).

Mean weight of the breast part after exposure was 143 ± 1.5 g (71 out of 76 groups could be used for analysis). The proportion of the breast part in the whole of the carcass was constant at 33.2 ± 0.1%, and was not affected by treatments. The dry matter (DM) content of the breast part increased with increasing T_a in water deprived pigeons, whereas temperature did not affect DM in pigeons with access to water (Figure 3). This resulted in a significant interaction between temperature and water treatment (p≤0.001). Similar to BW loss, T_{uc} of DM content for water deprived pigeons was estimated at 32.1°C. At higher temperatures, DM content increased by 0.83%·°C^{-1} (p≤0.001). Again, regression estimates were different between water treatments (p≤0.001).

The results of the hematocrit measurements after exposure are shown in Figure 4. Since observations at 39°C were removed from analysis, only values at 19, 27, 33 and 35°C were used. Hematocrit values were significantly affected by age (p≤0.05). For "First Year" groups,

Hct was on average 55.7%, while a value of 53.6% was found in "Old" groups. Water deprivation tended to increase Hct by 1.2%, but this effect was not significant (P>0.18).

Figure 4. Group means of hematocrit values after exposure. Water deprived pigeons (● and ▲); pigeons with access to water (○ and △); "First Year" pigeons (●,○); "Old" pigeons (▲,△).

DISCUSSION

Water availability and optimal temperature zone

Water deprivation lowers the upper critical temperature for an increase in heat production, body weight loss and dry matter content of the breast part to values between 32 and 33°C. When giving pigeons access to water, no increase in the above mentioned parameters was observed below the upper limit of the experimental temperature interval, set at 39°C.

Although water deprivation had little effect on HP_{tot} as such, the different regression estimates between water treatments for the effect of T_a on HP_{tot} are likely to be meaningful. Heat production of pigeons with access to water decreased with increasing T_a until 20°C was reached, and remained constant at higher temperature levels (Figure 1). According to the concept of thermoneutrality (Mount, 1974), 20°C can be regarded as the lower critical temperature (T_{lc}) of a thermoneutral zone. The upper critical temperature (T_{uc}) of this zone

is at or above 39°C. The lower boundary of 20°C is comparable to the T_{lc} of thermoneutral ranges found in literature, ranging from 23 to 36.5°C (Calder and Schmidt-Nielsen, 1967) and from 20 to 35°C (Webster et al., 1985). For water deprived pigeons, however, the observed T_{uc} of 32.7°C is more than 2°C lower than literature data, obtained from individually kept pigeons. The higher relative humidity (Smith, 1972) and longer period of water deprivation in our experiments (Arad, 1983) may be related to this difference. However, it is likely that the lower T_{uc} from our experiment is also due to group confinement. This is in accordance with findings in other bird species (Brown and Foster, 1992). No T_{lc} was found in water deprived birds. Hence, T_{uc} can be regarded as the T_a-level at which T_{lc} and T_{uc} coincide, in accordance with findings in broiler chickens (Kettlewell and Moran, 1992).

At high ambient temperature levels, birds resort manly to water evaporation for heat loss, thus maintaining normal body temperature levels (Mount, 1974). Water deprivation prevents repletion of body water reserves. As demonstrated by our body weight data, this results in an increase in BW loss of $1.3\%\cdot°C^{-1}$ above 32.1°C, measured over a 23-h exposure period (Figure 2). Using the body weight at start of exposure as a reference, relative BW loss reaches 16.2% at 39°C. From a practical point of view, the choice of the reference weight is important, as illustrated by the 9.2% weight loss during the 16-h adaptation period before start of the exposure period. During this adaptation period, all pigeons were housed at thermoneutral conditions with access to water, but with no feed available. The observed 9.2% BW loss probably results from the absence of feed intake, and feed related water intake. A ratio water intake to dry matter intake of 2:1 is reported in literature (Griminger, 1983).

The physiological consequences of this body weight loss (dehydration) through a combination of heat exposure and water deprivation were reflected in a rise in body temperature (data not published), an increase in Hct, an increased dry matter content of the breast part, and, above all, mortality. The mortality observed at 39°C fits well with heat tolerance experiments on 1-d old chickens (Henken et al., 1988). Body weight loss of dead birds during exposure was $18.0 \pm 1.6\%$ (mean $\pm$ sd, 12 out of 13 observations used). This indicates that chronic, and not acute exposure to 39°C caused their death by reaching a lethal BW loss threshold of about 18%. This suggests that exposure to temperatures lower than 39°C would involve more time to reach the threshold value, whereas at higher T_a-levels mortality would have occurred sooner. This confirms that not the level of temperature exposure as such, but the combined effect of temperature level and duration of exposure to that level determines the mortality rate, not only in 1-d old chickens, but also in racing pigeons.

An increase in Hct following water deprivation, most prominent at 39°C (Figure 4), is in agreement with literature data (Arad et al., 1987; Thornton, 1986). During flight, a low Hct is known to promote blood flow through a decreased blood viscosity, thus reducing the heart load (Bordel and Haase, 1993). Hence, an increase in Hct due to dehydration after transport may have an adverse effect on flight performance. Moreover, dehydrated pigeons are known to regulate plasma volume at the expense of interstitial water reserves (Arad et al.,

1989). Assuming that the water content of bones is not affected by dehydration, our data on dry matter content of the breast part (Figure 3) confirm that water extraction from the breast muscle tissues increases with increasing T_a-levels above 32.1°C. And, since the inert bone fraction is incorporated in the calculations of the dry matter content, the estimated increase in DM of the breast part of 0.83%·°C^{-1} above 32.1°C clearly underestimates the actual increase in DM content of the breast muscle tissue. Again, adverse effects on flight performance can be expected. During pigeon flight, body temperature increases by 1.5 to 3°C (Hirth et al., 1987), and water evaporation exceeds metabolic water production, resulting in net water loss (Biesel and Nachtigall, 1987). Hence, starting a flight with decreased water reserves will result in additional hyperthermia. In horses, hyperthermia is known to decrease the time to muscle fatigue (Hodgson et al., 1994). Alternatively, dehydration may also urge pigeons to interrupt their flight for water intake. Either which way, (partial) dehydration prior to flight is likely to have an adverse effect on flight performance and on the capacity to home.

Within water deprived groups, a link between BW loss and body weight (size) could be established. A regression of individual relative BW loss on T_a-classes above T_{uc} (33, 35, 37 and 39°C) was performed with BW at start as a covariable. This analysis showed that the relative BW loss was positively related to body weight at start (p ≤ 0.05):

$$BW\ loss\% = T_a\text{-class} + 0.0057 \times BW_{start}\ (g), \qquad R^2 = 0.70,\ n = 201 \qquad [2]$$

So, heavier birds lose proportionally more weight during heat exposure, indicating that small birds can cope better with hot environments where water is scarce. These findings, based on within-species comparison, are consistent with a between-species comparison (Weathers, 1981). Small bird species depend less on evaporative cooling at the upper critical temperature.

As stated before, no T_{uc} could be estimated for heat production, mean BW loss and DM content of the breast part of pigeons with access to water. In contrast, mean BW loss decreased by 0.35%·°C^{-1} above 35.7°C (Figure 2). The reason for this decline in BW loss at high T_a-levels remains unclear. An overconsumption of water seems plausible. Nevertheless, also for normally hydrated pigeons one parameter increased with T_a-levels above 32.1°C : The BW loss coefficient of variation within groups (Figure 2). Group confinement may explain this temperature-dependent increase in CV. Due to social interactions within a group of pigeons, interaction-related (locomotory or non-locomotory) heat production, and consecutively the need for evaporative heat loss, may differ substantially between individuals within that group. Furthermore, water availability for a group of pigeons as a whole does probably not equal summarized water intake by each individual. Individual differences in drinking thresholds and social inhibition on drinking ability are likely to be present. Hence, climatic control during transport is also useful when water is available. Keeping the temperature below 32°C reduces the variation in BW loss within a group, and thus the variation in individual hydration status of the birds at the time of release.

Age and optimal temperature zone

The optimal temperature zone was the same for "First Year" and "Old" pigeons, as indicated by the absence of interactions between temperature and age. For some parameters, however, mean levels were different between age classes.

Heat production of "First Year" pigeons was, on average, 5% higher than HP_{tot} of "Old" birds. "First Year" pigeons have not yet reached their mature, full-grown size. This results in a higher energy requirements for growth processes, and consequently in higher HP_{tot}. In contrast, energy requirements for "Old" birds depend no longer on growth, but on maintenance of body tissues (Blaxter, 1989).

Age did not affect mean body weight loss during exposure. However, the variation between birds, as measured by the coefficient of variation, tended to be higher in "First Year" pigeons. This may reflect the confounding of "experience" and "age". Although the experimental environment and procedure was new to all pigeons, the experimental conditions and housing were not. "Old" pigeons had an additional experience of at least one racing season, encountering conditions similar to the experimental housing. Hence, the lower variation in BW loss in "Old" birds may reflect an adaptation to a familiar environment. Hematocrit values were significantly higher in "First Year" pigeons by 2.1%. Possibly, the higher Hcr for young pigeons is linked with the higher heat production, requiring a higher oxygen supply.

In conclusion, we can state that 32°C is the upper critical temperature for pigeons housed under transport conditions. When pigeons have access to water, the variation in body weight loss within a group is increased above T_{uc}. Water deprivation increases heat production, body weight loss, dry matter content of the breast part and mortality at temperatures above T_{uc}. The resulting dehydrated state probably reduces the flying capacity of the pigeon. Hence, water deprivation and heat exposure during transport for homing contests may increase bird losses.

CHAPTER 2:

Diurnal Variation in the Thermogenic Effect of Ambient Temperature on Pigeons as Affected by Water Deprivation

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ABSTRACT

The effect of water deprivation on the diurnal variation in the relationship between heat production (HP) and ambient temperature (T_a) was studied in group confined pigeons. During 23 h and starting at 10.30 h, 80 groups of 15 or 18 pigeons were exposed to one of 10 constant T_a-levels between 15 and 39°C. Forty groups were water deprived and 40 groups had access to water. Lights were off between 20.30 and 07.30 h. The relationship HP-T_a was quantified based on 2-h sliding time averages. A continuous two-phase linear regression model was used for data analysis. An upper critical temperature (T_{uc}) was found in water deprived pigeons, not in pigeons with access to water. For water deprived birds, the lower critical temperature (T_{lc}) coincided with T_{uc} at 32 $\pm$ 1.5°C. No diurnal variation was evident, and T_{uc} was not affected by the on-going dehydration due to prolonged heat exposure without access to water. For birds with access to water, the estimated threshold temperature corresponded with T_{lc}; T_{lc} ranged between 20 and 26°C. The coefficient of cold strain (c_s), the slope relating HP and T_a below T_{lc}, was not affected by water deprivation. On average, c_s was 50% lower during "lights off" compared with a value during "lights on" of 0.10 W·kg^{-1}·°C^{-1}. The variation is c_s was unaffected by differences in locomotor activity levels. A clear within photoperiod variation was present, both during "lights on" and "lights off". The coefficient of heat strain (h_s), the slope relating HP and T_a above T_{uc}, indicated that the combination of water deprivation and exposure to high T_a-levels only resulted in a significant increase in HP after about 10 h of exposure. This increase from 0.06 to 0.32 W·kg^{-1}·°C^{-1} was not observed in groups with access to water, where h_s approached zero. The increase in h_s was photoperiod-dependent, showing an increase immediately after onset of darkness and prior to "lights on". Our findings indicate that the duration of water deprivation plays a decisive role for the presence of an increase in HP in water deprived, heat exposed birds.

INTRODUCTION

Transport of racing pigeons (<u>Columba livia</u>) for racing contests is characterized by group confinement, transport duration of 12 to 72 h, and deprivation of water and feed during periods of 12 to 24 h. Additionally, pigeons are at risk of periodical or chronical exposure to high ambient temperatures due to inadequate climatic control (Gorssen et al., 1993). Although the pigeon is one of the most investigated birds with regard to thermoregulation, and to circadian rhythm and sleep influences on thermoregulation (Graf et al., 1989), the thermal requirements of pigeons housed under transport conditions are not available from literature.

To assess the effect of ambient temperature (T_a) on homeotherms, the concept of thermoneutrality (Mount, 1974) is commonly used. In this concept, a zone of thermoneutrality with T_a-independent heat production (HP) is bordered by two critical T_a-levels. At T_a-levels above the upper critical temperature (T_{uc}), the increase in HP with increasing T_a is quantified by the slope h_s. In birds, Weathers (1981) designated h_s "the coefficient of heat strain", the integrated cost of thermoregulation in hot environments. Similarly, the increase in HP at T_a-levels below the lower critical temperature (T_{lc}), can described by the slope c_s, the coefficient of cold strain. Metabolic responses towards thermal stimuli are known to differ between light and dark conditions, as shown in pigeons (Graf, 1980b; Graf et al., 1989). For T_a-levels at and below thermoneutrality, the reduced T_a-sensitivity of HP during rest periods (darkness) compared with activity periods (light) has been stressed repeatedly (Aschoff, 1981b; Aschoff and Pohl, 1970). For T_a-levels above thermoneutral conditions the available information is scarce, especially with respect to T_{uc} and h_s. Moreover, it can be expected that variation in the effect of T_a on HP is not only present between photoperiods, but also within photoperiods (Aschoff, 1981a). Locomotory activity is likely to affect this variation. Activity increases HP, and may influence heat loss from the animal (Zerba and Walsberg, 1992; Schrama et al., 1993).

With respect to the effect of dehydration on HP in birds, Arad (1983) revealed some contradictory reports. Different methods employed to induce dehydration might explain the lack of consistency between reports. Both in fowls and in pigeons, 48 h-water deprivation resulted in an increased HP during heat exposure (Arad, 1983; Arad et al., 1987). However, there are no reports on the time-dependent development of the combined effect of dehydration and T_a on HP.

In the present study, pigeons housed under transport conditions were exposed to a constant T_a during 23 h. We studied the impact of water deprivation on the between- and within-photoperiod variation in the relation between T_a and HP, as quantified by T_{uc}, c_s and h_s.

MATERIAL AND METHODS

In total, 80 groups of experimentally naïve racing pigeons were allocated to treatments according to a factorial design with T_a (10 levels) and water availability (two levels) as factors, with four groups per treatment. The ambient temperature was set at one of 10 constant levels: 15, 19, 23, 27, 29, 31, 33, 35, 37 or 39°C. Birds had access to water or were deprived of water. For each group, pigeons of both sexes were obtained. For purposes not discussed in this paper, group size was 15 in 68 groups and 18 in 12 groups. For all groups, the available space per bird was constant at 280 cm². The experimental procedure consisted of three periods. A pre-experimental period of 7 to 10 d from the day of arrival of the birds onwards was followed by an adaptation period of 24 h, and the exposure period of 24 h.

Pigeons were allotted to groups during the first day of the pre-experimental period. During this period, animals were housed in a half-open outdoor loft, and were fed a commercial mix of whole grains at 09.00 and 16.00 h. Water was available ad libitum. Natural photoperiod was 15 L:9 D at start of the experiment (August), and 10 L:14 D at the end of the experiment (October). The adaptation period started at 09.00 h on the day before start of the exposure period. From this time on, the diet was changed to whole grain corn in order to avoid feed selection (Moon and Zeigler, 1979). Immediately after the afternoon feeding (16.00 h), two groups were transferred from the loft to the laboratory. Each group was confined to a metal transport crate in which they had free access to water, but received no feed. Three crate sides were constructed of perforated aluminium, the other was half-open with aluminium bars. The crate top was made of a wooden grid, and the floor consisted of a synthetic grid. For groups of 15 pigeons, the inner dimensions of the crate were 0.60 m width × 0.70 m length × 0.25 m height. For groups of 18 pigeons (23, 31 and 37°C), crate inner dimensions were 0.72 × 0.70 × 0.25 m. Water was supplied by means of two removable drinking troughs attached to the crate on the half-open outside.

The exposure period started between 10.00 and 10.10 h, and lasted until 09.45 h of the next day. The crate was placed on a platform in one of two climate-respiration chambers of 1.8 m³ each, as described by Verstegen et al. (1987). Ambient temperature was measured by means of a thermocouple placed 0.05 m above the top of the crate. Relative humidity was maintained at a constant level of about 70% up to 35°C. At 37 and 39°C, it decreased to respectively 64 and 56%. At those T_a-levels the absolute humidity was thus maintained at the 35°C-level. According to Smith (1972), the thermoregulatory consequences of this minor change in relative humidity in the T_a-levels 35 to 39°C are small. During the adaptation and the exposure period a 13 L:11 D photoperiod was adopted. Lights were off between 20.30 and 07.30 h.

From 10.30 to 09.30 h, the total heat production (HP_{tot}) was measured by indirect calorimetry at 9-min intervals on the basis of the exchange of CO_2 and O_2, as described by Verstegen et al. (1987). A Hartmann and Braun Uras 3G infrared absorption CO_2 analyzer and a Servomex 1100 H paramagnetic O_2 analyzer were used. Analyzers were calibrated

every 24 h, and all gas volumes were converted to standard temperature and pressure, dry. Heat production was calculated according to Romijn and Lokhorst (1961), and was expressed as $W \cdot kg^{-1}$, using body weight at start of the exposure period. The respiratory quotient was calculated as the ratio between the amount of CO_2 produced and O_2 consumed. Activity was measured using Doppler-radar activity meters (Radar MD5, Vierpool, Amsterdam, The Netherlands), placed about 1 m above the birds. Each movement of the animals was interpreted as a frequency change in the reflected ultrasound waves emitted by the meters. These changes were transformed to counts, and added over the same 9-min measurement interval as for HP_{tot}, resulting in a 9-min activity score. For each group, all 9-min measurements of HP_{tot} and activity were used for a linear regression of HP_{tot} on activity. The resulting regression coefficient was used to estimate the activity related HP (HP_{ac}) from the activity score. Finally, activity free HP (HP_{af}) was calculated by subtracting HP_{ac} from HP_{tot}.

Calculations and statistical analyses were performed on 2-h sliding time averages (STA) of HP_{tot} and HP_{af}. For each group, 22 STA's were calculated. The first STA included measurements between 10.30 and 12.30 h, STA-22 covered measurements between 07.30 and 09.30 h.

On the absence or presence of a zone of thermoneutrality in birds, contradictory findings are published. Nichelmann (1983) rejected the existence of such a zone. Van Kampen et al. (1979) stressed the importance of light as an experimental factor, reporting that the presence of light may reduce the width of thermoneutral zone, resulting in just a point of flexure. In this case, T_{lc} coincides with T_{uc}. Hence, a continuous two-phase linear regression model can be adopted for the estimation of the metabolic effect of T_a on HP. Preliminary analysis showed that no thermoneutral zone was present in water deprived groups, where T_{lc} coincided with T_{uc}. For groups with access to water, both T_{lc} and a thermoneutral zone were found, but T_{uc} was at or above the upper T_a-level of 39°C adopted in the experiment.

The relationship between HP_{tot} (HP_{af}) and T_a was estimated per STA for each water treatment separately. A continuous two-phase regression method for the estimation of physiological thresholds was adopted (Nickerson et al., 1989), using the actually measured T_a in that time period as independent variable. This procedure focuses primarily on the identification of T_{uc} using the "minimal total error sum of squares" criterion. Hence, estimates for c_s and h_s are sensitive to fluctuations in the estimated T_{uc}. To make slopes independent of the fluctuations in the estimated T_{uc}, two linear regressions covering separate T_a-intervals were performed. The first regression interval to estimate c_s included six lower T_a-classes (15 to 31°C), the second regression to estimate h_s included the four upper T_a-classes (33 to 39°C). Only estimates for c_s and h_s based on separate T_a-intervals will be presented. For each STA, regression estimates were compared between water treatments using a general linear test statistic (Nickerson et al., 1989).

In all water deprived groups at 39°C, some animals could not cope with the experimental treatment. For one group, all measurements were used in the analyses. Sliding time averages that include measurements from 00.30 h onwards (STA > 13) were removed

from analyses in a second group, and from 01.30 h onwards (STA > 14) in the other two groups. Due to technical problems, results of one water deprived group at 19°C and one group with access to water at 29°C were removed completely from the analyses.

RESULTS

The relationship between HP and activity levels, averaged for all groups, is illustrated in Figure 1. Both HP_{tot} and HP_{af} decreased during the first hours of exposure. Towards "lights off", HP_{tot} increased whereas HP_{af} did not. Activity related HP, as indicated by the ratio HP_{ac}/HP_{tot}, increased from 10.62 ± 0.67% during STA-1 to 19.47 ± 1.06% during STA-9 (mean ± SEM, n = 78). Activity levels during the dark period were low, as indicated by a HP_{ac}/HP_{tot} ratio of about 6%. Activity increased immediately following "lights on" during the second day, resulting in HP_{tot}-levels of 7.35 ± 0.09 $W \cdot kg^{-1}$ during STA-22. Nevertheless, also HP_{af} increased from night-time levels of about 4.9 $W \cdot kg^{-1}$ to 6.20 ± 0.10 $W \cdot kg^{-1}$ (n = 75). The respiratory quotient decreased from 0.83 during STA-1 to 0.71 during STA-9, whereafter respiratory quotient remained at this level.
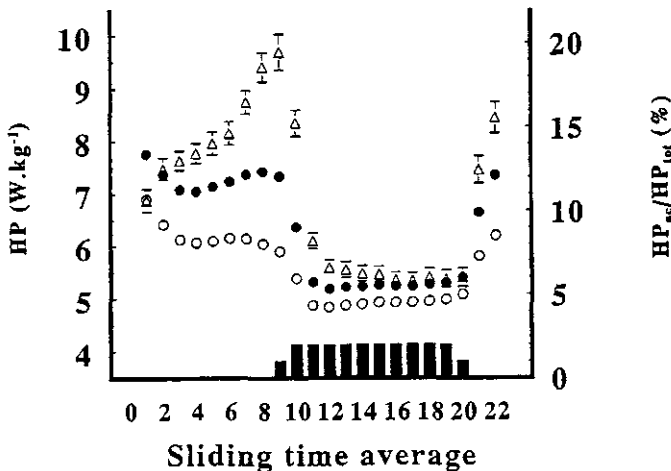
Figure 1. Overall means (± SEM) of total heat production (HP_{tot}; ●) and activity free heat production (HP_{af}; ○; left Y-axis) and the proportion of activity related heat production in HP_{tot} (HP_{ac}/HP_{tot}; △; right Y-axis) per sliding time average.

In Figure 2, the two-phase regression procedure is illustrated for HP_{tot} of both water treatment groups during STA-8 and STA-14. During STA-8, e.g., T_{uc} of water deprived pigeons was 32.6°C, whereas c_s and h_s were respectively 0.105 and 0.095 $W \cdot kg^{-1} \cdot {}^{\circ}C^{-1}$.

Access to water

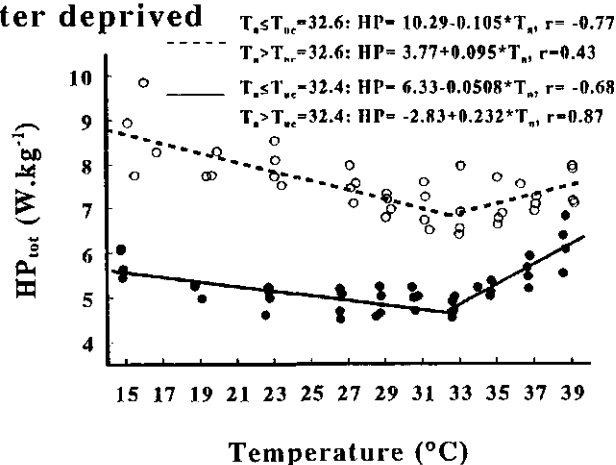$T_a \leq T_{lc} = 20.4$: $HP = 13.93 - 0.317 \cdot T_a$, $r = -0.68$
$T_a > T_{lc} = 20.4$: $HP = 7.99 - 0.027 \cdot T_a$, $r = -0.32$
$T_a \leq T_{lc} = 20.4$: $HP = 8.83 - 0.194 \cdot T_a$, $r = -0.68$
$T_a > T_{lc} = 20.4$: $HP = 4.36 + 0.025 \cdot T_a$, $r = 0.33$

Water deprived

$T_a \leq T_{uc} = 32.6$: $HP = 10.29 - 0.105 \cdot T_a$, $r = -0.77$
$T_a > T_{uc} = 32.6$: $HP = 3.77 + 0.095 \cdot T_a$, $r = 0.43$
$T_a \leq T_{uc} = 32.4$: $HP = 6.33 - 0.0508 \cdot T_a$, $r = -0.68$
$T_a > T_{uc} = 32.4$: $HP = -2.83 + 0.232 \cdot T_a$, $r = 0.87$
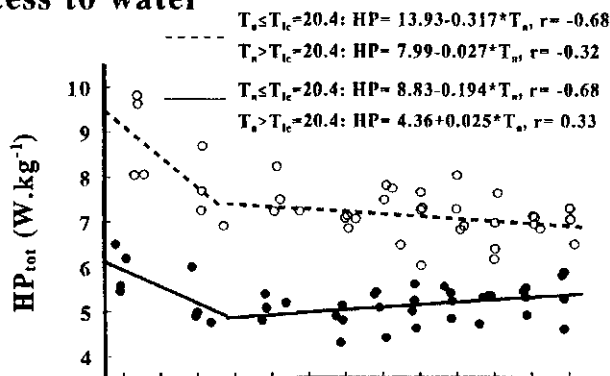
Figure 2. Relation between ambient temperature and total heat production (HP_{tot}) measurements from 17.30 to 19.30 h (STA-8; ○) and from 23.30 to 01.30 h (STA-14; ●). The presented estimates of the continuous two-phase linear regression model are drawn in overlay.

In pigeons with access to water, estimates for the threshold temperature were highly variable, especially during "lights on" (Figure 3.a). Estimates varied between 19.3 and 36.5°C for HP_{tot} and between 20.3 and 30.0°C for HP_{af}. For water deprived birds, the estimated threshold temperature corresponded with T_{uc} throughout the exposure period. Estimates for T_{uc} were relatively constant, especially for HP_{af} (Fig 3.b). Whereas T_{uc} for HP_{af} varied between

31.6 and 33.0°C from STA-1 to STA-9, estimates based on HP_{tot} ranged between 27.7 and 34.2°C for the same time period. During "lights off", T_{uc} was relatively constant, being about 32.5°C for HP_{tot} and 31.5°C for HP_{af}.
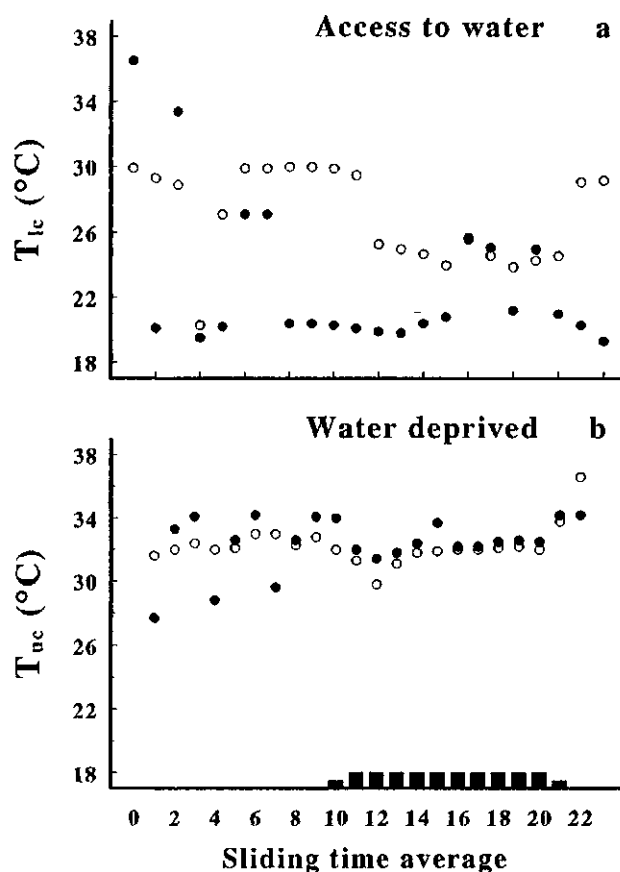
Figure 3. Estimates per sliding time average (STA) for the lower critical temperature (T_{lc}) for groups with access to water (part **a**) and the upper critical temperature (T_{uc}) for groups deprived of water (part **b**) based on data for total heat production HP_{tot} (●) and activity free heat production HP_{af} (○). Black bars indicate the proportion of measurements during "lights off" per STA (50% or 100%).

In Figure 4, estimates for c_s based on the discrete regression of HP on T_a for the 15-31°C interval are presented. Estimates were comparable between water deprived pigeons and pigeons with access to water ($p > 0.05$). In both water treatments, a clear between- and within-photoperiod variation was present in the regression estimates for c_s. A maximum in c_s

was reached at STA-7, whereafter c_s decreased towards the night. In general, nighttime values for c_s were only 50% of the day time estimate, which was, on average, $0.10 \ W \cdot kg^{-1} \cdot {}^{\circ}C^{-1}$. Also during the night, within-photoperiod variation was present. From STA-19 onwards, c_s increased again towards "lights on". Locomotor activity did not affect c_s, as indicated by the estimates obtained for HP_{tot} and HP_{af} (Figure 4).
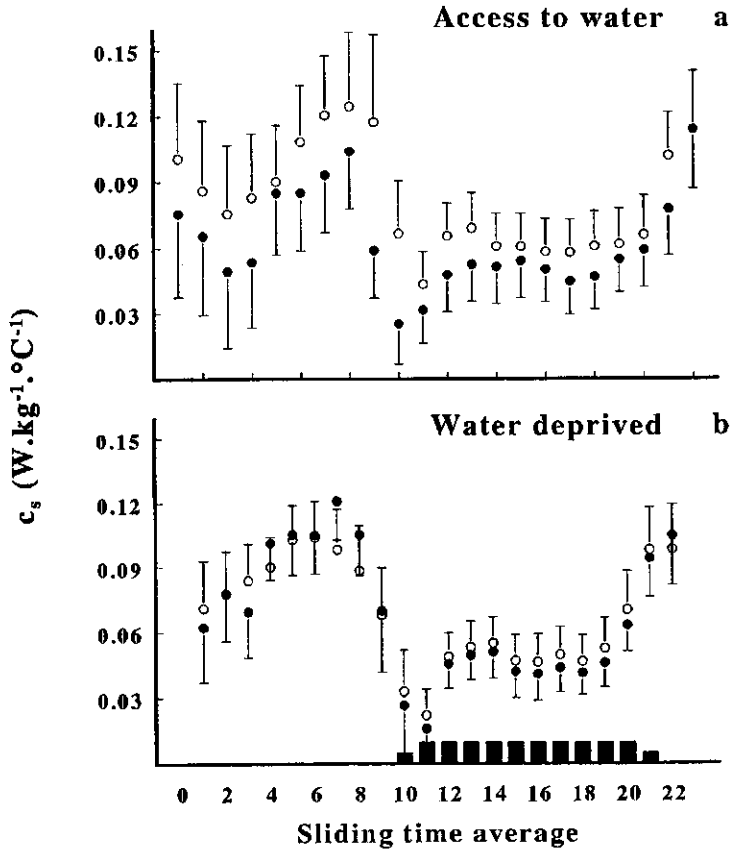
Figure 4. Estimates of the coefficient of cold strain (c_s, $\pm$ SE) per sliding time average (STA) based on data for total heat production HP_{tot} (●) and activity free heat production HP_{af} (○) for groups with access of water (part a) and groups deprived of water (part b). Black bars indicate the proportion of measurements during "lights off" per STA (50% or 100%).

For pigeons with access to water, estimates for h_s obtained from the regression of HP_{tot} and HP_{af} on T_a-levels between 33 and 39°C where less than or about equal to zero (Figure

5). Estimates based on HP_{tot} were only significantly negative during STA-3, STA-9 and STA-10 ($p \leq 0.05$). For HP_{af}, none of the h_s estimates differed from zero, indicating that T_a did not affect HP_{af} in the 33-39°C interval. Hence, exposure to T_a-levels higher than 31°C did not cause an increase in heat production when water was available. This indicates that the estimated threshold temperature, presented in Figure 3.a, corresponded with a T_{lc}.

In contrast with pigeons with access to water, h_s estimates of water deprived pigeons increased with time, resulting in significantly positive values ($p \leq 0.05$) for h_s from STA-10 onwards (Figure 5).
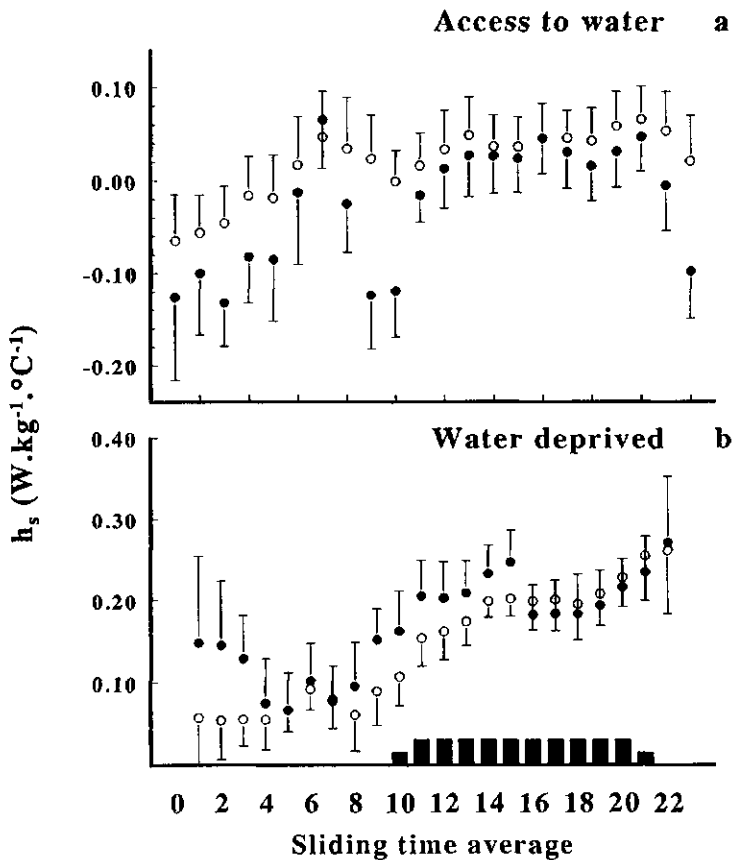

Figure 5. Estimates of the coefficient of heat strain (h_s, $\pm$ SE) per sliding time average (STA) based on data for total heat production HP_{tot} (●) and activity free heat production HP_{af} (○) for groups with access of water (part a) and groups deprived of water (part b). Black bars indicate the proportion of measurements during "lights off" per STA (50% or 100%).

Comparison of both water treatments showed that concurrently estimates for h_s became significantly higher for water deprived groups ($p \le 0.05$) (Figure 5). This indicates that exposure to ambient temperature levels at and above 33°C resulted in an increasingly higher response in HP to T_a as temperature exposure and water deprivation continued (Figure 5). For both HP_{tot} and HP_{af}, the coefficient of heat strain increased with time between STA-1 and STA-22. Also, an effect of photoperiod was present, as can be seen from the stepwise increase in h_s at the light-dark (STA-9 to STA-11) and dark-light (STA-20 to STA-22) transition. Also within the dark period, a variation pattern in h_s was observed. The coefficient of heat strain increased during the late part of the night, starting few hours before "lights on" (STA-19 and STA-20) (Figure 5).

When comparing water treatments, the influence of locomotor activity on h_s was small and not consistent. In general, estimates based on HP_{tot} resulted in steeper regression slopes compared with estimates based on HP_{af} (Figure 5). This was most consistent in pigeons with access to water. Estimates for h_s differed between HP_{tot} and HP_{af} during the day, when activity was high (Figure 1). During the night, when activity was low, estimates were comparable. For water deprived pigeons, the role of locomotor activity was not clear. During the first part of the night, activity appeared to increase h_s although activity levels were low. No difference was found between HP_{tot} and HP_{af} during STA-21 and STA-22, when activity levels were high.

DISCUSSION

Water deprivation and diurnal variation in T_{uc}

An upper critical temperature was found in water deprived pigeons, but not in pigeons with access to water. For birds with access to water, the estimated threshold temperature corresponded with T_{lc} rather than T_{uc} (Figure 3, Figure 5). Hence, a thermoneutral zone was found in pigeons with access to water, with T_{lc} as the lower boundary. This means that the 2-phase linear regression estimate of the threshold T_a yields a different physiological interpretation for pigeons with or without access to water. The variation in T_{lc} estimates throughout the exposure period was probably due to the experimental design. This research was aimed at defining physiological threshold temperatures for racing pigeons housed under transport conditions. Since heat exposure was the main point of interest, emphasis was placed on identification of T_{uc}. Hence, the interval between T_a-levels was set at 4°C from 15 to 27°C, which had a negative effect on the accuracy of threshold temperature estimates below 27°C.

For water deprived birds, no zone of thermal neutrality was found, indicating that T_{lc} coincided with T_{uc}. Throughout the exposure period, T_{uc} was relatively constant at 32 ± 1.5°C. So, no diurnal variation was evident, and T_{uc} appeared to be unaffected by the on-going dehydration due to prolonged heat exposure without access to water. According to Graf (1980b), spinal thermosensitivity to heat is increased during darkness. This results in the onset

of panting at a spinal temperature which is more than 1 °C lower compared with light. Hence, a lower T_{uc} during "lights off" could be expected from our experiments. This, however, could not be confirmed by our data presented in Figure 3. The higher variability in T_{uc} during "lights on" compared with "lights off" makes comparison difficult. Most T_{uc}-estimates fluctuate between 31 and 33°C. This variation in T_{uc} might be a reflection of a measurement variation, caused by the estimation procedure. The adopted T_a measurement interval of 2°C around T_{uc} might be too wide to allow T_{uc}-estimates of 1 °C accuracy or less.

Water deprivation and diurnal variation in c_s

During "lights on", c_s was about two times the value during "lights off" (Figure 4). For "minimal conductance", the slope relating T_a and HP_{tot} below the lower critical temperature, Aschoff (1981b) reported a "activity time" value of 1.5 times the "rest-time"-value. Since the respiratory quotient in our experiments reached fasting levels of 0.71 at about the start of the dark period, the lower value of c_s during "lights off" compared with the first light period may be partially caused by a food deprivation-effect. Graf et al. (1989) showed that the spinal cord threshold temperature for inducing an increase in HP decreased with duration (days) of food deprivation. This effect of fasting was only found during the night, not during the day. This is in agreement with our data, which show that the values for c_s attained during the second light period are comparable to non-fasting values before onset of darkness. However, also differences in thermoregulatory behaviour between wakefulness and sleep may (partially) account for the lower cold sensitivity of HP during darkness (Hohtola et al., 1980).

A clear within photoperiod variation is present. Estimates for c_s during "lights on" suggest the presence of two distinct maxima in temperature sensitivity of HP, one shortly before the onset of darkness, and one at start of the light period (Figure 4). Also during "lights off", a within-photoperiod variation was observed. The increase in c_s from STA-19 onwards confirms findings by Graf (1980b), who reported an increased sensitivity of HP to thermal stimuli during the late dark phase, prior to "lights on".

Estimates for c_s were similar for HP_{tot} and HP_{af}. This indicates that differences in c_s between light (activity) and dark (rest) periods were not caused by differences in activity levels. It suggests that photoperiod dependent differences in both activity levels and thermoregulatory effector mechanisms are regulated by the same oscillator. Oshima et al. (1989) demonstrated that the rhythmicity in circulating melatonin is important for the control of circadian rhythms of both locomotor activity and body temperature in pigeons. Body temperature, however, represents the accumulated heat in the body, resulting from the balance between heat production and heat loss (Aschoff, 1981a). Therefore, it seems likely that circulating melatonin levels are not only involved in the control of body temperature rhythms as such, but also in the control of the underlying rhythms in thermoregulatory effector mechanisms. This susceptibility of thermoregulatory effector mechanisms to changes in the photo-environment suggests a direct or indirect impact of circulating melatonin on thermoregulation. More research into the thermoregulatory effects of melatonin may identify

the underlying physiological mechanisms for the observed influence of light on the relationship between T_a and HP.

Water deprivation and diurnal variation in h_s

As indicated by h_s, the combination of water deprivation and exposure to high T_a-levels only resulted in a significant increase in HP after about 10 h of exposure (Figure 5). This time-related effect of water deprivation also appeared when comparing estimates for h_s between water treatments. The discussion concerning between and within-photoperiod variation in h_s as observed in this experiment has to take into account this confounding of "time of day" and "duration of deprivation". Nevertheless, the increase in h_s was not continuous in a photoperiod-dependent way. A first, clear increase occurred at the onset of darkness, consistent with the lowered temperature threshold for heat production responses during darkness (Graf, 1980b). Graf (1980a) reported an increase in respiratory rate after "lights off". The resulting increase in HP due to muscular activity for respiration may explain the observed rise in h_s. The second increase in h_s started during the night from STA-19 onwards. As for c_s, this indicates an increased T_a-sensitivity of HP during the second part of the night.

The overall increase of h_s with time in water deprived pigeons might be a result of dehydration. An increase in circulatory energy requirements due to a gradually increasing blood viscosity (Arad et al., 1987), and an increase in HP due to a higher body temperature (van 't Hoff-effect) may explain the increase in h_s over time. In agreement with Arad (1983), our findings indicate that the duration of water deprivation plays a decisive role for the presence and the degree of increase in HP in water deprived, heat exposed birds. For transport, this implies that not the level of temperature exposure as such, but the combination of water deprivation, temperature exposure, and duration of exposure to that temperature level determines the intensity of the thermoregulatory stress, experienced by the pigeons.

ACKNOWLEDGMENTS

CHAPTER 3:

Diurnal Variation in Thermoregulation of Group Confined Pigeons (<u>Columba livia</u>) in Relation to Ambient Temperature and Water Deprivation

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ABSTRACT

This study examines the thermoregulatory responses of group confined pigeons to water deprivation, and their ability to recover from the resulting dehydration. Two experiments are described. Pigeons were kept in groups, food deprived, and exposed to a constant ambient temperature of 23, 31 or 37°C during 48 h. During a 24-h dehydration period and an appending 24-h recovery period, heat production and body temperature (Experiment 1) and evaporative water loss (Experiment 2) were measured. Results of both experiments were combined to estimate dry thermal conductance during "lights on" and "lights off" periods. Evaporative water loss measurements indicated that the upper critical temperature was above 31 and below 37°C. At 23 and 31°C, water deprivation did not affect body temperature, evaporative water loss and heat production. At 37°C, water deprivation increased body temperature and reduced evaporative water loss from 8 h after start of exposure onwards, whereas heat production was not affected. Within 30 min after rehydration the effects of previous dehydration disappeared. Dry thermal conductance increased with ambient temperature. At 37°C, conductance of dehydrated birds was lowered. Compared with "lights on", "lights off" values for dry thermal conductance were lower at 23°C and higher at 37°C, whereas no diurnal variation was found at 31°C. Lower conductance during "lights on" at 37°C may be caused by increased locomotor activity.

INTRODUCTION

Transport of both racing pigeons (Columba livia) and poultry is associated with group confinement and a risk of exposure to adverse thermal conditions (Gorssen and van der Hel, 1993; Webster et al., 1993). Typically for racing pigeons, transport lasts 1 to 3 d with periods of water deprivation from 12 to 24 h (Gorssen and van der Hel, 1993). From a welfare point of view, not only the momentary effect of adverse conditions on pigeon thermoregulation is of interest, but also the pigeon's ability to recover from them. Dehydrated pigeons almost fully replenish body water reserves within 30 min when given access to water (Arad et al., 1989). It is, however, unknown at what rate and to what degree heat production

(HP_{tot}), body temperature (T_b) and evaporative water loss (EWL) return to values attained by normally hydrated birds.

Arad et al. (1987) showed that dehydrated pigeons increase HP_{tot} and T_b and reduce EWL when exposed to heat. However, information concerning the transition phase from the normally hydrated towards the dehydrated state is lacking. Also, it remains unclear how water deprivation affects the well-established diurnal variation in HP_{tot}, EHL and T_b (Robinson et al., 1993; Stewart and McClure, 1993). Since HP_{tot}, EHL, T_b and ambient temperature (T_a) determine dry thermal conductance (C_{dry}) (McNab, 1980; Brown and Foster, 1992), a diurnal variation in C_{dry} is likely. Aschoff (1981b) suggested that C_{dry} will be low during rest periods compared to activity periods within the zone of metabolic thermoneutrality, whereas C_{dry} should be maximal and constant in very warm environments. To our knowledge, no information is present in literature on this hypothesis and on its possible dependence on water deprivation.

In this paper, we report on two experiments with group confined pigeons exposed to T_a-levels of 23, 31 and 37°C. Alterations of HP_{tot} and T_b (Experiment 1) and EWL (Experiment 2) with time were studied during a dehydration period of 24 h. To assess the pigeon's ability to recover from dehydration, all birds had access to water during the second 24-h period. Combining the results of both experiments, diurnal variation in C_{dry} was studied in relation to T_a and water availability.

MATERIAL AND METHODS

General

The design of both experiments was similar. Twelve groups were randomly assigned to a 2 × 3 factorial design, with water availability at two levels, and T_a at three levels (23, 31 or 37°C). These groups consisted of adult, experimentally naive pigeons (both male and female). The exposure period was partitioned over a dehydration period and a recovery period, both lasting 24 h. Pigeons had access to water during both periods (AW groups), or during the recovery period only (DW groups). Before the experiments, birds were housed in a half-open outdoor aviary under natural photoperiod, humidity and temperature, and fed twice daily. Water was available ad libitum. Following the second feeding (16.00 h) on the day before start of the exposure period, two groups were transferred to a laboratory room. Here, each group was placed in an experimental crate and deprived of food. Water was available by drinking troughs (0.35 m long, 0.07 m^3 content), attached to the outside of the crate.

The dehydration period in the adjacent climate-respiration chambers started at 10.10 h of the next day. Between 09.30 and 09.45 h of the next day, the crates were moved back to the laboratory room during 30 min. Thereafter, the 24-h recovery period followed with water available for all groups. Inside the climate-respiration chambers, relative humidity was

kept at 70% at 23 and 31°C, and at 64% at 37°C. Lights in the laboratory room and in the climate-respiration chambers were off between 20.30 and 07.30 h.

In both experiments, activity was measured continuously by Doppler-radar activity meters (Radar MD5, Suther, Vierpool, Amsterdam, The Netherlands) (Wenk and Van Es, 1976; Verstegen et al., 1987). Mean activity scores per hour were normalized for each exposure period and group separately (Robinson et al., 1993). Body weight (BW) of each animal was recorded ($\pm$ 1 g) at start and end of the dehydration period, and at the end of the recovery period.

Experiment 1: heat production and body temperature

In this experiment, 18 pigeons per group were used. The pigeons arrived at the aviary 2 wk before start. Transport crates were used with sides of perforated aluminium, and a synthetic floor with a 0.01 × 0.01 m grid. Inner dimensions of the crate were 0.72 m width × 0.70 m length × 0.25 m height. The crate was placed on a platform in one of two climate-respiration chambers of 1.8 m^3 each, as described by Verstegen et al. (1987). Between the dehydration and recovery period, four birds were removed at random from the crate for purposes not further discussed in this paper. In order to keep the available surface per bird similar during the recovery period, the inner dimensions of the crate were reduced to 0.70 × 0.60 × 0.25 m.

From about 45 min after closing the chambers onwards, total heat production (HP_{tot}) was measured indirectly per chamber from the exchange of CO_2 and O_2 measured in successive 9-min intervals (Romijn and Lokhorst, 1961). The infrared absorption CO_2-analyzer (Hartman and Braun Uras 3G) and paramagnetic O_2-analyzer (Servomex 100 H) were calibrated daily. All gas volumes were converted to standard temperature and pressure, dry. Heat production was expressed as $W \cdot kg^{-1}$, with body weight at start of the dehydration period as a reference. The respiratory quotient was calculated as CO_2 produced over O_2 consumed.

Body temperatures (T_b) were recorded in successive 10-min intervals using a telemetry system. All transmitters were calibrated against a standard mercury thermometer before and after each implantation (van der Hel et al., 1992). Four days before start of the exposure period, a transmitter (12 g weight) was implanted in the abdomen of three pigeons per group. Location of the transmitters in the abdomen was ventral to the intestines, dorsal to the right abdominal air sac, and caudal to the liver. After one night recovery, the birds were moved back to the outdoor aviary. In both 31°C-DW groups and in one 23°C-DW group, telemetry data from one pigeon could not be obtained due technical failure.

Experiment 2: evaporative water loss

In a second experiment, 12 groups of six pigeons were used from a stock which was present in the aviary for about one year. For this experiment, one large climate-respiration-chamber (80 m^3) was used (Verstegen et al., 1987), but only as climate-controlled room.

During each of six exposure periods, two groups (one AW, one DW) were confined to wire cages (0.42 × 0.40 m, 280 cm^2·animal^{-1}). To prevent evaporation from the excreta, the cages were placed on top of a mineral oil bath, . The groups were visually isolated from each other.

The cage, the mineral oil bath, and the water trough (if appropriate according to treatment) were weighed (± 1 g) at 10.30, 12.00, 13.30, 15.00, 16.30, 18.00, 19.30, 20.30, 21.30, 23.00, 06.30, 07.30, 08.30 and 09.30 h during the dehydration and recovery period, and at the start of the recovery period (± 10.00 h). During weight recordings in the dark, a dim red light illuminated the weighing site. Pigeon locomotor activity remained low under these conditions. Water intake was calculated as the weight loss of the drinking trough, corrected for water evaporation. This evaporation was estimated from the weight of a dummy water trough, placed in the chamber to which the birds had no access. Water temperature from a second dummy was measured in successive 30-min intervals to calculate heat loss through the ingestion of water adopting 4.2 J·g^{-1}·°C^{-1} as the specific heat of water (Blaxter, 1989).

Excretion was calculated from the weight gain of the oil bath between measurements. For each weighing interval, evaporative water loss (EWL) was calculated as:

$$EWL = \text{Crate weight}_{start} - \text{crate weight}_{end} - \text{excretion} + \text{water intake} \qquad [1]$$

Water intake, excretion rate and EWL were expressed as mg·g^{-1}·h^{-1}, with BW at start of the dehydration period as a reference.

At 23 and 31°C, aggressive pecking behavior resulted in head injuries. Therefore, afflicted pigeons were removed from the group during exposure, and isolated for recovery. In total, three birds were removed during the dehydration period (two of 31°C-DW, one of 23°C-AW), and another six birds during the recovery period (four of 23°C-DW, two of 31°C-DW).

Assuming 2.429 kJ·g^{-1} water evaporated (Weathers, 1981), measurements of EWL in Experiment 2 were converted to evaporative heat loss (EHL). Combined with HP$_{tot}$ and T$_b$ measured in Experiment 1, C$_{dry}$ (W·kg^{-1}·°C^{-1}) was estimated per photoperiod according to McNab (1980):

$$C_{dry} = [HP_{tot} - EHL] \times [T_b - T_a]^{-1} \qquad [2]$$

Statistical analysis and calculations

All data for BW, T$_b$, HP$_{tot}$, respiratory quotient, EWL, water intake and excretion rate were subjected to 2-way analysis of variance, with group as the experimental unit. Body weight loss at the end of the dehydration and recovery period was calculated relatively (%) to BW at start of the dehydration period. Data of semi-continuous measurements were analyzed on

main photoperiod means ("lights on": 10.30-20.30 h; "lights off": 20.30-07.30 h) for the dehydration and recovery period separately. Paired differences between the dehydration and recovery period were assessed for "lights on" and "lights off" periods separately by paired t-test and subsequent ANOVA. Within the dehydration and recovery period, the same procedure was adopted to assess the difference between "lights on" and "lights off".

RESULTS

Common measurements: Body weight loss and activity

The activity pattern was similar during the entire exposure period for both Experiment 1 and 2 (Figure 1). Activity increased during "lights on", with a peak before and after the onset of darkness. Activity was low during "lights off", with an increase 1 to 2 h prior to "lights on".
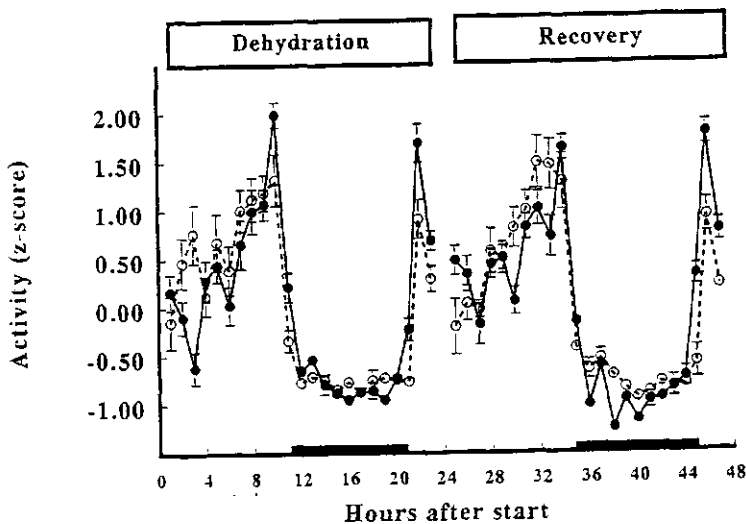
Figure 1. Standardized activity scores ($\pm$ SEM, n = 12) per experiment, pooled for all treatments. Experiment 1 (●——●); Experiment 2 (○----○); "lights off" (▬▬▬).

In Table 1 (Experiment 1) and Table 2 (Experiment 2), BW loss results were presented. At start of the dehydration period, BW was 448 $\pm$ 14 g in Experiment 1, and 504 $\pm$ 19 in Experiment 2 (mean $\pm$ S.D., n = 12). At the end of the dehydration period, BW loss was affected by the interaction between T_a and water availability (p $\leq$ 0.05). During

the dehydration period, BW loss was highest for 37°C-DW groups (Table 1 and 2). At the end of the recovery period, differences between treatments in BW loss were reduced. Body weight loss for DW groups was consistently lower, although not significantly ($p \leq 0.25$; Table 1 and 2).

Table 1. Least squares means during "lights on" and "lights off" of total heat production (HP_{tot}), body temperature (T_b) and body weight (BW) loss of group confined pigeons in relation to water availability and ambient temperature.

| | Period | Lights[3] | Treatment[1,2] | | | | | | Root M.S.E[4] |
| | | | 23 °C | | 31 °C | | 37 °C | | |
			DW	AW	DW	AW	DW	AW	
HP_{tot}	Dehydration	On	7.28	7.51	6.93	7.21	6.92	7.00	0.61
($W \cdot kg^{-1}$)		Off	5.07[AB]	5.25[AB]	4.98[A]	4.94[A]	5.49[B]	5.35[B]	0.13
	Recovery	On	6.22	6.59	6.26	6.05	5.55	5.82	0.43
		Off	4.74	4.72	4.53	4.53	4.43	4.60	0.19
T_b	Dehydration	On	41.06	41.15	41.21	41.25	41.67	41.23	0.29
(°C)		Off	39.30[a]	39.94[ab]	39.80[ab]	39.75[ab]	42.04[c]	40.38[ab]	0.16
	Recovery	On	40.88	41.03	40.89	41.05	40.76	40.91	0.22
		Off	38.86[A]	39.60[A]	39.48[A]	39.37[A]	40.06[B]	39.78[B]	0.25
BW	Dehydration[5]		6.43[ab]	5.04[b]	7.63[a]	4.93[ab]	13.60[c]	4.42[b]	0.60
Loss									
(%)	Recovery[6]		7.65	8.13	7.47	7.72	5.75	7.39	0.71

[1]   DW: deprived of water; AW: access to water.
[2]   Non-overlapping superscripts within a row indicate significantly different treatment results ($p \leq 0.05$). Capital letters indicate significant main effects, small letters indicate a significant interaction effect ($p \leq 0.05$).
[3]   Lights on (10.30-20.30 h); lights off (20.30-07.30 h).
[4]   Mean square error
[5]   BW loss is calculated as the difference between BW at end and start of the dehydration period
[6]   BW loss is calculated as the difference between BW at end of the recovery period and at start of the dehydration period

Experiment 1: Heat production and body temperature

During the dehydration period and "lights on", HP_{tot} was unaffected by the experimental treatments (Table 1). Only a T_a effect on HP_{tot} was present during "lights off" ($p \leq 0.01$), being 5.16, 4.96 and 5.42 $W \cdot kg^{-1}$ at 23, 31 and 37°C, respectively. During the dehydration period no interaction effect between T_a and water availability was present (Table 1). Even at 37°C, no effect of water availability on HP_{tot} was found (Figure 2.a). During the recovery period, no treatment effects were present regarding HP_{tot}.

Heat production was lower during "lights off" compared to "lights on" ($p \leq 0.001$; Table 1). The difference between photoperiods in HP_{tot} was 1.96 $W \cdot kg^{-1}$ during the dehydration period and 1.49 $W \cdot kg^{-1}$ during the recovery period. Averaged over photoperiods, HP_{tot} was lower during the recovery period than during the dehydration period ($p \leq 0.01$; Table 1).

The respiratory quotient was not affected by treatments. Immediately after start of exposure, respiratory quotient was 0.88. The fasting level of 0.71 was reached from 10 h after start of the dehydration period onwards.

With progression of time during the dehydration period, the interaction effect between T_a and water availability on T_b appeared. The interaction effect on T_b was absent during "lights on" ($p > 0.4$), but was highly significant during "lights off" ($p \leq 0.001$; Table 1). Water deprivation during the dehydration period increased T_b at 37°C from 8 h after start of exposure onwards (Figure 2.b). Neither at 23°C nor at 31°C, T_b was affected by water availability (Table 1). During the recovery period, no effects of previous water deprivation on T_b were present (Table 1, Figure 2.b).

Body temperature was lower during "lights off" compared to "lights on", except for 37°C-DW groups. During the dehydration period, T_b during "lights on" was higher by 1.5°C at both 23 and 31°C. At 37°C, T_b was 0.85°C higher during "lights on" for AW groups. For 37°C-DW groups, however, T_b during "lights off" was 0.37°C higher than during "lights on" (Table 1 and Figure 2.b). Body temperature was lower during the recovery period ($p \leq 0.05$) than during the dehydration period. The difference between recovery and dehydration period in T_b was different between AW and DW groups ($p \leq 0.01$). For AW groups, this difference in T_b was 0.21°C during "lights on", and 0.44°C during "lights off" and for DW groups 0.47 and 0.91°C, respectively.

Experiment 2: Evaporative water loss, water intake and water temperature

During the dehydration period, EWL increased with increasing T_a ($p \leq 0.01$, Table 2). From 6 to 8 h after start of the dehydration period onwards, EWL of 37°C-DW groups was lowered compared with 37°C-AW groups (Figure 2.c). At that time, 37°C-DW groups had lost evaporatively 3.9% of their BW at start (Figure 3.a). As a result, the interaction between T_a and water availability was nearly significant during "lights off" ($F(2,11) = 4.97$, $p = 0.053$). During the recovery period, EWL was affected by T_a ($p \leq 0.001$), but not by water availability ($p > 0.55$).
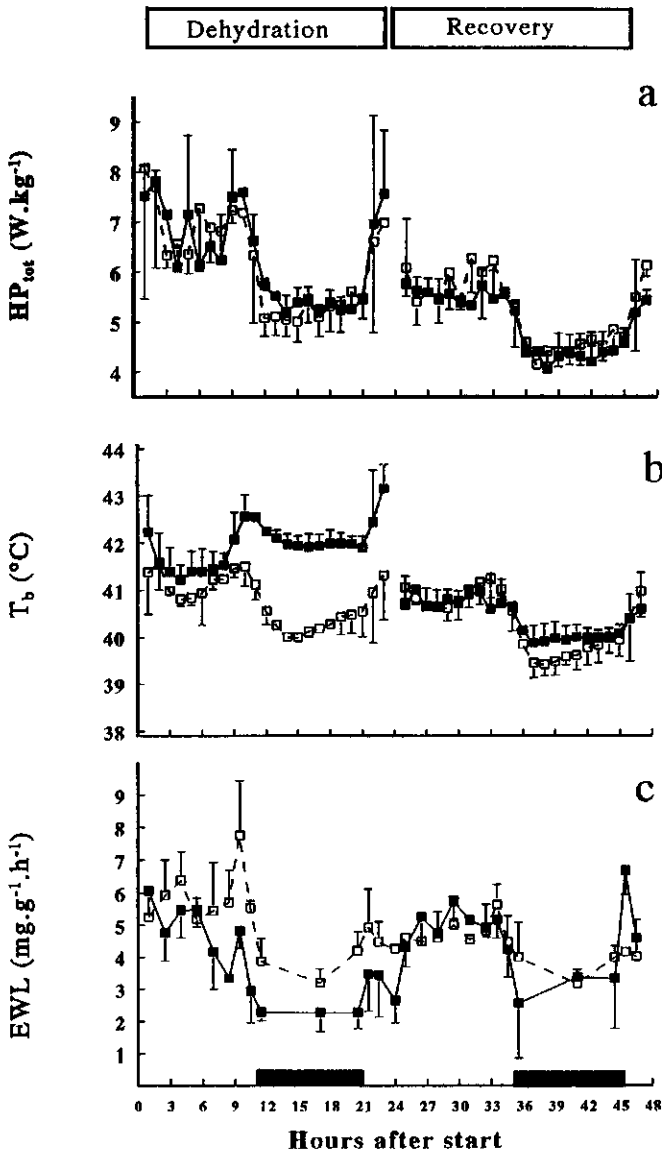
Figure 2. Hour means (± SD, n = 2) of total heat production (HP$_{tot}$; part a) and body temperature (T$_b$, part b), measured in Experiment 1, and weighing period means of evaporative water loss ((± SD, n = 2; part c), measured in Experiment 2, of groups exposed to 37°C. Deprived of water (■———■); access to water (□····□); "lights off" (▬▬▬).

Evaporative water loss was lower during "lights off" than during "lights on" ($p \leq 0.01$; Table 2). "Lights off" values for EWL were 1.77 mg·g^{-1}·h^{-1} and 1.09 mg·g^{-1}·h^{-1} lower during the dehydration and the recovery period, respectively.

Table 2. Least squares means during "lights on" and "lights off" of evaporative water loss (EWL), water intake, excretion (Excret.) rate and body weight (BW) loss of group confined pigeons in relation to water availability and ambient temperature.

	Period	Lights	23 °C		31 °C		37 °C		Root M.S.E
			DW	AW	DW	AW	DW	AW	
EWL	Dehydration	On	2.34^A	2.63^A	2.50^A	3.38^A	4.86^B	5.86^B	0.79
(mg.g^{-1}.h^{-1})		Off	1.41^A	1.14^A	1.12^A	1.46^A	2.33^B	3.49^B	0.32
	Recovery	On	1.78^A	1.58^A	2.48^B	2.40^B	4.83^C	4.74^C	0.25
		Off	1.08^A	0.97^A	1.28^A	1.22^A	3.31^B	3.40^B	0.21
Water	Dehydration	On	-	2.82	-	3.79	-	6.63	1.02
Intake		Off	-	0.07	-	0.39	-	0.85	0.41
(mg.g^{-1}.h^{-1})	Recovery	On	3.53^A	1.55^B	6.26^A	3.17^B	12.82^C	6.40^D	1.16
		Off	0.0	0.22	0.01	0.51	2.09	1.65	0.38
Excret.	Dehydration	On	0.80	1.08	0.82	0.95	0.82	1.13	0.30
Rate		Off	0.50	0.67	0.51	0.57	0.49	0.47	0.12
(mg.g^{-1}.h^{-1})	Recovery	On	0.92	0.90	1.08	1.02	1.09	0.85	0.32
		Off	0.59	0.64	0.48	0.60	0.72	0.45	0.18
BW Loss	Dehydration		5.95^a	3.92^a	5.90^a	3.34^a	9.90^b	3.79^a	0.85
(%)	Recovery		7.65	8.13	7.47	7.72	5.75	7.39	0.96

[1] See Table 1 for legend

During the dehydration period and "lights on", water intake tended to increase with increasing T_a ($p = 0.07$; Table 2). Water intake during the recovery period and "lights on" was affected by T_a ($p \leq 0.001$) and water availability ($p \leq 0.001$), and tended to be influenced

by their interaction effect (p=0.06). At all T_a-levels, DW groups drank more than AW groups during "lights on" of the recovery period. Water intake was low or absent during "lights off" (Table 2). As can be seen from the steeper increase in Figure 3.b, water intake during "lights on" was highest immediately before "lights off". Excretion rate was lower during "lights off" compared to "lights on" (Table 2). No significant treatment effects on the excretion rate were found.
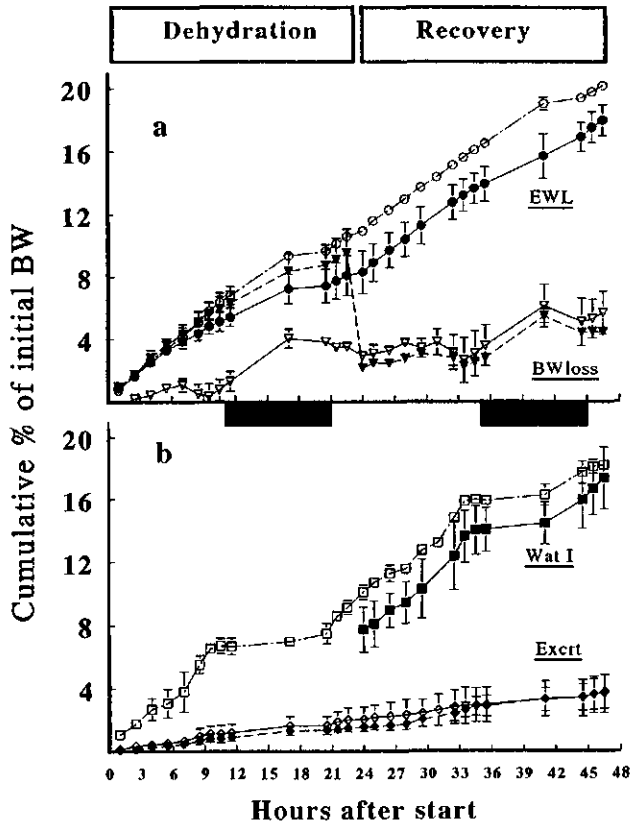
Figure 3. Cumulative evaporative water loss (EWL, part **a**), body weight (BW) loss (part **a**), water intake (Wat I, part **b**) and excretion (Excrt, part **b**) during Experiment 2, expressed relative to body weight at start of the dehydration period. Symbols represent weighing interval means ($\pm$ SD, n=2). Deprived of water ($\bullet$——$\bullet$, ▲——▲, ■——■ and ◆——◆); access to water (○----○, △----△, □----□ and ◇----◇); "lights off" (▬▬▬).

Water temperature in the trough was consistently lower than T_a for all temperature levels. Within 3 h, water temperature in the dummy trough stabilized at 22 , 29 and 34°C for T_a-levels of 23, 31 and 37°C, respectively.

Dry thermal conductance

Dry thermal conductance increased with increasing T_a during both "lights on" and "lights off" (Figure 4). The photoperiod-related change in C_{dry}, measured as the ratio (%) between "lights off" and "lights on", varied with T_a. At 23 and 31°C, C_{dry} was lower during "lights off". At 37°C, however, C_{dry} was higher during "lights off", except for 37°C-DW groups during the dehydration period, where C_{dry} was the same (Figure 4). During "lights on" and "lights off" of the recovery period, C_{dry} was similar between water availability levels at all T_a-levels. Levels of C_{dry} tended to be lower during both "lights on" and "lights off" of the recovery period (Figure 4).
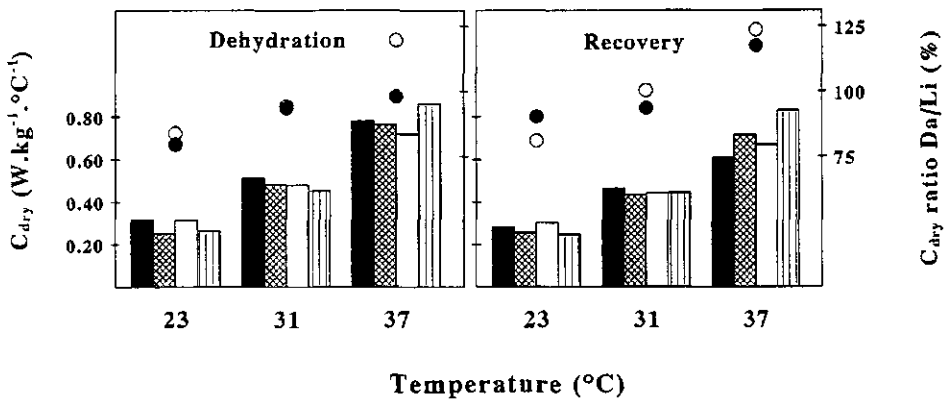
Figure 4. Dry thermal conductance (C_{dry}) during the dehydration period (left part) and the recovery period (right part). C_{dry}: Water deprived groups during "lights on" (■) and "lights off" (□ cross-striped); groups with access to water during "lights on" (□) and during "lights off" (□ striped horizontally). Ratio of C_{dry} during "lights off" (Da) to C_{dry} during "lights on"(Li): Water deprived groups (○); groups with access to water (○).

DISCUSSION

Effects of water deprivation

During the dehydration period, the effects of water deprivation on T_b and EWL depended on the T_a-level and on the duration of exposure (Table 1 and 2), whereas HP_{tot} depended only on T_a (Table 1). At 23 and 31°C, water deprivation did not affect the thermoregulatory parameters. Water deprivation at 37°C increased T_b (Figure 2.b), and reduced EWL (Figure 2.c). This might be due to an osmotically triggered reduction in EWL, resulting in body water savings (Arad et al., 1989). Dehydration resulting from water deprivation increases serum electrolyte and protein concentrations (Thornton, 1986). Brummermann and Rautenberg (1989) also demonstrated that osmotical stress reduces respiration frequencies in pigeons, with a concomitant skip to behavioral thermoregulation to maintain normothermia. The increase in T_b and the decrease in EWL only developed from 6 to 8 h after start of water deprivation onwards (Figure 2.b and 2.c). At that time, 37°C-DW groups in Experiment 2 had evaporated about 3.9% of their initial body weight as water (Figure 3.a). Assuming a total body water content of 65% (Arad et al., 1989), the reduction in EWL was initiated when about 7% of the total body water was lost. Also in dehydrated fowls ($\pm$ 10% BW loss), reduced EWL and relative hyperthermia during heat exposure were reported (Arad, 1983). Heat exposed, dehydrated fruit-bats (Rousettus aegyptiacus), in contrast, defend a normal T_b-level at the expense of an increase in EWL (Korine and Arad, 1993). This difference in coping strategies may be explained by the better tolerance to high T_b-levels in birds compared with flying mammals. Highest T_b-levels in flying bats are about 3°C lower than those observed in birds (Thomas et al., 1991; Torre-Bueno, 1976).

In contrast with T_b and EWL (Figure 2.b and 2.c), the effect of dehydration on HP_{tot} at 37°C was small and not consistent in time (Figure 2.a). This indicates an ability to dissociate an increase in T_b from an increase in HP_{tot}, contradictory to the Arrhenius-van 't Hoff law (Q_{10}-effect). According to Weathers (1981), small birds (BW < 150 g) use this strategy to enhance water economy by facilitating non-evaporative heat loss. Our data on pigeons show that this strategy is also adopted by birds with a higher body weight.

Remarkably, also normally hydrated birds at 37°C showed an increase in T_b within the "lights off" period. Body temperature of normally hydrated birds increased from 40.0°C at 4 h after "lights off" to 40.5°C prior to "lights on" (Figure 2.b). This was parallel to an increase in HP_{tot} from 5.0 to 5.5 W·kg^{-1} over the same time interval (Figure 2.a). This increase in HP_{tot} may be explained by a dehydration-induced shift in water loss mechanisms. As shown in Figure 3.a, BW loss of pigeons with water available increased rapidly during the "lights off" period. Due to low water intake, body water reserves became depleted as time progressed within the "lights off" period. This shows that, during darkness, heat exposed pigeons become dehydrated although water is available. Arad et al. (1987) showed that normally hydrated, heat exposed pigeons rely mainly on cutaneous water loss, whereas

dehydrated pigeons resort to increased respiratory water loss, requiring additional energy expenditure. As this process proceeds, a shift from cutaneous to respiratory water loss may have occurred, with the consecutive increase in HP_{tot}. Hence, the rise in T_b in 37°C-AW birds within the "lights off" period (Figure 2.b) can be regarded as a passive consequence of an increase in HP_{tot} rather than a Q_{10}-effect because no concomitant increase in EHL occurred.

Recovery from dehydration

During the recovery period, water was available for all groups. Recovery of body weight from dehydration at 37°C was fast and almost complete. Within 30 min after giving the pigeons access to water, T_b was similar for both water availability treatments (Figure 2.a). This is in accordance with findings in fowls (Arad, 1985). The recovery in EWL (Figure 2.c), however, was slow compared to the quick normalization of BW loss (Figure 3.a) and T_b (Figure 2.b). As water in normally hydrated pigeons is mainly evaporated through the skin (Arad, 1987), the slower recovery in EWL for previously dehydrated pigeons may reflect the time needed to restore the normal hydration status of the skin structures involved (Webster et al., 1985). However, the delayed recovery in EWL may also result from a reduced need for evaporative cooling during the first hours of the recovery period. Within this period, dehydrated birds drank about 7% of their initial BW (Figure 3.b). The temperature of the fresh drinking water during that period was 26°C, providing a sensible heat loss of 1.2 $W \cdot kg^{-1}$ due to the ingestion of water. The volume of water drunk was equivalent to the mean weight loss (corrected for excreta) in the dehydration period (Figure 3), in accordance with Thornton (1986).

Factors affecting diurnal variation in HP_{tot}, T_b and EWL

This study shows that also in dehydrated, heat exposed pigeons a diurnal variation in HP_{tot}, T_b and EWL is present (Figure 2). Because the reduction in EWL and the consecutive increase of T_b in 37°C-DW groups started shortly before "lights off", water deprivation at 37°C resulted in a larger decrease in EWL, and a smaller decrease in T_b compared to normally hydrated birds.

From 10 h after start of the dehydration period onwards, respiratory quotient was at the fasting level of 0.71. Hence, the pigeons depended on body energy reserves during the second part of the dehydration period, and during the entire recovery period. Compared to the dehydration period, food deprivation might have lowered HP_{tot}, T_b and EWL during the recovery period.

The difference in T_b between the recovery and the dehydration period was higher during "lights off" than during "lights on" (Table 1), which is in accordance with Graf et al. (1989). In contrast with T_b, the difference in HP_{tot} between the dehydration period and the recovery was largest during "lights on", not "lights off" (Table 1). Remarkably, the difference in EWL between the recovery period and dehydration period was higher during "lights on"

compared with "lights off" (1.05 vs. 0.16 mg·g^{-1}·h^{-1}; Table 2). As already suggested by Phillips et al. (1991), our data confirm that high T_b-levels under fasting conditions during "lights on" are enabled by a reduction in heat loss, and is not caused by an increase in HP_{tot}.

Locomotor activity increases T_b (Oshima et al., 1989), HP_{tot} (Zerba and Walsberg, 1992) and EWL (Biesel and Nachtigall, 1987). During "lights on", all three parameters follow a pattern similar to that of locomotor activity (Figure 1 and 2), with two peaks. One peak occurs prior to "lights off", the second immediately after "lights on". Activity during "lights off" is low. Therefore, higher "lights on"-levels for HP_{tot}, T_b and EWL are partially due to activity. The low activity levels and suppression of water intake during "lights off" are in accordance with Yamada et al. (1988).

Diurnal variation in C_{dry}: role of T_a and dehydration

Aschoff (1981b) expected that differences in C_{dry} between active and rest periods would be present at and below thermoneutral conditions, but not at higher T_a-levels. Our data on EWL indicate that the upper critical temperature for an increase in EWL is intermediate between 31 and 37°C. Hence, a diurnal variation in C_{dry} is expected at 23 and 31°C, not at 37°C. During active periods, with a higher activity-related HP_{tot}, C_{dry} should be high to facilitate heat loss. During rest periods, however, the extra HP_{tot} due to activity is absent. Hence, C_{dry} during rest at and below thermoneutral conditions is lowered to reduce heat loss, resulting in energy savings.

In our experiments, C_{dry} was highest during "lights on" at 23 and 31°C, but not at 37°C. This shows that, indeed, the difference between rest and activity periods decreases with higher T_a-levels (Figure 4). At 23 and 31°C, no effect of water deprivation on the diurnal variation in C_{dry} was found. In birds exposed to 37°C, however, water deprivation affected C_{dry} during the dehydration period. For water deprived groups, "lights off"- and "lights on"- estimates of C_{dry} were similar, in accordance with Aschoff's hypothesis (Aschoff, 1981b). For normally hydrated pigeons, however, C_{dry} at 37°C was higher during "lights off" compared with "lights on". The higher estimates of C_{dry} were found for water deprived groups during the recovery period, and for groups with access to water during both the dehydration and the recovery period. Therefore, the higher C_{dry} during "lights off" at 37°C can be considered the "normal" case, whereas the lower value for C_{dry} during "lights off" for dehydrated pigeons reflects an abnormal situation, where water economy (through a reduced EWL) is paid for by a reduced thermal conductance due to an increase in T_b. Hence, C_{dry} of normally hydrated heat exposed pigeons is maximal during the resting phase, not during the active phase. These findings on group confined pigeons are in disagreement with the hypothesis put forward by Aschoff (1981b).

This discrepancy between our experiments and literature might be explained by the fact that Aschoff's hypothesis was based on observations of individually confined birds. In contrast with individually housed pigeons, activity of group confined pigeons consists mainly of aggressive social interactions: Pecking, threatening and running away (personal observations).

As a consequence, HP_{tot}, EHL and T_b increase. This increase in T_b may have two causes. First, the increase in EHL may be not sufficient to cover the increase in HP_{tot}, resulting in heat storage in the body. Second, heat stress reduces capillary blood flow to inner body organs (Wolfenson et al., 1981). This allows maximal sensible heat loss at the body surface. Locomotor activity, however, causes a shift in blood flow towards muscular tissue, resulting in a decreased sensible heat loss and an increase in T_b. In both cases, a decrease in C_{dry} seems likely, since C_{dry} is the ratio between a heat storage component ($HP_{tot} - EHL$) and a temperature difference ($T_b - T_a$). The heat storage components are both increased by activity, and the resulting difference may be constant or increasing. At 37°C during "lights on", the temperature difference (in °C) is larger than the heat storage component (in $W\,kg^{-1}$). The temperature component consists of an activity-dependent T_b and a constant T_a, which always increases with increased activity. Since C_{dry} is the ratio of both components, this results in a lower C_{dry} when activity levels increase.

A second explanation for the lower C_{dry} during "lights on" due to group confinement might be the light-dependent spatial distribution of the pigeons within the crate. Aggressive behavior during "lights on" of one or few pigeons within the group may force other pigeons to clustering (personal observations), thus reducing average C_{dry} for the group (Brown and Foster, 1992). Absence of aggressive behavior during "lights off" may facilitate a more dispersed distribution within a crate, resulting in an overall higher C_{dry}.

However, also endogenous mechanisms not related to group confinement can be invoked to explain the higher values of C_{dry}. The nightly increase in HP_{tot} in normally hydrated birds at 37°C, discussed previously, is associated with an increase in T_b, but not in EWL. Hence, the resulting increase in dry thermal conductance will cause body water savings by the reduction of evaporative water loss for thermoregulatory purposes.

CONCLUSIONS

This study has demonstrated the capacity of dehydrated heat-exposed pigeons to reduce EHL at a constant HP_{tot}. This capacity is paid for by an increase in T_b and a reduction in C_{dry}. Diurnal variation in HP_{tot}, T_b and EWL was still present in dehydrated pigeons exposed to 37°C. After the dehydration period, when all birds were given access to water, T_b of previously dehydrated pigeons exposed to 37°C dropped almost immediately to T_b levels attained by normally hydrated birds. The recovery from dehydration as measured by EWL, however, was delayed. Dry thermal conductance increased with T_a. In accordance with Aschoff (1981b), C_{dry} was higher during "lights off" at 23°C whereas no diurnal variation was found at 31°C. The lower value for C_{dry} during "lights on" compared to "lights off" at 37°C may be caused by increased locomotor activity, not present in individually housed birds, or by endogenous water saving mechanisms. Dry thermal conductance was lower during the recovery period. This resulted from a decrease in HP_{tot}, T_b and EWL.

CHAPTER 4:

Activity and Thermogenesis in Pigeons Exposed to Temperature fluctuations

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Activity and Thermogenesis in Pigeons Exposed to Temperature Fluctuations

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ABSTRACT

In group confined pigeons housed under transport conditions, responses in activity and thermogenesis to one of three temperature fluctuation patterns were studied at two levels of ambient temperature ("15°C" or "35°C"). During the 23-h exposure period, one fluctuation pattern had zero amplitude ("Constant"), the second and the third an amplitude of 7°C, starting at the maximum ("Cosine") or starting at the mesor and increasing thereafter ("Sine"). At "35°C", activity patterns were affected by temperature fluctuations, but not at "15°C". For both "Sine" and "Cosine" at "35°C", activity increased with temperature at levels exceeding 35°C. Mean heat production was 5.87 $W \cdot kg^{-1}$ at "15°C" and 5.30 $W \cdot kg^{-1}$ at "35°C", but was not affected by temperature fluctuations. For "Sine" and "Cosine" at "15°C", the heat production pattern differed from the activity pattern. At "35°C", however, activity and heat production patterns were similar for all temperature patterns. Body weight loss at "15°C" was about 9% and was not affected by temperature fluctuation patterns. At "35°C", body weight loss depended on the temperature fluctuation pattern, being 11.8% for "Constant", 14.3% for "Cosine" and 15.0% for "Sine". Data on heat production and body weight loss showed that at "15°C" the pigeon's thermoregulatory capacity is sufficient to cope with fluctuating temperatures. At "35°C", however, fluctuating temperatures increased the risk of exceeding the pigeon's thermoregulatory capacity.

INTRODUCTION

In birds, thermoregulatory responses often involve adaptation of activity levels. Under cold conditions, higher activity levels in quail increase heat production, which substitutes for extra-thermoregulatory heat production (Zerba and Walsberg, 1992). In hot environments, individually kept pigeons (Columba livia) reduce activity levels, thus reducing heat production, and consequently the need for heat loss (Marder and Gavrieli-Levin, 1986; Brummermann and Rautenberg, 1989). Group confinement of racing pigeons, however, allows for aggressive social interactions, such as pecking, which may elicit escape responses (Goodwin, 1983). This behavior may interfere with the normally expected response in activity, as suggested by Marder (1983). He observed an increase in aggressive behavior in heat exposed, group confined

pigeons, where a decreased activity was expected.

Under outdoor conditions, ambient temperature (T_a) varies with time according to a predictable diurnal rhythm reaching a maximum during the day, and a minimum during the night. In the microclimate of free-ranging birds, this variation in T_a is not only a passive result from external, uncontrollable factors, but also from microhabitat selection during the bird's active phase (Prinzinger, 1982). The ability to switch between microhabitats, i.e., T_a-levels, is limited for racing pigeons on transport to their release sites. The transport procedure involves group confinement in crates during 24 to 72 h, with extended periods of food and water deprivation (Gorssen et al., 1993). Furthermore, T_a fluctuations within the transport vehicle are often no longer predictable for the bird. Via the variation in heat loss from the vehicle (e.g.,, due to variation ventilation rate), T_a fluctuations at the animal level depend heavily on driving procedures (Webster et al., 1993). As shown by Kettlewell and Mitchell (1993), T_a fluctuations inside poultry vehicles depend mainly on vehicle speed, not on fluctuations in the outside T_a. Highest T_a-levels are reached when the vehicle is not moving. In pigeon transport, stationary periods occur prior to departure, during relax breaks for the driver, and after arrival at the release site. Hence, the moment of transport (day vs. night) is decisive for the time at which pigeons are challenged with maximal T_a-levels.

Heat production is also directly affected by T_a. Although the effect of constant T_a levels on energy metabolism is well established, fluctuating T_a levels have received little attention (Prinzinger, 1982). Since the effect of T_a on heat production is known to vary between the active and resting phase (Aschoff and Pohl, 1970), different temperature fluctuation patterns within a day are likely to result in a different daily energy expenditure.

In the present paper, we report on activity and thermogenesis in group confined, water deprived fasted pigeons. Responses to one constant and two fluctuating, sinusoidal temperature patterns were compared during a 23-h exposure to cold ("15°C") and warm ("35°C") conditions in order to assess the effect of fluctuating temperatures on thermogenesis and activity of racing pigeons housed under transport conditions.

MATERIAL AND METHODS

Animals, design and housing

In total, 360 experimentally naïve, adult pigeons (male and female) were allotted to 24 mixed groups of 15 birds. The experiment was conducted in late autumn. The experiment followed a 2-way factorial design with four replicates per treatment combination, with group as the experimental unit. Average temperature (two levels) and temperature fluctuation pattern (three levels) were included as factors. Birds were allotted to groups about 2 months before start of the experiment.

During this pre-experimental period, the birds were housed in a half-open outdoor aviary under natural photoperiod, humidity and temperature, with four groups per aviary

compartment (4 m length × 2 m width × 2 m height). Twice a day, the pigeons were fed a commercial diet of whole grains (mainly peas, corn, beans and barley) in a daily ration of ± 45 g per bird with water ad libitum. At the last day of the pre-experimental period (Day 0), diet composition was changed to whole grain corn.
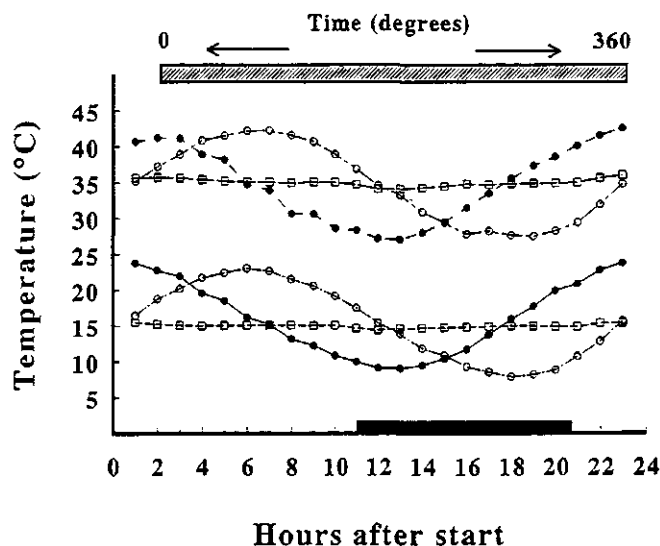
Figure 1. One hour means of ambient temperature during the exposure period for each fluctuation pattern at "15°C" or "35°C". "Cosine" (●); "Constant" (□); "Sine" (○). Black bar (bottom) indicate "lights off". Hatched bar (top) marks the 22-h period (360 degrees) used for acrophase estimation by non-linear regression.

Procedure

The experimental period consisted of an adaptation period (18 h), an acclimation period (23 h) and an exposure period (23 h). The adaptation period started immediately after the second feeding at Day 0 (16.00 h). Two groups of pigeons were transferred to a laboratory room. Each group was confined to a transport crate (0.60 m width × 0.70 m length × 0.25 m height) with aluminium sides, half-open wooden top and hard plastic grid floor. No feed was available. Water was supplied by drinking troughs which were attached to the outside of the crate.

The acclimation period started at 09.15 h of the next day (Day 1). The crate with appending drinking troughs was placed on a platform in one of two climate-respiration chambers of 1.8 m^3 each, as described by Verstegen et al. (1987). The temperature was constant at either 15 or 35°C, according to treatment. The T_a-level of 15°C reflects common transport conditions at start of the Dutch racing season (April), whereas the 35°C-level

represents conditions that can be encountered during summer transports. At 08.40 h of Day 2, the drinking troughs were removed from the crates.

The exposure period started at 09.15 h of Day 2. For each group, average T_a during the acclimation and exposure period was similar. During the exposure period, however, temperature fluctuated around this average according to one of three sinusoidal patterns, each with a 23-h period. One pattern had zero amplitude, so was "Constant", a "Cosine" pattern had a 7°C amplitude starting at the maximum, and a "Sine" pattern with a 7°C amplitude, starting at the average T_a and increasing afterwards (Figure 1). At 08.40 h of Day 3, the exposure period ended.

Throughout the experimental period, lights were off between 19.30 and 06.30 h. Average relative humidity was kept at about 70% for all patterns at "15°C". At "35°C", relative humidity was kept at approximately 63%.

Data collection

The individual body weights (BW $\pm$ 1 g) were recorded at the start of the adaptation and the acclimation period, and at start and end of the exposure period.

During both the acclimation and the experimental period, heat production was measured by indirect calorimetry in successive 9-min intervals on the basis of the exchange of CO_2 and O_2, as described by Verstegen et al. (1987). A Hartmann and Braun Uras 3G infrared absorption CO_2 analyzer and a Servomex 1100 H paramagnetic O_2 analyzer were used. Analyzers were calibrated every 24 h, and all gas volumes were converted to standard temperature and pressure (dry). Air flow through the chambers was 17 l·min^{-1}. Total heat production (HP_{tot}) was calculated in kJ·d^{-1} according to Romijn and Lokhorst (1961). Using BW at start of the acclimation period, HP_{tot} was expressed in W·kg^{-1}. Activity was measured using Doppler-radar activity meters (Radar MD5, Vierpool, Amsterdam, The Netherlands), which were placed about 1 m above the crate. Each movement of the animals was interpreted as a frequency change in the reflected ultrasound waves emitted by the meters. Frequency changes were transformed to counts, which were added over the 9-min measurement interval for HP_{tot}. This resulted in a 9-min activity score (# counts·9 min^{-1}).

Data preparation and analysis

Body weight loss at the end of the acclimation and exposure period were analyzed using BW at start of the acclimation period as a reference. Group means of absolute (g) and relative BW loss (%) were analyzed for the effects of average temperature, temperature fluctuation pattern, and their interaction by means of 2-way ANOVA.

The diurnal variation in HP_{tot} and activity was quantified for the acclimation and exposure period separately. For this purpose, only measurements between 10.30 and 08.30 h were considered, resulting in a 22-h period covering 11 h of "lights on" and 11 h of "lights off" (Figure 1). Nine-minute data on HP_{tot} and activity were averaged over 30-min periods, resulting in 44 observations per group for both the acclimation and exposure period. To allow

comparison between groups, activity scores were first normalized for each group (Robinson et al., 1993). A sine wave was fitted through these data ($n = 44$) for each group (NLIN procedure, SAS, 1989). For HP_{tot}, estimates of mesor, amplitude and phase-shift were subjected to ANOVA. For activity, ANOVA was performed on phase-shift estimates only. Estimates of phase-shift were expressed as the time (in degrees) at which the estimated peak levels of HP_{tot} and activity occurred.

Furthermore, the slope relating HP_{tot} and T_a was estimated in "Cosine" and "Sine" groups for "lights on" and "lights off" periods separately. This linear regression was based on 30-min values of HP_{tot} and T_a.

All analyses of variance were performed for the acclimation and exposure period separately.

RESULTS

General

In six groups at "35°C", some pigeons could not cope with the exposure. In two groups of the "Cosine" treatment one pigeon was lost. For the "Sine" treatment, losses increased between replicates from group 1 (two birds) to group 2 (three birds) and group 3 (four birds). Consequently, it was decided to stop the exposure period of group 4 after 7 h of exposure. However, also in this group two pigeons had already succumbed when opening the chamber. All data of group 4 were removed from the exposure period analyses. Activity measurements during the exposure period of one "35°C-Constant" group were missing. This resulted in a total of 24 observations for the acclimation period, and respectively 23 (BW and HP_{tot}) and 22 (activity) observations for the exposure period.

Activity

Activity patterns during the acclimation period, quantified by the time at which maximum activity was estimated, were similar between treatments. Peak estimates occurred at about 5 h after start of exposure. Although T_a was constant during the acclimation period, an interaction between average T_a and the fluctuation pattern was observed ($F(2,18) = 5.41$, $p \leq 0.05$). This resulted from the value obtained for the "15°C-Cosine" treatment, for which the activity peak occurred at 6 h 23 min (88 degrees) after start, more than 1 h later than for the other treatments.

As shown in Figure 2, activity patterns during the exposure period differed between temperature fluctuation patterns at "35°C". At "15°C", no difference in activity patterns was present. In both "Cosine" and "Sine" temperature fluctuations at "35°C", T_a-levels approaching 42°C were associated with increased activity levels (Figure 1, Figure 2). For all other treatments, activity patterns during the exposure period were similar.
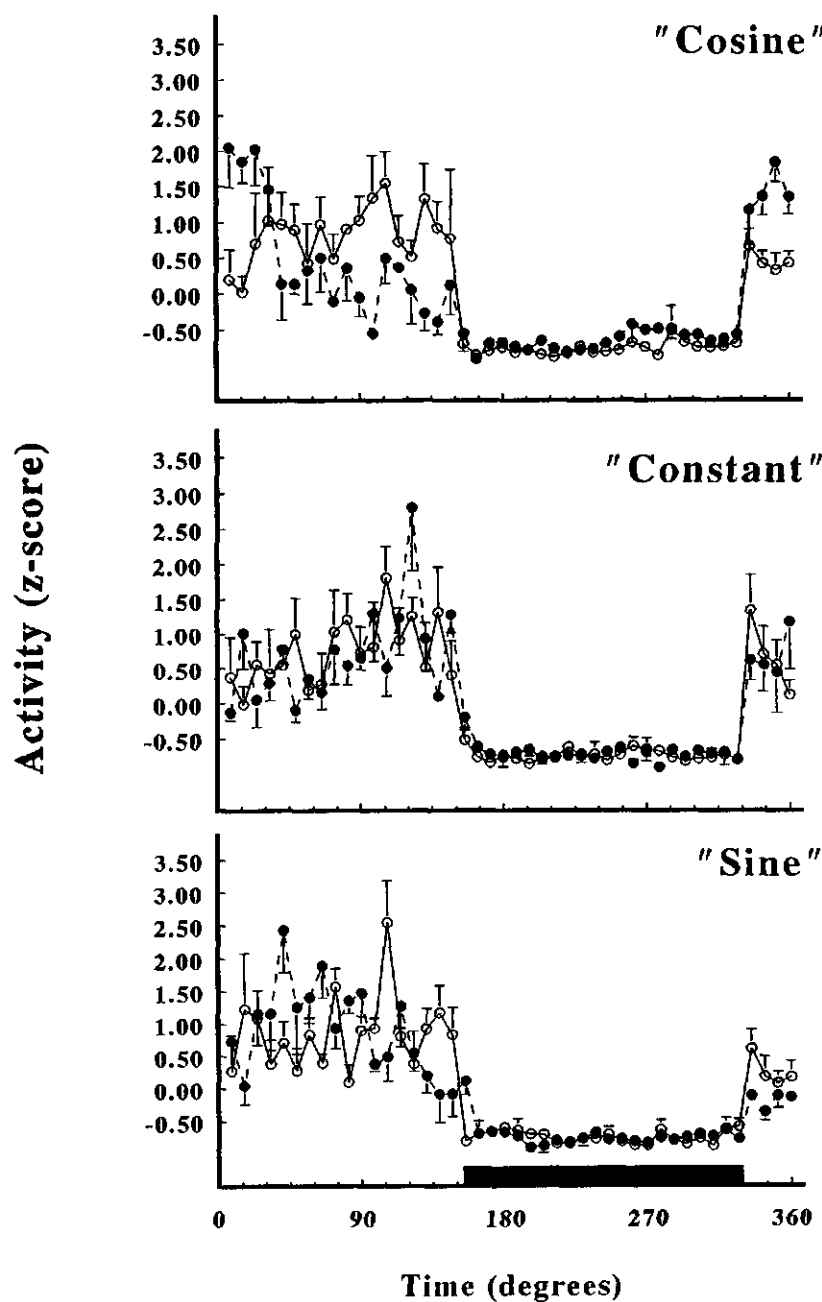
Figure 2. Exposure period half-hour means ($\pm$ SEM, n=3 or 4) of normalized activity counts (z-scores) per fluctuation pattern at each average T_a-level. "15°C" ($\bigcirc$); "35°C" ($\bullet$); "lights off" (▬▬▬).

For these treatments, maximum activity was estimated at about 5 h 15 min after start of exposure (70 degrees), as shown in Table 1. This corresponds with the estimation of maximum activity during the acclimation period. For "35°C-Cosine" groups, the estimated activity peak occurred earlier, at 2 h 40 min after start of exposure. As a result, an interaction between average T_a and fluctuation pattern was found for the phase-shift in activity $(F(2,16)=9.13, p\leq0.01)$.

Table 1. Sinusoidal regression estimates for heat production and activity during the exposure period. Data are presented as least squares means $\pm$ SE.

Temperature	Fluctuation Pattern	Heat Production[1]			Activity
		Mesor $(W\cdot kg^{-1})$	Amplitude $(W\cdot kg^{-1})$	Acrophase[2] (h:min)	Acrophase[2] (h:min)
"15°C"	"Cosine"	5.73[ab] ±0.11	1.38[a] ±0.10	5:50[a] ±0:12	5:13[a] ±0:19
	"Constant"	5.82[a] ±0.11	1.49[a] ±0.10	3:55[b] ±0:12	5:14[a] ±0:19
	"Sine"	5.99[a] ±0.11	1.18[ab] ±0.10	2:47[c] ±0:12	5:23[a] ±0:19
"35°C"	"Cosine"	5.23[bc] ±0.11	1.55[a] ±0.10	2:18[c] ±0:12	2:40[b] ±0:19
	"Constant"	5.07[c] ±0.11	0.87[b] ±0.10	4:56[a] ±0:12	5:21[a] ±0:22
	"Sine"	5.29[bc] ±0.13	2.14[c] ±0.11	5:37[a] ±0:14	4:59[a] ±0:22

[1] Different, non-overlapping superscripts within a column indicate significant treatment differences $(p\leq0.05)$.

[2] Acrophase (h:min after start) is transformed from the estimate in degrees by equalling 1 h to 16.36 $(=360/22)$ degrees, starting at 1:00 after start.
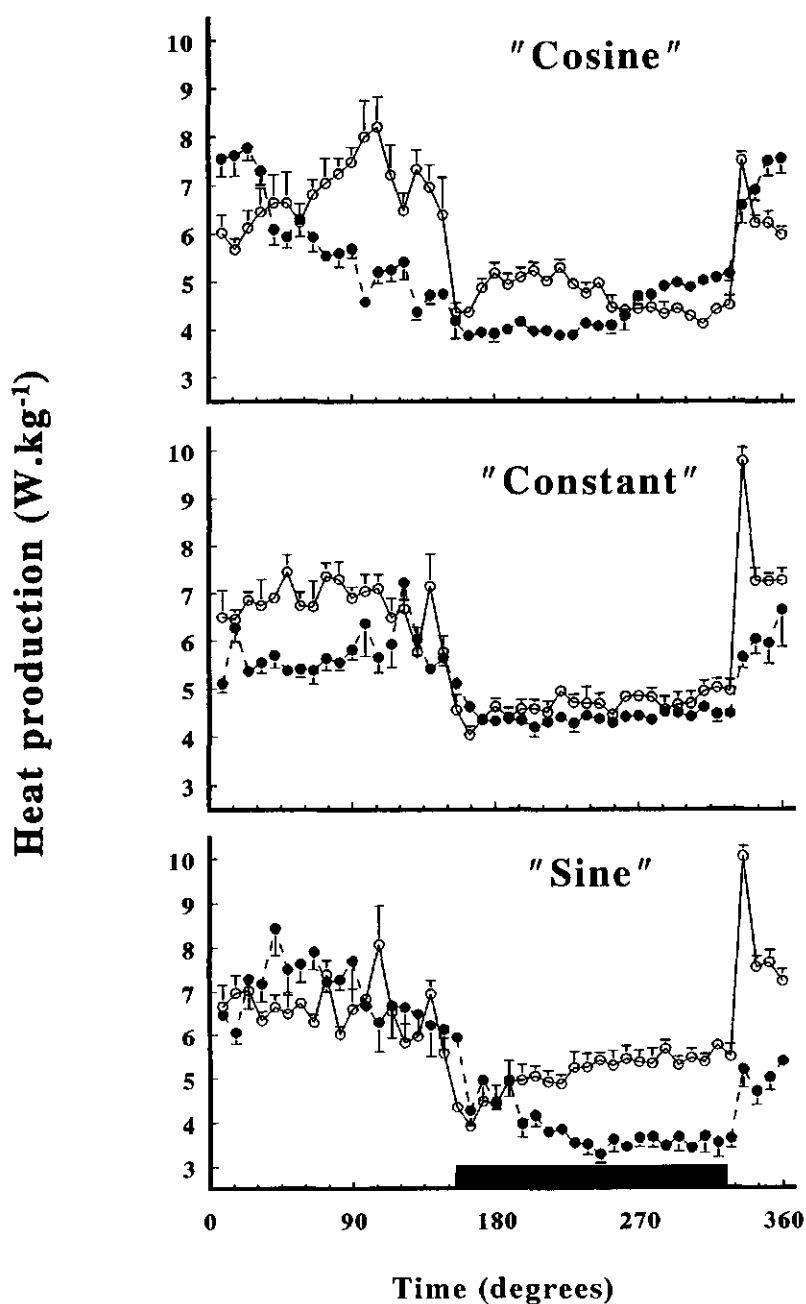
Figure 3. Exposure period half-hour means ($\pm$ SEM, n=3 or 4) of heat production measurements per fluctuation pattern at each average T_a-level. "15°C" (○); "35°C" (●); "lights off" (▬▬▬).

Heat production

During the acclimation period, HP_{tot} was 6.62 $W \cdot kg^{-1}$ at "15°C" and 5.78 $W \cdot kg^{-1}$ at "35°C" ($F(1,18)=84.59$, $p \leq 0.001$). Also during the exposure period, HP_{tot} was affected by average T_a ($F(1,17)=33.94$, $p \leq 0.001$). Heat production was 5.87 $W \cdot kg^{-1}$ and 5.30 $W \cdot kg^{-1}$ at "15°C" and "35°C", respectively. Limiting the analysis to the "Constant" groups, HP_{tot} was lower during the exposure period compared with the acclimation period (paired t-test, $p \leq 0.001$). This decrease in HP_{tot} for "Constant" groups was 0.73 $W \cdot kg^{-1}$ at "15°C" and 0.55 $W \cdot kg^{-1}$ at "35°C" ($F(1,6)=27.53$, $p \leq 0.001$).

Table 2. Body weight loss and heat production during the exposure periode. Data are presented as least squares means $\pm$ SE.

Temperature	Fluctuation Pattern	Heat[1] Production ($W \cdot kg^{-1}$)	Body weight[1,2] Loss	
			(g)	(%)
"15°C"	"Cosine"	$5.708^a \pm 0.115$	$42.4^a \pm 1.4$	$8.61^a \pm 0.27$
	"Constant"	$5.875^a \pm 0.115$	$42.3^a \pm 1.4$	$8.39^a \pm 0.27$
	"Sine"	$6.018^a \pm 0.115$	$47.1^a \pm 1.4$	$9.22^a \pm 0.27$
"35°C"	"Cosine"	$5.319^b \pm 0.115$	$73.7^c \pm 1.4$	$14.26^c \pm 0.27$
	"Constant"	$5.153^b \pm 0.115$	$59.3^b \pm 1.4$	$11.83^b \pm 0.27$
	"Sine"	$5.443^{a,b} \pm 0.133$	$78.1^c \pm 1.6$	$14.96^c \pm 0.32$

[1] Different, non-overlapping superscripts within a column indicate significant treatment differences ($p \leq 0.05$).

[2] Body weight loss was calculated with body weight at start of the acclimation period as a reference.

As shown in Table 2, differences in HP_{tot} between temperature fluctuation patterns were not significant during the exposure period ($F(2,17)=2.13$, $p=0.149$). At "15°C", mean HP_{tot} for the "Cosine" pattern was 0.17 $W \cdot kg^{-1}$ lower compared with the "Constant" pattern, and 0.31 $W \cdot kg^{-1}$ lower than the "Sine" pattern. At "35°C", HP_{tot} for the "Constant" pattern was lowest, being 0.17 $W \cdot kg^{-1}$ lower than the "Cosine" pattern, and 0.29 $W \cdot kg^{-1}$ lower than the "Sine" pattern (Table 2). No interaction between average T_a and fluctuation pattern was found on HP_{tot} ($F(2,17)=1.05$, $p=0.37$).

The estimated time of maximum HP_{tot} during the acclimation period varied between 4 h 07 min and 4 h 51 min after start. For the exposure period, estimates of the sinusoidal

regression parameters are shown in Table 1. Estimates for the mesor were comparable with the data for mean HP_{tot} presented in Table 2. With respect to the amplitude, an interaction between average T_a and fluctuation pattern was found ($F(2,17)=29.67$, $p \le 0.001$). At "15°C", the amplitude tended to be lower for "Sine" groups, which had the highest mesor. At "35°C", the amplitude of the "Constant" treatment was 0.68 $W \cdot kg^{-1}$ lower than for the "Cosine" pattern, and 1.27 $W \cdot kg^{-1}$ lower than for "Sine" groups. As can be seen from Figure 3, the effect of the fluctuation pattern on the time at which HP_{tot} was maximal depended strongly on the average T_a. Analysis of acrophase estimates showed a clear interaction between average T_a and the fluctuation pattern ($F(2,17)=119.14$, $p \le 0.001$). At "15°C", peak HP_{tot} is reached first for the "Sine" treatment, followed by the "Constant" pattern about 1 h later, and last for the "Cosine" pattern about 6 h after start of exposure (79 degrees). At "35°C", however, the estimated peak in HP_{tot} was reached first in the "Cosine" treatment at 2 h 18 min after start (21 degrees), being significantly earlier than the "Sine" or "Constant" peak ($p \le 0.05$).

Table 3. Regression coefficients relating heat production and ambient temperature during the exposure period

Temperature	Lights	Fluctuation Pattern	Regression Coefficient $(W \cdot kg^{-1} \cdot °C^{-1})$	Temperature interval (°C)	
				Mean	Range
"15°C"	On	"Cosine"	-0.085 ± 0.06	17.9 ± 0.7	13.4 ± 1.9
		"Sine"	-0.180 ± 0.03	19.9 ± 0.1	10.7 ± 0.6
	Off	"Cosine"	-0.059 ± 0.02	13.5 ± 0.6	12.5 ± 1.6
		"Sine"	-0.130 ± 0.02	11.2 ± 0.4	10.5 ± 0.2
"35°C"	On	"Cosine"	0.205 ± 0.02	36.6 ± 0.2	14.2 ± 0.3
		"Sine"	0.248 ± 0.02	39.3 ± 0.4	10.9 ± 1.0
	Off	"Cosine"	0.095 ± 0.01	32.5 ± 0.1	13.8 ± 0.2
		"Sine"	0.180 ± 0.07	30.4 ± 0.2	11.0 ± 0.5

In Table 3, regression coefficient estimates of HP_{tot} on T_a are presented for the "lights on" and "lights off" period separately. At "15°C" treatments, HP_{tot} decreased with increasing T_a, while at "35°C", HP_{tot} increased with increasing T_a. Regression coefficients at the "15°C" treatment were higher during "lights off" compared to "lights on". Regression coefficients at the "35°C" treatment were lower during "lights off" compared to "lights on". This indicates that at both "15°C" and "35°C" treatment, HP_{tot} during "lights off" was less affected by T_a.

Comparison of regression coefficients for the "Sine" and "Cosine" patterns within photoperiods shows that HP_{tot} is less affected by T_a at the "Cosine" than at the "Sine" pattern. This indicates that the apparent sensitivity of HP_{tot} to changes in T_a is lower when adopting a "Cosine" temperature fluctuation pattern. However, when comparing between and within photoperiods it should be realized that the mean and the range of T_a was not constant (Table 3).

Body weight

Mean BW at start of the acclimation period was 508.7 ± 3.3 g (mean $\pm$ SEM, $n = 24$). Body weight loss during the acclimation period was affected by average T_a only. Body weight after the acclimation period was 484.0 g at "15°C" and 487.4 g at "35°C" ($F(1,17) = 12.51$, $p \leq 0.01$). This corresponds with a BW loss of 4.88 and 4.20% at "15°C" and "35°C", respectively ($F(1,17) = 17.39$, $p \leq 0.001$). At the end of the exposure period, relative BW loss was affected by an interaction between average T_a and the temperature fluctuation pattern ($F(1,17) = 17.11$, $p \leq 0.001$). The highest BW loss was found at "35°C" (Table 2). "Sine" and "Cosine" fluctuation patterns at "35°C" resulted in a higher BW loss compared with the "Constant" treatment, being 15.0%, 14.3% and 11.8%, respectively. At "15°C", BW loss was not affected by the fluctuation pattern (Table 2).

Weight loss of both dead pigeons for the "35°C-Cosine" treatment was 17.1%. For the "35°C-Sine" treatment, five pigeons had a BW loss between 15.2 and 18.0%, three pigeons had lost between 10.5 and 12.5%, and three birds lost less than 10% (range 8.4 - 9.9%). Among the latter category were both birds of group 4, where exposure was stopped after 7 h.

DISCUSSION

Temperature fluctuations and activity levels

Heat exposed pigeons are expected to reduce activity levels, thus reducing the need for heat loss by a decrease in heat production (Marder and Gavrieli-Levin, 1986; Brummermann and Rautenberg, 1989). For group confined pigeons, our results show that an increase in temperature from 35°C to 42°C results in an increase in activity levels. No such response in activity was found under cold conditions, where temperature increased in a similar way from 15 to 22°C.

From a thermoregulatory perspective, the observed increase in activity of water deprived pigeons exposed to heat is counterproductive. Under hot conditions, maintenance of physiological homeostasis depends mainly on the capacity for evaporative heat loss. Hence, a combination of both physical activity and water deprivation severely affects water economy of heat exposed pigeons (Arad et al., 1987). But, although the resulting effect of higher activity levels is not in accordance with the need to reduce the thermoregulatory burden, the

underlying cause for the increased activity may fully comply with the goal of maintaining physiological homeostasis. Three hypotheses, thermoregulatory in nature, can be put forward: a search for water, heat avoidance and the increase in sensible heat loss.

The increased activity might be due to a search for water. Pigeons had access to water during the acclimation period, but not during the exposure period. To compensate for increased water evaporation under hot conditions, pigeons may have become increasingly eager to drink water with increasing temperature. However, Thornton (1986) suggested that drinking in pigeons is stimulated by an osmoreceptor mechanism, specifically by an increase in plasma sodium concentrations. Dehydration through water deprivation induces such an increase (Arad et al., 1989). The activity patterns presented in Figure 2 do not support the "water search" hypothesis. Activity peaks for the "Cosine" pattern follow immediately after start of the exposure period, so only 2 h after water removal. This period seems too short to induce a sufficiently high level of dehydration. Furthermore, as temperature decreased again, also a drop in activity levels was observed, although birds became more dehydrated as exposure continued.

The second hypothesis, avoidance of heat exposure, seems more adequate to explain the increased activity above 35°C. Prinzinger (1982) pointed at the bird's capacity for micro-habitat selection during the active phase. In hot environments, the most sensible strategy for a bird to adopt is heat avoidance (Blaxter, 1989). In our experiment, avoidance of the temperature increase was impossible. Although the type of behavior was not studied, it is most likely that aggressive social interactions (pecking, threatening, escaping etc.) explain most of the observed activity. Goodwin (1983) reported serious fights among pigeons at over-crowded communal roosts, when pigeons try to defend the space immediately around themselves. The group confinement adopted in our experiments, with an available space of no more than 280 cm^2 per bird, may be comparable with an over-crowded roost. Attempts to avoid the increasing ambient temperature cause displacements within the crate. This way, pigeons who are moving around are bound to enter area's defended by other, stationary, pigeons, thus eliciting an aggressive response. As shown by Cross and Goodman (1988), body movements of the attacked bird invoke more attacks from the aggressor than immobility.

For the third hypothesis, the increase in sensible heat loss, we refer to Figure 1 and Figure 2. Activity levels and ambient temperature are positively correlated above 35°C, in both the increasing and decreasing temperature phase. This suggests that the frequency of heat avoidance, and the resulting aggression levels, depend on the level of heat exposure. Probably, the heat induced increase in activity is explained by the temperature dependent size of the area defended by the pigeon. Keeping ambient temperature constant, thermal insulation is higher when the number of birds per surface unit increases. Under cold conditions, clustering illustrates very well the importance of animal interspace for thermoregulation without extra-thermoregulatory heat production (Brown and Foster, 1992). Under hot conditions, however, thermoregulation demands a lowered thermal insulation, and an increase on heat loss. For water economy, sensible heat loss (radiation, conduction, convection) is to be preferred to

evaporative heat loss. Group confined pigeons dealing with increasingly high temperatures can maintain sensible heat loss by increasing the distance with other birds, hence by defending a larger space around themselves. In a crate of fixed size with a constant number of animals, this implies that the risk of interfering with an adjacent pigeon increases, and, consequently, the frequency of aggressive social interactions.

However, all three hypotheses are based upon closely related thermoregulatory arguments. Hence, it is likely that each of the proposed hypotheses contributes to the observed heat-induced increase in activity. Nevertheless, the relative contribution of each hypothesis may vary with time and between groups.

Fluctuations in T_a and thermogenesis

The interpretation of the thermogenic effect of temperature fluctuations is different between the "15°C" and the "35°C" treatment. As discussed in the previous paragraph, an increase in temperature above 35°C results in an increased activity, thus in an increased heat production (Figure 3, Table 1). Hence, the higher heat production in "Cosine" and "Sine" groups (Table 2) is not only due to the direct thermogenic effect of temperature, but also to the indirect effect of ambient temperature through activity. The increased demand for evaporative heat loss due to the higher heat production is reflected in the higher body weight loss for "Cosine" and "Sine" groups (Table 2), in accordance with Arad et al. (1987). As indicated by the mortality encountered in both treatments, with body weight losses higher than 15%, continuing heat exposure leads to lethal dehydration levels. However, a body weight loss of less than 10% in three dead pigeons of the "35°C-Sine" treatment suggests that not only chronic exposure to heat, but also a relatively short, acute heat exposure may be lethal, even when the birds are not severely dehydrated. Probably, these birds suffered from irreversible hyperthermia, resulting from a high ambient temperature, high locomotor activity levels and an insufficient capacity for evaporative and non-evaporative heat loss. Mortality occurred at lower temperature levels than known from literature. Marder (1983) reported on individually kept pigeons, surviving heat loads of 60°C during 270 min. Although these birds were given access to water every 2 h, also a beneficiary effect of solitary confinement on survival seems likely.

At "15°C", activity patterns were not affected by ambient temperature fluctuations (Figure 2, Table 3). As shown in Table 2, heat production during the exposure period was lowest for the "Cosine" treatment, and highest for the "Sine" treatment, the "Constant" treatment being intermediate. Comparing the heat production for the "Cosine" and "Constant" treatment, a higher HP_{tot} for "Cosine" was expected. Prinzinger (1982) demonstrated in quail that temperature fluctuations increase the energy consumption compared with a constant temperature exposure, probably by an overshoot of the feedback control system when adapting the energy metabolism to the new temperature conditions. In the light of these findings, the even larger difference in heat production between "Cosine" and "Sine" treatments is remarkable, since both treatments differ only in a 90 degrees phase shift.

In our opinion, they might reflect a within-photoperiod variation in the thermogenic effect of ambient temperature on heat production. Aschoff and Pohl (1970) already demonstrated that the increase in heat production with a decrease in temperature below the lower critical temperature is lower in the resting phase compared with the active phase. As shown in Figure 2, "lights on" corresponds with the active phase, and "lights off" with the resting phase in pigeons. Aschoff (1981) also postulated that, similar to body temperature and heat production, this variation may also be present within photoperiods. In accordance with Aschoff and Pohl (1970), regression coefficients were higher during "lights off" in both fluctuation patterns (Table 3). The sensitivity of HP_{tot} to lower temperature levels was, however, higher for "Sine" groups during both the "lights on" and "lights off" period. This complies with mean HP_{tot} data for the exposure period in Table 2. At the same average temperature, a "Sine" fluctuation causes a higher energy consumption than a "Cosine" fluctuation, suggesting that a within-photoperiod variation is present in the effect of low ambient temperature levels on heat production. This might be important for a generally accepted method to test the relationship between basic metabolism and ambient temperature by measuring heat production at a sequence of different temperature levels in one night or one day (e.g., Saarelaa and Vakkuri, 1982). Prinzinger (1982) already argumented that these short-term ambient temperature changes cause artificially high values for basic metabolic rate due to the testing procedure, and, consequently, cannot produce reasonable estimates. To this criticism, we might add that estimates based on this testing procedure may also be biased by a within-photoperiod variation in the effect of ambient temperature on heat production.

    In conclusion, we can state that fluctuations in ambient temperature exceeding 35°C increased activity levels. The drive for this increased activity probably is thermoregulatory in nature. At a temperature level of "15°C", heat production tended to differ between temperature fluctuation patterns. This might be due to a within-photoperiod variation in the effect of low ambient temperature levels on heat production.

ACKNOWLEDGEMENTS

CHAPTER 5:

Behavior and Thermogenesis of Group Confined Pigeons under Crowded Conditions

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ABSTRACT

Racing pigeons are transported to their release site under crowded conditions. No quantitative data on behavior and thermogenesis under these conditions are available. In a first experiment - using 'old' males - different heat exposures (26 vs. 36°C) and water deprivation (access vs. deprived) during one day had no specific significant effects on behavior or heat production measurements. However, the frequency of threatening behavior and the proportion of activity related heat production in the total heat production increased during the experimental period. Behavior patterns differed between pecked and non-pecked birds but remained rather constant during the period. Pecked birds showed more cyclic transitions between immobility and retreat, indicating their subordinate position. No extinction of pecking behavior was found. In a second experiment - using young and old male and female pigeons under 36°C conditions and with access to water - young birds were more immobile than old pigeons, whereas heat production was lower in old pigeons. Male groups had a higher activity related heat production, pecked relatively more with contact and had more head injuries than females. Again no extinction of aggressive behavior or changes in behavior patterns with time were found. Individual variation in body weight was consistent with variation in behavior patterns and head injuries: Higher body weight coincided with more threatening behavior, lower mobility, and less head injuries. The consistent pattern of behavior of pecked and non-pecked birds without obvious adaptation in time causing consistent predictable injuries indicates that a ceiling effect in adaptation is reached under these transport conditions, in which expected effects of the experimental conditions are overruled. Serious considerations must be given to transport racing pigeons under less crowded conditions, under which behavioral adaptation might be possible.

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 range from 225 to 300 cm^2 space allowance per bird. The conditions within a transport crate may be comparable to over-crowded roosting perches, where serious fights take place (Goodwin,

1983). At present, no quantitative data are available on the occurrence of (aggressive) behavior of pigeons housed under transport conditions.

Transport conditions are not only determined 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 during 12 to 24h 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 (Arad et al., 1987). It remains unclear to what extent dehydration affects the behavior of pigeons at low available space levels.

Apart from this physiological variation in transport conditions, also the social environment 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 classes: "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 behavior only occurs in "old", male groups. Murton et al. (1972a), however, adopted 6 months as the cut off value for the discrimination between non-breeding juvenile and potentially breeding adult pigeons. This suggests that the differences in behavior between "young" and "old" male pigeons are smaller than those assumed by pigeon fanciers.

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

MATERIAL AND METHODS

Design, animals and pre-experimental housing

Two experiments were performed. In each experiment, 80 pigeons were allotted to 8 groups of 10 birds. Both experiments were set up according to a 2-way factorial design.

In Experiment 1, water availability (access to water versus deprived of water) and ambient temperature (26 and 36°C) were included as experimental factors. Only adult male pigeons were used. These were kept at the university's facilities during 1 year before start of the experiment in September 1993.

In Experiment 2, conducted in October 1993, the experimental factors were age and sex. A constant temperature of 36°C was adopted to mimic the high crate temperatures which may occur during warm summer days. All groups had continuous access to water, in compliance with recently established transport guidelines in the Netherlands. At the end of the racing season, 3 weeks before start of the experiment, 40 pigeons of about 6 months old

("young") and 40 pigeons older than 1 year ("old") arrived at the university's facilities. The age classes consisted of 20 males and 20 females.

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 2 (w) x 4 (l) x 2 (h) m. Each compartment contained 4 or 5 groups of 10 pigeons. Male and female pigeons were separated, with no visual contact between male and female groups. Each morning at 0800 h, the pigeons were fed a commercial diet of whole grains (mainly peas, corn, beans and barley) in a daily ration of $\pm$ 40 g per bird with water ad libitum.

Procedure

Both experiments consisted of four periods comprising two groups of 10 pigeons. Each period started at 0800 h of Day 0, when the diet composition was changed to whole grain corn. At 1100 h of the same day, two groups were transferred to the laboratory. Here, 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 to assure correct visual identification of the individuals. Each group was confined to a transport crate (50 x 56 x 25 cm) 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 1300 h, the exposure period started. Until 1210 h of Day 1, each crate was placed on a platform in one of two climate-respiration chambers of 1.8 m^3 each, as described by Verstegen et al. (1987). Throughout the experimental period, lights were off between 1930 and 0700 h. Relative humidity level was kept at 70% at 26°C and at 44% at 36°C.

Data collection and parameters

The individual body weight (BW $\pm$ 1 g) of the pigeons was recorded at start and end of the exposure period. During the exposure period, heat production was measured by indirect calorimetry in successive 9-min intervals on the basis of the exchange of CO_2 and O_2, as described by Verstegen et al. (1987). A Hartmann and Braun Uras 3G infrared absorption CO_2 analyzer and a Servomex 1100 H paramagnetic O_2 analyzer were used. Analyzers were calibrated every 24 h, and all gas volumes were converted to standard temperature and pressure, dry. Air flow through the chambers was 10 $l \cdot min^{-1}$. Total heat production (HP_{tot}) was calculated according to Romijn and Lokhorst (1961). Using BW at start of the exposure period, HP_{tot} was expressed in $W \cdot kg^{-1}$. Activity was measured using Doppler-radar activity meters (Radar MD5, Vierpool, Amsterdam, The Netherlands), which were placed about 1 m above the crate. Each movement of the animals was interpreted as a frequency change in the reflected ultrasound waves emitted by the meters. These frequency changes were counted over the 9-min measurement interval for HP_{tot}, resulting in a 9-min activity score (# counts·9 min^{-1}). Activity related HP (HP_{ac}) was estimated per group by linear regression of 9-min HP data on 9-min activity counts. From HP_{tot} and HP_{ac}, activity-free HP (HP_{af}) was calculated.

Inside both climate-respiration chambers, a video-camera was installed about 1 meter above the crate. The camera's were connected with a monitor and a real-time recorder placed next to the chambers. During 6 periods of 30 min each (starting at 1500, 1700, 1845, 0715, 0930 and 1115 h) video-recordings were taped for behavioral analyses after completing the experiment. The resulting 48 periods for the whole experiment were analyzed in random order, using focal sampling. Each 30 min period was divided in 10 non-overlapping sampling intervals of 150 s. During each interval, the behavior of 1 pigeon was recorded and stored on a personal computer, using a software package designed for event recording (Observer: Noldus, 1993).

The adopted ethogram 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, 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 behavior 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 behavior from another bird) were added to the ethogram.

Furthermore, videotapes were used to record alterations in the location of each bird within the crate. At start of each 30-min interval, the position of the head was located in 1 of 4 quadrants, whereafter this procedure was repeated at 5-min intervals. As a measure of mobility, the total frequency of position changes between consecutive 5-min intervals was used.

After exposure, 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). In total, 4 areas were examined per pigeon: 2 ceres (white protuberances) at the base of the bill, and 2 eye surroundings. Each area was attributed a score of 0, 1 or 2. If no lesions were visible, the score for that area was "0". Minor, point-like lesions corresponded with score "1", and major, dispersed lesions corresponded with score "2". For each bird, the scores for each of the 4 areas were added to an overall lesion score, ranging from 0 (no damage) to 8 (severely damaged). Lesions were scored independently by three observers. The individual lesion score was calculated as the mean of these three observations.

Data preparation and analysis

The group was the experimental unit used in the statistical analysis. For both experiments, results were analyzed using a two-way ANOVA-model. Heat production data were analyzed for "lights on" and "lights off" separately. Prior to analysis, some behavioral elements were combined to behavioral categories. "Avoidance" included 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-min intervals before and after the dark period, the behavioral observations (frequencies or durations) were summated. Paired differences between the periods before and after darkness were averaged at group level, and analyzed by ANOVA.

Measurements on individual animals (behavioral and non-behavioral) 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 behavior data (Observer: Noldus, 1993) were analyzed 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 two observation periods (before and after "lights off") and two lesion score classes ("pecked" and "non-pecked"), observed observational 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 behavior upon the preceding behavior is calculated by the standardized residual 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 behavior sequence for values of q larger than three (Fagen and Mankovich, 1980). Kinematic path diagrams are made for visualizing behavioral frequencies and significant interactions.

RESULTS

Experiment 1

Behavioral measurements

Neither temperature nor water availability affected the behavioral measurements (Table 1). Immobility was observed during more than 63% of the observed time (Table 1). An interaction between temperature and water availability tended to be present with respect to immobility ($F(1,4) = 7.3$, $p = 0.054$). The time spent threatening ranked second, with more than 14% of the observed time. Autonomous behavior was displayed during 9 to 13% of the observed time. Grooming was a minor component of the observed behavior patterns. Pecking

frequencies were not affected by the experimental factors. The proportion of the pecks-with-contact in the total of all observed pecks (with or without contact) was 0.62, not affected by the experimental factors.

Table 1. Behavioral measurements during for Experiment 1 and 2.

Experiment 1[1]

	26°C[2,3]		36°C			
	DW	AW	DW	AW	SE	Units
Immobile	71.8	65.7	63.1	74.3	4.2	% of observed time
Threaten	16.9	17.7	19.6	14.1	3.9	% of observed time
Autonomous	9.4	13.0	11.4	9.0	3.3	% of observed time
Avoidance	0.7	1.4	2.6	1.2	0.9	% of observed time
Grooming	0.6	0.9	0.3	0.0	0.4	% of observed time
Peck, no contact	3.7	7.5	13.7	7.2	4.7	times·pigeon^{-1}
Peck, contact	2.5	4.4	9.3	3.8	3.1	times·pigeon^{-1}

Experiment 2

	Young		Old			
	♂♂	♀♀	♂♂	♀♀	SE[4]	Units
Immobile	69.2[a]	71.2[a]	57.2[b]	56.9[b]	4.4	% of observed time
Threaten	14.4	12.6	21.0	16.3	3.2	% of observed time
Autonomous	11.7	10.4	8.4	13.4	3.0	% of observed time
Avoidance	2.0	2.5	10.8	9.4	4.7	% of observed time
Grooming	1.1	1.7	0.4	1.9	1.0	% of observed time
Peck, no contact	7.4	8.2	9.2	11.5	1.9	times·pigeon^{-1}
Peck, contact	4.4	3.4	4.6	3.7	0.8	times·pigeon^{-1}

[1]   Least square means of the untransformed values are presented. ANOVA yielding statistical differences was performed using an arsin($\sqrt{\%}$)-transformation for proportions, and a $\sqrt{}$-transformation for frequencies; n = 8 for each measurement

[2]   Different superscripts within a row indicate significant differences (p ≤ 0.05)

[3]   DW: deprived of water; AW: access to water

[4]   SE: standard error of least squares means

Heat production and non-behavioral measurements

Heat production was affected by neither ambient temperature ($F=0.33$, $p=0.60$) nor 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 ($F=4.22$, $p=0.11$).

Lesion scores were not affected by the experimental factors (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, not presented in Table 1, was measured as the coefficient of variance (CV). The CV was 13.6% for water deprived groups and 26.2% for groups with access to water ($F=4.64$, $p=0.10$).

Time effects

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

In Figure 1, behavioral sequences during Experiment 1 are presented for non-pecked pigeons (lesion score 1.5 ± 0.7, mean $\pm$ s.d., $n=24$) and for pecked pigeons (4.8 ± 1.0). The observed behavior patterns were predominantly associated with aggressive interactions. The interaction-related behavioral elements are located at the left and upper side of each diagram. The immobile state was the central behavioral element in both pecked and non-pecked groups, as well before as after the dark period. In pecked pigeons, an alternation between immobility and retreat (avoidance) was present. This alternation was absent in non-pecked birds, where also the "retreat" frequency was consistently lower than in birds with high lesion scores. No direct transition was found between the left and upper side of the diagram on one hand (bowing, pecking, avoidance), and the autonomous behavioral elements at the right side of each diagram (preening, roosting, looking around).

Again, the difference between the behavioral 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, presented in Table 4, were relatively weak between behavioral and non-behavioral measurements. Nevertheless, Table 4 indicates that pigeons with a relatively high body weight at start had a lower mobility score, i.e., 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 behavior, and spent less time immobile.

Experiment 2

Behavioral measurements

Also in Experiment 2, pigeons were predominantly immobile (Table 1). Old pigeons were immobile during 57.1% of the time, young pigeons 70.2% ($F = 16.6$, $p = 0.015$). An interaction between temperature and water availability tended to be present with respect to immobility ($F = 7.3$, $p = 0.054$).

Table 2. Heat production measurements during "lights on" and non-behavioral measurements for Experiment 1 and 2.

Experiment 1[1]

	26°C		36°C			
	DW	AW	DW	AW	SE	Units
HP_{tot}[2]	4.32	4.40	4.55	4.43	0.22	$W\,kg^{-1}$
HP_{af}[3]	3.57	3.31	3.14	3.26	0.21	$W\,kg^{-1}$
HP_{ac}/HP_{tot}	0.17	0.25	0.31	0.26	0.04	
Lesions	2.5	3.1	3.6	3.2	0.5	
BW start[4]	0.548	0.552	0.545	0.565	0.030	kg
BW loss	8.5	7.7	11.8	7.9	1.61	%

Experiment 2

	Young		Old			
	♂♂	♀♀	♂♂	♀♀	SE	Units
HP_{tot}	7.51	7.18	7.26	6.79	0.15	$W\,kg^{-1}$
HP_{af}	5.80^a	5.95^a	5.18^b	5.53^b	0.16	$W\,kg^{-1}$
HP_{ac}/HP_{tot}	0.23^a	0.17^b	0.29^a	0.18^b	0.01	
Lesions	1.7^a	1.2^b	2.0^a	1.4^b	0.3	
BW start	0.506^a	0.450^b	0.530^a	0.480^b	0.016	kg
BW loss	8.7^a	8.2^a	6.1^b	5.8^b	0.85	%

[1]   Data are presented as least squares means, $n = 8$ for each measurement
[2] HP_{tot}: Total heat production
[3] HP_{ac}: Activity free heat production
[4]   BW: Body weight
       For further legenda: See Table 1.

Old pigeons tended to threaten more than young pigeons (18.7% vs. 13.5%; $F=6.05$, $p=0.07$). A similar tendency was observed with respect to avoidance behavior (10.1% vs. 2.3%; $F=5.45$, $p=0.08$). Grooming behavior tended to occur more in females (0.7% vs. 1.8%; $F=6.62$, $p=0.06$) (Table 1).

As in Experiment 1, pecking frequencies were not affected by the experimental factors. In Experiment 2, the proportion peck-with-contact in the total number of pecks was 0.35 in male groups and 0.27 in female groups ($F=13.3$, $p=0.022$).

Heat production and non-behavioral measurements

For young pigeons, HP_{tot} during "lights on" was 7.35 $W \cdot kg^{-1}$, being 0.32 $W \cdot kg^{-1}$ higher than for old pigeons ($F=4.7$, $p=0.10$) (Table 2). This was not due to a higher activity-related HP, as indicated by the higher HP_{af} (5.88 vs. 5.35 $W \cdot kg^{-1}$; $F=9.9$, $p=0.034$). For male and female groups, HP_{ac} during "lights on" was 1.90 respectively 1.25 $W \cdot kg^{-1}$ ($F=32.8$, $p=0.005$). 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). For none of the HP_{tot}-related measurements, interactions were present.

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 attained on average 1.7 ($F=1.7$, $p=0.26$).

Females had lower body weight than males (0.465 vs. 0.518 kg; $F=20.9$, $p=0.01$). Start weight of old and young birds was 0.518 kg and 0.465 kg, respectively ($F=5.41$, $p=0.08$). The relative body weight loss of young pigeons was 8.5%, compared with a loss of 6.0% for old pigeons ($F=17.5$, $p=0.014$). The weight loss variation within groups was affected by neither sex ($p=0.81$) nor age ($p=0.70$).

Time effects

Also in Experiment 2, the occurrence of aggressive behavior did not extinguish with time (Table 3). Differences between the first and last part of the exposure period were smaller than in Experiment 1 (Table 3).

The behavioral sequences during Experiment 1, presented in Figure 1, are representative for the behavioral sequences observed during Experiment 2.

Individual variation in measurements

The body weight at start of exposure had a predictive value for the subsequent behavior during exposure (Table 4). Pigeons with the highest body weight at start were better capable of maintaining their position in the crate, as indicated by a negative correlation between the body weight at start and the mobility score during exposure ($r=-0.42$). A high body weight at start was also associated with a increase in the time spent threatening ($r=0.27$), and with lower lesion scores ($r=-0.32$).
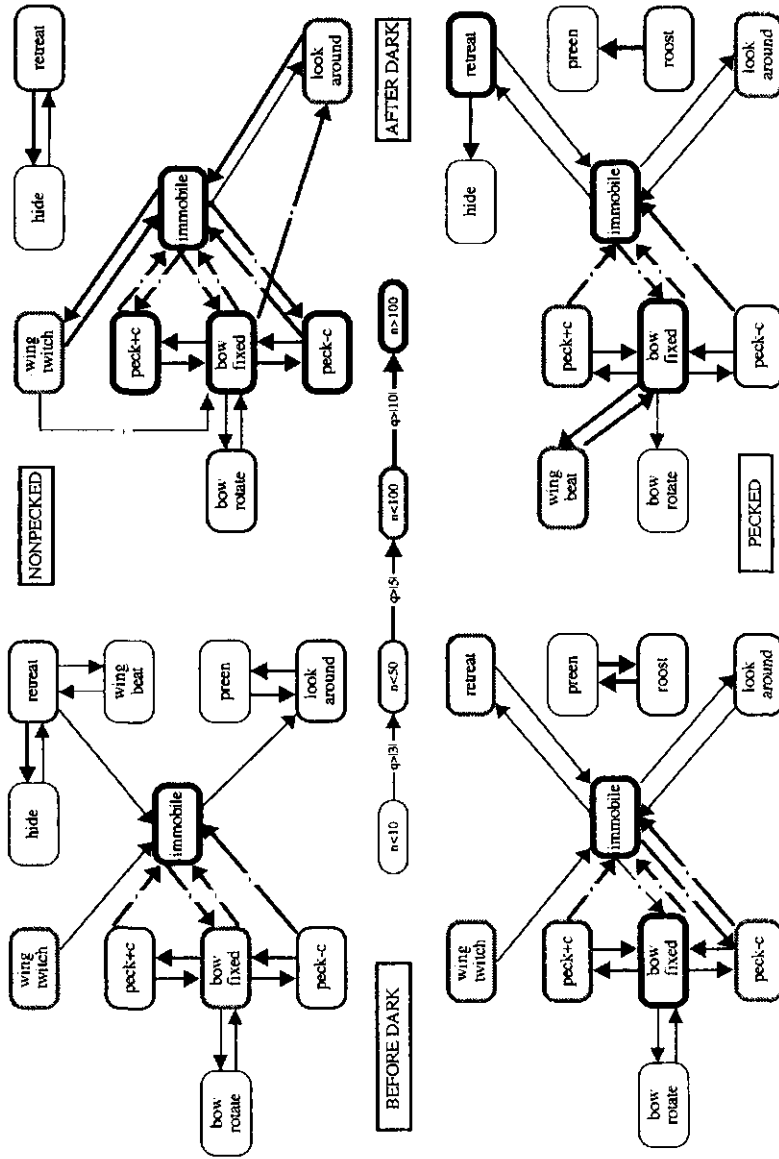
Figure 1. Behavior sequences during Experiment 1 before and after "lights off". Within each of 8 groups, behavior recordings of 3 birds with highest lesion score (pecked) and 3 birds with lowest lesion score (non-pecked) were selected, and pooled (24 birds per diagram).
"q" = strength of association; "n" = frequency.

Table 3. Comparison between mean observations made during the first (before "lights off") and last (after "lights off") part of the exposure period ($\pm$ SE, n=8)

	Experiment 1			Experiment 2			
	BL[1]	AL[2]	p-value[3]	BL	AL	p-value	Units
HP_{ac}/HP_{tot}	0.21 $\pm$0.03	0.30 $\pm$0.02	**	0.21 $\pm$0.06	0.23 $\pm$0.05	ns	
Immobile	72.1 $\pm$2.44	65.3 $\pm$2.29	*	65.3 $\pm$3.78	62.0 $\pm$2.32	ns	% of observed time
Threaten	12.1 $\pm$1.55	22.0 $\pm$2.07	**	13.6 $\pm$2.50	18.5 $\pm$1.52	ns	% of observed time
Autonomous	12.8 $\pm$2.29	8.6 $\pm$1.45	ns	12.6 $\pm$1.67	9.2 $\pm$0.91	ns	% of observed time
Peck, no contact	3.2 $\pm$0.96	4.8 $\pm$1.21	ns	4.1 $\pm$0.78	5.0 $\pm$0.53	ns	times·pigeon^{-1}
Peck, contact	1.8 $\pm$0.51	3.3 $\pm$0.95	ns	2.2 $\pm$0.39	1.8 $\pm$0.24	ns	times·pigeon^{-1}

[1]   BL: Means for the time interval before "lights off"
[2]   AL: Means for the time interval after "lights off"
[3]   p-value of the paired t-test on differences between BL and AL (ns: $p > 0.05$; *: $p \leq 0.05$; **: $p \leq 0.01$).

Lesion scores provided a retrospective indication for the behavior displayed by the pigeon during exposure. A high lesion score was positively correlated with a high mobility score ($r = 0.44$), and negatively correlated with threatening behavior ($r = -0.37$). Pigeons with a high mobility score, hence with an unstable position in the crate, displayed less threatening behavior ($r = -0.54$), less autonomous behavior ($r = -0.44$), and pecked less ($r = -0.53$ for pecking without contact).

As shown in Table 4, body weight loss was a weak retrospective indicator for the behavior during exposure. Pigeons who showed much threatening behavior tended to have a lower body weight loss ($r = -0.29$), whereas birds with a high mobility score tended to have a higher body weight loss ($r = 0.26$).

Table 4. Spearman rank correlations on pooled individual measurements, ranked within groups, for Experiment 1 (above the diagonal) and Experiment 2 (below the diagonal). Correlations in **bold** print indicate significant correlations (p ≤ 0.05) (Krauth, 1993)

	BW_s[1]	BW_l[2]	Lesion	Mobsco[3]	Threat	Immobile	Auton.	$Peck_{nc}$[4]	$Peck_c$[5]
BW_s	\	0.07	0.03	-0.25	0.18	-0.23	0.19	0.17	0.10
BW_l	0.08	\	0.16	-0.06	-0.25	0.16	0.02	-0.30	-0.21
Lesion	-0.32	-0.14	\	0.16	-0.14	0.06	0.00	0.04	-0.10
Mobsco	**-0.42**	0.26	**0.44**	\	-0.32	0.27	-0.25	-0.22	-0.06
Threat	0.27	-0.29	**-0.37**	**-0.54**	\	**-0.80**	0.02	**0.71**	**0.56**
Immobile	-0.10	0.23	0.20	**0.40**	**-0.56**	\	**-0.44**	**-0.62**	**-0.40**
Auton.	0.22	-0.16	-0.18	**-0.44**	0.25	**-0.48**	\	0.01	-0.05
$Peck_{nc}$	0.27	-0.21	-0.23	**-0.53**	**0.60**	**-0.41**	**0.40**	\	**0.75**
$Peck_c$	0.19	-0.13	-0.09	-0.21	**0.44**	-0.24	0.23	**0.75**	\

[1] Body weight at start
[2] Body weight loss
[3] Mobility score
[4] Peck without contact
[5] Peck with contact

DISCUSSION

In this paper, two experiments on pigeons housed under crowded conditions are presented. First, the persistence of aggressive behavior patterns with time will be discussed. Next, the relation between the observed behavior patterns and the initial body weight of the pigeons will be dealt with. Finally, the relation between heat production, body weight loss and behavior patterns will be discussed.

Behavior patterns: persistence of aggressive behavior with time

The persistence of the predominance of aggressive behavior patterns with time was demonstrated in both experiments (Figure 1, Table 3). This fits well into the general framework that no fixed hierarchy develops within groups of pigeons in a pigeon loft (Heinroth and Heinroth, 1949). In paired aggression tests involving male pigeons, however, the number of aggressive attacks decreased with time once a dominant-subordinate relationship was established (Cross and Goodman, 1988). In our 23-h experiments, adopting a group size of 10 pigeons, no decrease in aggression levels with 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 in solitary confinement. Introduction of a higher ranking pigeons in the observation chamber, however, resulted in a clear decrease in the test performance of the low-ranking bird, whereas the test performance returned to the previously established levels after removal of the high-ranking individual.

Table 4 also showed that pigeons with a high mobility score, so with an unstable position in the crate, were more at risk of having a high lesion score. Pecked pigeons did not alter their behavioral strategy with time (Figure 1). Hence, the positive correlation between lesion scores and mobility scores is not a consequence of an increase in avoidance behavior once the pigeons were injured. This complies with Cross and Goodman (1988), who found that body movements provoke more aggressive attacks than immobility. The aggression preventing effect of immobility may also explain the predominance of this type of behavior (Table 1, Figure 1). Since aggressive encounters have a cost for both winners and losers in terms of energy cost and injuries (Cross and Goodman, 1988), immobility is the most sensible strategy to adopt under the crowded conditions present in both experiments.

Under crowded conditions occurring during pigeon transport, the on-going character of the aggressive encounters has major implications for the injuries (or lesion scores) that will finally result. An increase in the duration of the transport, so a lengthened 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 start: the relation with subsequent behavior patterns

In both Experiment 1 and Experiment 2, the pigeon's rank within a group as determined by the body weight at start of exposure had a predictive value for the behavior displayed during exposure. Pigeons with the highest weight rank in a group had a more stable position in the crate, spent more time threatening, and had a higher pecking frequency (Table 4). This is in agreement with the higher frequency of aggressive encounters in high ranking birds observed in a pigeon loft (Diebschlag, 1941).

Also in free-ranging feral pigeons, the behavior within a group was associated with the

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). Central birds had a higher food intake at a lower activity-related energy cost compared with pigeons in the periphery of the feeding flock.

In general, correlations with body weight at start were stronger in Experiment 2. Comparison of the start weight of the old males in Experiment 1 with the corresponding group in Experiment 2 shows a difference of on average 35 g per pigeon (Table 2). Also, total heat production was clearly lower in Experiment 1. In our opinion, these differences can be attributed to the pre-experimental treatment. Experiment 1 was performed with pigeons that were housed at the University during 1 year before start of the experiment. They had limited possibilities for physical exercise since they were housed in a compartment of 2 x 4 x 2 m, and frequent feed remainders indicated that they were fed at or nearly at the ad libitum level. Experiment 2, however, used pigeons that had participated in racing contests until about 3 weeks before start of the experiment.

Obviously, the trained pigeons of Experiment 2 were better comparable to the very competitive situation among the feral pigeon population studied by Murton et al. (1972b).

The relation between behavior patterns, heat production and body weight loss

Pigeons housed at high stocking density are not able to decrease activity levels during heat exposure. From a thermoregulatory viewpoint, 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 behavior was expected for water exposed pigeons exposed to 36°C. The higher body weight loss in water deprived birds at 36°C compared to 26°C (Table 2) indicates an increase in evaporative water loss. Hence, 36°C may be well above the upper critical temperature of pigeons housed under crowded conditions (Mount, 1974). Since an increase in activity at 36°C increases not only heat production, but also the burden 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 significance levels were not attained, the activity-related heat production was highest in water deprived groups at 36°C (Table 2).

Combining the high activity related heat production with the equally high results for pecking frequencies and threatening behavior (Table 1), our results comply with a remark made by Marder (1983). During a heat acclimation period prior to the actual measurements, pigeons had to be housed separately, since aggressive behavior was well developed at temperature levels exceeding 50°C.

In Experiment 2, young pigeons had a higher activity-free heat production than old pigeons (Table 2). As indicated by the lower body weight at start, young pigeons were not yet fully grown. Hence, the higher metabolism due to growth may explain the higher heat production levels in young groups (Blaxter, 1989). The higher metabolism in young pigeons may also be related to the 2.5% higher body weight loss in young 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 was rarely observed. This was not surprising, since the total observation time for each pigeon was only 15 min, and the total observable time during "lights on" was more than 11 h. Hence, the behavioral observations do not permit a quantitative analysis of possible differences in water intake between age groups. However, the time spent immobile was 13% higher in young groups (Table 1), which may represent a general tendency of young birds to be less active, movements to and from the drinking trough included.

Also in Experiment 2, males had a higher activity-related heat production than females (Table 2). As indicated by the time spent threatening (Table 1) and by the lesion scores (Table 2), this might be explained by the stronger tendency in males to become involved in aggressive interactions. This is in agreement with observations made by Diebschlag (1941) in a pigeon loft. Fabricius and Jansson (1963) came to a similar conclusion. When observing paired pigeons in the pre-incubation time, bowing and attacking was displayed more by males. This probably results in an increased activity-related heat production due to muscular activity.

CONCLUSIONS

From Experiment 1, we can conclude that neither temperature nor water availability had a specific significant effect on behavior or heat production. The frequency of threatening behavior and the proportion of activity related heat production in the total heat production increased with time. Between pecked and non-pecked birds, differences in behavior patterns were present, and these differences remained rather constant during the experiment. In general, no extinction of aggressive behavior patterns was found.

The results from Experiment 2 showed that young birds were more immobile than old pigeons, whereas heat production was lower in old pigeons. Male groups had a higher activity related heat production, pecked relatively more with contact and had more head injuries than females. Again, no extinction of aggressive behavior or changes in behavior patterns with time were found. Body weight at start of the experiment had a predictive value for the subsequent behavior in the crate. A higher body weight was associated with more threatening behavior, a lower mobility, and less head injuries.

The consistent pattern of behavior of pecked and non-pecked birds without obvious adaptation in time indicates that, under crowded conditions, a ceiling effect in adaptation is reached. Under these transport conditions, expected effects of the experimental factors are overruled. Hence, the transport of racing pigeons under less crowded conditions must be given serious consideration.

CHAPTER 6:

Effect of Crate Space Allowance and Sex on Behavior and Thermogenesis of Racing Pigeons

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ABSTRACT

Behavior and thermogenesis of racing pigeons were studied in relation to space allowance and sex. During a 23-h period, 20 groups consisting of either males or females were confined to transport crates at one of 5 space allowance levels. The time pigeons spent immobile decreased from 85% at 210 cm^2 to 37% at 630 cm^2. This was compensated by an increase in autonomous and grooming behavior. An increase in space allowance was accompanied by a decreased activity related heat production, and by a decrease in head injuries at the bill base and around the eye. Compared to the reference level of 350 cm^2 per pigeon, a space allowance of 630 cm^2 had a sparing effect on the occurrence of injuries. The risk of having major injuries was increased 9-fold for pigeons at 210 cm^2, and 5-fold at 280 cm^2. A level of 420 cm^2 was risk-neutral. The effects of space allowance levels on activity related heat production, behavior and lesion scores were present in both male and female pigeons. Male pigeons, however, had a higher activity related heat production, which was probably related to threatening behavior. Males were 3 times more at risk of having major injuries than females.

INTRODUCTION

Racing pigeons (Columba livia) are group confined in crates during transport for homing contests. In the Netherlands, the time between placing the pigeons in the crate and opening the crates at the release site may take 12 to 72 h. During this period, the birds are at risk of exposure to high ambient temperature levels (Gorssen et al., 1993). Group confinement allows for aggressive social interactions within a group. At communal roosting sites, pigeons are known to defend a space around themselves. This may cause serious fights, which result in selective pecking at areas around the base of the bill and around the eyes (Goodwin, 1983). Group confinement in a crate can be comparable with an overcrowded roosting site. The resulting aggressive behavior may not only yield lesions at the attacked areas, but may also cause increased activity within a group, and, consequently, increased activity related heat production. Most frequently, pigeons are transported in groups consisting of either males or

females. Regarding group behavior of only male or female pigeons, little is known so far. Moreover, no information is available concerning the effect of space allowance in a crate on group behavior. Actual transport guidelines adopted by the Dutch racing pigeon fanciers organisation (NPO), range from 225 cm^2 per bird for transport durations below 24 h to 300 cm^2 per bird for 72 h-transports. No physiological nor behavioral base is available for these guidelines. To improve transport conditions, more insight is needed in the consequences of the space allowance for the pigeon.

In the present study, the effect of space allowance per pigeon on behavior, heat production and head injuries of groups consisting of either males or females was investigated. The objective of this experiment was to verify whether differences in behavior between sexes and between space allowance levels existed, and, whether they can explain possible differences in heat production and injuries.

MATERIAL AND METHODS

In total, 100 adult male and 100 adult female pigeons were randomly assigned to 20 groups of 10 birds of the same sex. The experiment was set up according to a 2-way factorial design. Space allowance per bird (5 levels: 210, 280, 350, 420 or 630 cm^2 per bird) and sex (male or female) were included as experimental factors. From 7 months before start of the experiment onwards, pigeons were housed in an outdoor half-open aviary under natural photoperiod, humidity and temperature. The pigeons were assigned to one of 4 compartments (2 x 4 x 2 m). Each compartment contained 5 groups of males or females. Between the male and female groups, no visual contact was possible. Each morning at 0800 h, the pigeons were fed a commercial diet of whole grains (mainly peas, corn, beans and barley) in a daily ration of $\pm$ 40 g per bird with water ad libitum.

Procedure

Each of 10 experimental periods started at 0800 h of Day 0, when the diet composition was changed to whole grain corn. At Day 1, the morning feeding consisted again of corn only. At 0830 h of the same day, 2 groups were transferred to the laboratory. Here, a description of each bird was made (colour, spots). If the appearance of birds within a group was similar, ink marks were sprayed on the back. Each group was confined to a transport crate with aluminium sides, wire grid top and hard plastic grid floor. The inner dimensions of the crate varied according to the space allowance level. For each level, a crate length-width ratio of 1.3 was maintained. No feed was available, but a drinking trough of 35 cm long was attached to the outside of the crate. At each space allowance level, pigeons had access to the full length of the drinking trough. The continuous availability of water is in compliance with Dutch transport guidelines, recently established by NPO. (unpublished observations).

At 1030 h of Day 1, the measurement period started. Until 0945 h of Day 2, each crate was placed on a platform in one of two climate-respiration chambers of 1.8 m^3 each, as described by Verstegen et al. (1987). Lights were off between 2030 and 0730 h. Ambient temperature was set at 36°C, while relative humidity was kept at 66%. These high values for both temperature and relative humidity mimic the crate microclimate during the warm summer months.

Data collection

The individual body weight (BW $\pm$ 1 g) of the pigeons was recorded at start and end of the measurement period. During this period, heat production was measured by indirect calorimetry in successive 9-min intervals on the basis of the exchange of CO_2 and O_2, as described by Verstegen et al. (1987). A Hartmann and Braun Uras 3G infrared absorption CO_2 analyzer and a Servomex 1100 H paramagnetic O_2 analyzer were used. Analyzers were calibrated every 24 h, and all gas volumes were converted to standard temperature and pressure, dry. Air flow through the chambers was about 10 l·min^{-1}. Heat production (HP) was calculated according to Romijn and Lokhorst (1961). Using BW at start, HP was expressed in W·kg^{-1}. Activity was measured using a Doppler-radar activity meter (Radar MD5, Vierpool, Amsterdam, The Netherlands), which was placed about 1 m above the crate. Each movement of the animals was interpreted as a frequency change in the reflected ultrasound waves emitted by the meter. These frequency changes were transformed into counts over the 9-min measurement interval for HP, resulting in a 9-min activity score (# counts·9 min^{-1}).

Inside both climate-respiration chambers, a video-camera was installed about 1 meter above the crate. The camera's were connected to a monitor and a real-time recorder placed next to the chambers. During 4 periods of 30 min each (starting at 1200, 1600, 2000 and 0800 h) video-registrations were taped for behavioral analyses after completing the experiment. Due to technical failure, one "1600" period was lost in two male groups, one at 210 cm^2 and one at 350 cm^2. The resulting 78 periods for the whole experiment were analyzed in random order. Each 30 min period was divided into 6 non-overlapping sampling intervals of 180 s. During each interval, the focal sampling procedure was adopted. The behavior of 1 pigeon was recorded and stored on a personal computer, using a software package designed for event recording (Observer: Noldus, 1993).

The adopted ethogram 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, all according to Goodwin (1983). Furthermore, immobile (standing still, feathers tight, rump patch covered), retreat (displacement as a consequence of aggressive behavior of another bird), hiding (lowering the head and hiding it under tail or breast of another pigeon), observing (looking around with head movements in both the horizontal and vertical plane), walking (displacement not due to aggressive behavior from another bird) and exploring (exploratory pecking at the sides, the top or the bottom of the crate) were added to the ethogram.

After exposure, lesions around the base of the bill and around the eyes were scored by 1 person. In total, 4 areas were examined per pigeon: 2 ceres (white protuberances) at the base of the bill, and 2 eye surroundings. Each area was attributed a score of 0, 1 or 2. If no lesions were visible, the score for that area was "0". Minor, point-like lesions corresponded with score "1", and major, dispersed lesions corresponded with score "2". For each bird, the area scores were summated to an "eye" and "bill" score separately (ranging from 0 to 4), and to an overall lesion score, ranging from 0 (no damage) to 8 (severely damaged).

Data preparation and analysis

Based on 9-min observations of total heat production (HP_{tot}) and activity scores, activity related HP (HP_{ac}) and activity free HP (HP_{af}) were calculated by linear regression of HP_{tot} on activity scores for each group. Mean HP_{tot}, HP_{af} (both in $W \cdot kg^{-1}$), and the proportion HP_{ac}/HP_{tot} (%) were calculated for each photoperiod separately ("lights on" or "lights off"). Subsequently, these parameters were statistically analyzed by a 2-way ANOVA.

For lesion scores and behavioral observations, "group" was the experimental unit for 2-way ANOVA. Prior to ANOVA, some behavioral elements were clustered. "Threatening" included wing twitching and the bowing display, "Autonomous behavior" consisted of observing, walking, roosting and exploring, "Grooming" covered preening, shaking and stretching, and "Pecking" included both pecking with and without contact. Durations, when expressed as a proportion of the observed time, as well as other proportions (e.g., HP_{ac}/HP_{tot}) were transformed prior to ANOVA by means of a arsine-square root transformation. Frequencies were square root-transformed prior to ANOVA.

Based on overall lesion scores, all birds were classified as "major injuries" (score 2 or higher) or as "minor injuries" (score of 0 or 1). Within each treatment combination, data for both groups were combined. Using logistic regression, odds ratios for having "major injuries" were calculated. An odds ratio (OR) is the measure of association between exposure (space allowance and sex) and health status. If there is no association the OR will have the value 1. The greater the deviance from 1, either larger or smaller, the stronger the association. If the OR is less than 1, the factor might be considered as a sparing factor. The factor may be seen as a risk factor if the OR is larger than 1. If the value 1 is outside the limits of the confidence interval, then the "sparing" or "risk" property of the factor is significant at the given confidence level (Martin et al., 1987).

In this experiment, the OR measures whether or not having major injuries is more common in the exposed group compared to the non-exposed group. The non-exposed situation was considered 350 cm^2 space allowance per bird for females. This is the maximal space allowance level applied in Dutch practice for the sex with least injury problems (unpublished observations). The methods applied in logistic regression use the same general principles as those used in linear regression, but the outcome variable is binary (major-minor injuries) instead of continuous (Hosmer and Lemeshow, 1989). Sex, space allowance and their interaction were initially included as regressors in the logistic regression model. Since the

interaction did not contribute significantly to the model, the final model included main effects only.

RESULTS

Heat production, body weight

Total heat production during "lights on" was 5.24 W·kg^{-1} for males and 4.79 W·kg^{-1} for females (F(1,10) = 16.4, p = 0.002) (Figure 1.a). Activity related heat production accounted for this difference in HP$_{tot}$. The proportion of HP$_{ac}$ in HP$_{tot}$ during "lights on" was lower in females than in males (13.4 vs. 18.8%, F(1,10) = 30.9, p ≤ 0.001) (Figure 2).
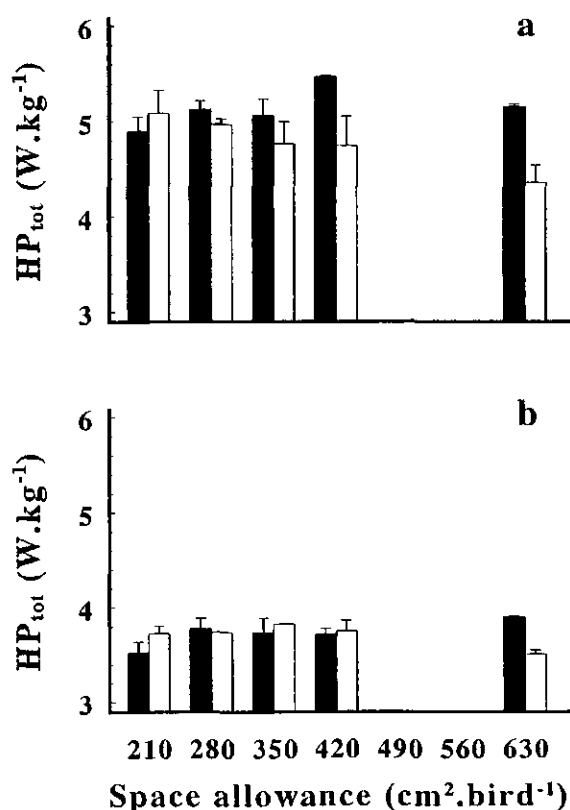
Figure 1. Total heat production (HP$_{tot}$) during "lights on" (part **a**) and "lights off" (part **b**) (mean ± SEM, n = 2). "Females" (□); "males" (■).

Consequently, HP_{af} was similar for males and females (4.25 vs. 4.14 W·kg^{-1}, F(1,10)=1.91, p=0.20). Figure 1.a shows that HP_{tot} decreased with increasing space allowance in females, but not in males. However, this interaction effect between sex and space allowance on HP_{tot} was not significant (F(4,10)=2.1, p=0.155). The proportion of HP_{ac} in HP_{tot} was affected by space allowance (F(4,10)=8.8, p=0.003) and by the interaction between sex and space allowances (F(4,10)=7.9, p=0.004). The proportion of HP_{ac} in HP_{tot} decreased with increasing space allowance, except for male groups at 420 cm^2 (Figure 2).

During "lights off", values of HP_{tot}, HP_{af}, HP_{ac}, and of the ratio between HP_{ac} and HP_{tot} were lower than during "lights on". Moreover, the differences between treatments were reduced during "lights off". During "lights off", mean HP_{tot} and HP_{af} were 3.79 and 3.49 W·kg^{-1}, respectively, and were both unaffected by the experimental factors (Figure 1.b). Similarly, space allowance affected neither HP_{ac} (F(4,10)=0.8, p=0.55) nor the ratio between HP_{ac} and HP_{tot} (F(4,10)=0.9, p=0.52) during "lights off". Despite the lower activity levels during "lights off", HP_{ac} was higher for males than for females (0.35 vs. 0.26 W·kg^{-1}, F(1,10)=7.3, p=0.02) and also the proportion of HP_{ac} in HP_{tot} was higher for males (9.2 vs. 6.8%, (F(1,10)=7.9, p=0.019).

Body weight at start was 518 ± 5 g (mean ± SEM, n=10) for male groups and 501 ± 5 g for female groups. Body weight loss during exposure was 4.4 ± 0.3 and 4.0 ± 0.2% for males and females, respectively.

Behavior, lesion scores

As shown at the top of Figure 2, the time spent "immobile" decreased sharply with increasing space allowance (F(4,10)=20.3, p≤0.001). The spent "immobile" did not depend on sex (F(1,10)=0.03, p=0.87). The decrease from more than 80% "immobile" at 210 cm^2 towards less than 40% at 630 cm^2.bird^{-1} was accompanied by a significant and sharp increase in autonomous behavior (F(4,10)=14.4, p≤0.001) and grooming behavior (F(4,10)=24.0, p≤0.001). Females spent more time "grooming" than males (5.1 vs. 3.1%, F(1,10)=5.1, p=0.047). The time spent "threatening" was 10.7% for males and 6.4% for females (F(1,10)= 7.6, p=0.02). Figure 2 suggests that the outcome of the statistical analysis was strongly affected by the value of 20.4% threatening, observed for male groups at 420 cm^2. The correspondence between the time spent threatening and the ratio HP_{ac}/HP_{tot}, apparent from Figure 2, was confirmed by a Pearson correlation of 0.66 (p≤0.01).

The total pecking frequency was on average 2.9 times·3-min^{-1}, affected by neither space allowance nor sex. In Figure 3.a and 3.b, the mean frequency per 3-min interval is presented for pecking with and without contact. Pecking without contact was not affected by the experimental factors, whereas pecking with contact was slightly affected by space allowance (F(4,10)=3.7, p=0.042). The proportion of the total "peck with contact"-frequency to the total pecking frequency, shown in Figure 3.c, decreased with increased space allowance (F(4,10)=30.2, p≤0.001).
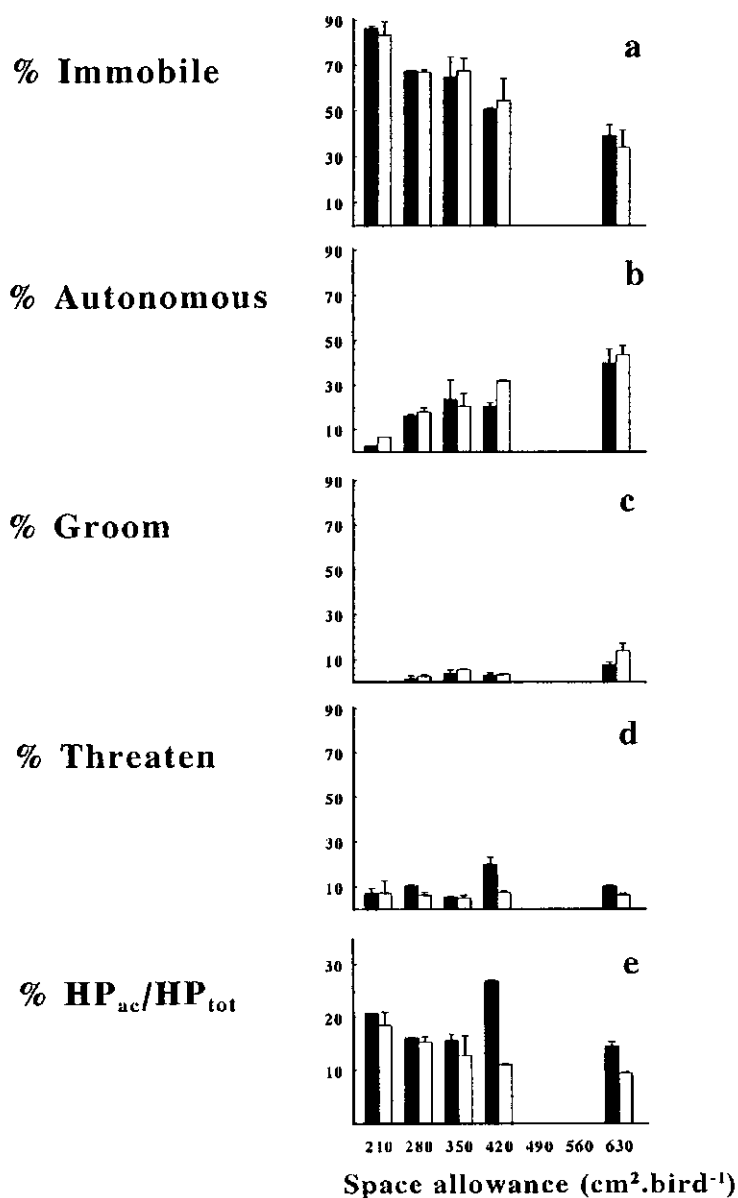
Figure 2. Treatment means of four behavior classes, expressed as a proportion of the total observed time (part a to d), and the ratio of the activity related heat production (HP_{ac}) to the total heat production (HP_{tot}) during "lights on" (part e) (mean ± SEM, n= 2). "Females" (□); "males" (■).
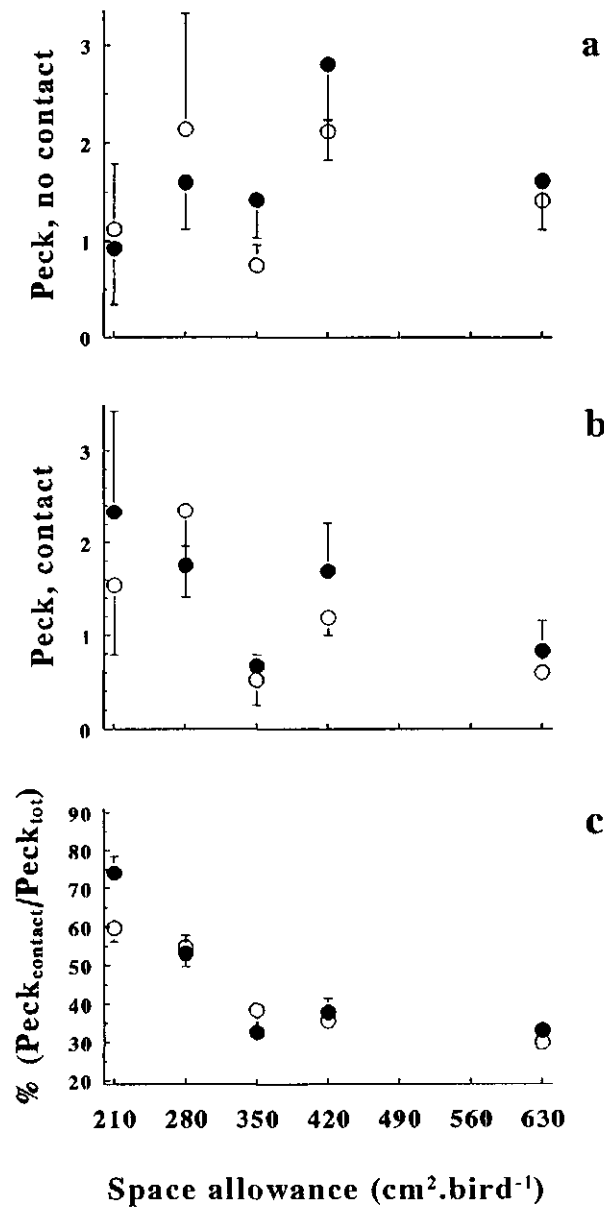
Figure 3. Mean pecking frequencies (counts·3-min^{-1} ± SEM) without contact (part **a**) or with contact (part **b**), and the proportion of the total frequency "pecking with contact" to the total pecking frequency (part **c**). "Females" (○); "males" (●).

Overall lesion scores decreased with increasing space allowance ($F(4,10) = 15.5$, $p \leq 0.001$), and were lower for female groups compared to male groups ($F(1,10) = 10.9$, $p = 0.008$). On average, the overall score was 2.1 for males and 1.5 for females. The difference between sexes was mainly attributable to a higher eye lesion score in males. The eye lesion score was 1.32 for males and 0.85 for females ($F(1,10) = 8.7$, $p = 0.015$), whereas bill scores were 0.80 and 0.64 ($p = 0.22$). Based on group means, Pearson correlation coefficients between the "peck with contact" proportion and eye respectively bill lesion scores were 0.72 respectively 0.79, whereas with the overall lesion score a correlation of 0.83 was found (all $p \leq 0.05$).

Table 1. Frequency distribution for overall lesion scores per treatment combination (number of birds out of 20 pigeons).

Lesion	Sex	Space allowance					Injuries	
		210	280	350	420	630	Minor	Major
0-1	♂♂	2	3	9	9	13	$\Sigma\delta\delta = 36$	
	♀♀	4	6	14	14	19	$\Sigma♀♀ = 57$	
2-3	♂♂	10	13	9	9	6		
	♀♀	11	12	4	6	1		
4-6	♂♂	8	4	2	2	1		$\Sigma\delta\delta = 36$
	♀♀	5	2	2	0	0		$\Sigma♀♀ = 43$

Odds ratio's

As shown in Table 1, a large variation in lesion scores was present between individuals within treatment combinations. Even at the highest space allowance level, pigeons with major injuries were found. In male groups, more birds with major injuries were found. These findings are also reflected in the odds ratio's, presented in Figure 4. As indicated by an OR of 3.2 with a 95% confidence interval excluding 1, males were more at risk of having major injuries than females ($p \leq 0.05$). Space allowance of 210 and 280 cm^2 per bird increased the risk of having major injuries by respectively 8.8 and 5.2 times compared to the reference value of 350 cm^2 per bird ($p \leq 0.05$). Increasing space allowance to 420 cm^2 dit not affect the risk of being injured, whereas a space allowance of 630 cm^2 significantly spared birds from having major injuries ($p \leq 0.05$). An inverse dose (space allowance) - response (injuries) relationship was apparent.
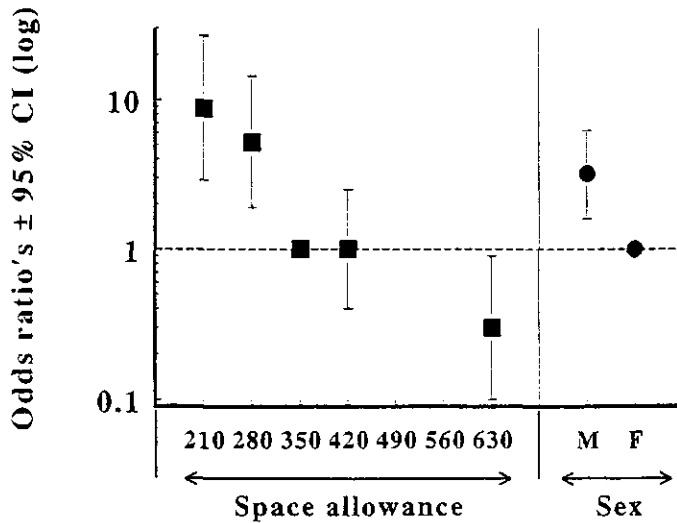
Figure 4. Log-plot of odds ratio's with 95% confidence intervals for having major injuries. Reference values were "350 cm²" for space allowance, and "female" for sex.

DISCUSSION

In the present study, differences in behavior between sexes and between space allowance levels were examined in relation to differences in heat production and lesion scores. The influence of space allowance and sex will be discussed separately.

Space allowance per pigeon

The effect of space allowance is characterized by an apparent contradiction between the different types of measurements: both the proportion of HP_{ac} in HP_{tot} and the time spent "immobile" decreased with increasing space allowance (Figure 2). This is apparently linked to the increase in autonomous and grooming behavior with increasing space allowance. As shown in Figure 2, the decrease in individual "immobile" behavior is compensated for by autonomous and grooming behavior, two types of behavior which are not related to the action of an adjacent pigeon. Hence, the time spent "immobile" is an indicator for neighbour-dependent behavior, probably aimed at the avoidance of aggressive interactions. This is consistent with findings by Cross and Goodman (1988), who demonstrated that silent, immobile target birds evoked the least number of aggressive attacks. At low space allowance levels, each observation of aggressive behavior on one individual probably has a higher energetic cost in terms of HP_{ac} which is measured at a group level.

Also a lack in correspondence was observed between lesion scores and the occurrence of aggressive interactions (threatening, pecking). However, the ratio between the frequency of pecks with contact and the frequency of all pecks (contact and no contact), plotted in Figure 3.c, is equivalent to the probability that an observed peck will result in contact. Since this probability decreased with increasing space allowance, it complies with the intuitive expectation that at low space allowance levels, where the average distance between birds is smaller, pecking with contact is more likely to occur, resulting in higher lesion scores. Hence, lesion scores appear to be a reliable and easily applicable indicator for the preceding behavior in the crate.

Furthermore, lesion scores provide an easy, retrospective base for the quantitative assessment of health risks associated with housing conditions such as space allowance and group composition. As shown in Table 1 and Figure 4, they allow for the calculation of odds ratio's and their confidence intervals, a helpful tool for both the evaluation of present transport conditions, and the design of new transport guidelines. The reference situation, used for the OR calculation, depends on the targets put forward. In this experiment, we showed that an increase in space allowance to the upper boundary of 350 cm^2 used in practice to date significantly reduces the risk of having major injuries. The significance for the pigeons of having injuries is twofold. First, there is the discomfort of the pecking injury itself. Second, observations in the loft after exposure indicate that pigeons with major eye lesions are more susceptible to eye infections, resulting in partial sight loss.

From a thermoregulatory point of view, it is noteworthy that the body weight loss is low, and that also the variation in body weight loss within a group, measured as the coefficient of variance, was not affected by the space allowance. Under the high temperature level of 36°C adopted in the experiment, the weight loss data indicate that water was accessible to all pigeons, even at low space allowance levels. Hence, continuous water availability is an effective measure for preventing dehydration due to heat exposure (Arad, 1987), even at high stocking densities. However, the cost of water intake, measured as the number of pecks received, is probably higher at low space allowance levels. Due to the shorter inter-individual distance, the aggression eliciting effect of body movements may increase the number of pecks (Cross and Goodman, 1988) when passing other pigeons on the way to and from the drinking trough.

The effect of sex

Male pigeons had a higher activity related heat production during "lights on", although the behavioral observations provide no clear explanation for this difference (Figure 2). The concurrence of an exceptionally high HP_{ac} and an equally extreme duration of threatening behavior in male groups at a 420 cm^2 space allowance indicates that the consistent difference in HP_{ac} between sexes is mainly due to differences in threatening behavior, too subtle for detection with a camera placed above the pigeons. As pointed out by Goodwin (1983), sex differences are present in the self-assertive bowing display. In this type of display, the pigeon turns around its own axis while cooing with an air filled, pulsating crop. Whereas the male

pigeon makes a complete turn, the female does not. Furthermore, observations at the loft indicate that the pumping of the crop is more explicit in male pigeons. The muscular exercise needed for both the displacement of the body and the pulsatile filling of the crop may explain for the increased HP_{ac} in male pigeons. In the experimental setting, where pigeons were observed from the top, the observation of this behavior, and not to mention the qualitative interpretation, was impossible.

Also the behavior leading to higher lesion scores in males may contribute to the higher HP_{ac}. First, the pecking force may be higher in males, which had on average 17 g higher body weight at start. Second, Goodwin (1983) states that the fighting movements are adapted to fighting on ledges, and attempting to hurl the opponent off them. For this purpose, the attacking pigeon tries to get a firm grip on the orbital skin around the eye, after which a violent pulling and pushing takes place. The resulting lesion score is probably higher in this type of fighting compared with a normal pecking bout with short contact. Although Goodwin (1983) did not report on sex differences in this peck-with-grip behavior, our data suggest that it occurs more in male groups than in female groups. As indicated by the odds ratio, the risk of having major injuries was 3 times higher in males compared to females.

However, it should be noted that there is a considerable individual variation in behavior, and in the resulting lesion scores. The background for this variation is not clear. It implies, however, that low group means of e.g., lesion scores hide the presence of birds within that group with considerable lesions. In this respect, the data presented in Table 1 are most illustrating: even at the highest space allowance level, 7 out of 20 male pigeons were classified as having major injuries. So, even a space allowance level of 630 cm^2 was not sufficient to prevent all pigeons from having major injuries. Put into a general framework, this finding illustrates the basic question to be answered before guidelines aimed at the improvement of pigeon welfare can be put forward: Should guidelines focus on an acceptable average outcome, disregarding individual variation, or should they focus on the most vulnerable individual within a group?

CONCLUSIONS

This study showed that an increase in space allowance per pigeon is accompanied by a decrease in activity related heat production, and an increase in autonomous and grooming behavior. Compared to the maximal space allowance level of 350 cm^2 per pigeon actually applied in practice, levels of 210 and 280 cm^2 increase the risk of having major injuries by respectively 8.8 and 5.2 times. At the experimental temperature of 36°C, body weight loss was low and not affected by space allowance level. This indicates that the continuous availability of water is an effective means to prevent dehydration due to heat exposure, even at high stocking densities. The effect of space allowance levels on activity related heat production, behavior and lesion scores were found in both male and female pigeons. Male

pigeons, however, had a higher activity related heat production, and were three times more at risk of having major injuries.

GENERAL DISCUSSION:

General Discussion

DISCUSSION OUTLINE

Columba livia, known as the price-winning racing pigeon, as the street-dwelling feral pigeon, or as the cliff-bound rock dove, is one of the few bird species occupying a place in the centre of the human spotlight. Limiting an elaboration of its popularity among man to the scientific environment, the pigeon is a widely appreciated model animal in psychology, in physiology, and, above all, in the study of bird orientation and navigation. However, the vast amount of literature available on pigeons proved to be insufficient to tackle a basically simple question, the general objective of this thesis research, rooted in problems encountered by pigeon fanciers in the field: How should transport conditions be altered to minimize the strain enforced upon the pigeon?

By nature and by name, the "general discussion" of a thesis ought to relate the main features of the different chapters to a common denominator. The bi-focal approach in methodology (thermoregulation vs. behavior) and the project's emphasis on practical relevance did not provide a clear-cut concept for such a denominator. Unlike literature, where a classic by Oskar and Käthe Heinroth, published in 1949, offered a most useful view angle. As a leitmotiv for this general discussion, I shall adopt the central theme of their detailed comparative study on the behavior of rock doves and racing pigeons in a pigeon loft:

Bei unsern langjährigen Beobachtungen der Haustauben im Vergleich zur Felsentaube ergab sich eine völlige Übereinstimmung der Verhaltensweise von Wildform und Zuchtrasse.

This chapter will root in the premise that the behavioral similarity between racing pigeons and rock doves can be extended to a physiological correspondence. The results presented in Chapter 1 to 6, obtained on racing pigeons housed under completely artificial conditions, will be discussed within an ecological reference frame. This framework will be constructed of available literature on the habitat, the behavior and the breeding biology of rock doves and feral pigeons. The discussion will focus on the role of time regarding two important characteristics of racing pigeons housed under transport conditions: Thermoregulation and behavior. With respect to thermoregulation, time related effects of water availability and the role of light in thermoregulatory characteristics will be considered. For behavior, emphasis will be placed on the inability of pigeons housed under transport conditions to adapt their behavior patterns with time in order to minimize the burden placed upon them by the physical and social environment, as well in terms of impaired thermoregulation as in terms of major head injuries and the occurrence of mortality.

The practical implications of the research covered by this thesis will be the last topic treated in the general discussion. Prior to a conclusive overview of the main research findings, the relative nature of an objective and quantitative risk assessment procedure will be discussed.

ROCK DOVES AND FERAL PIGEONS: LIVING ON THE EDGE

Hospitality is not the most typical feature of the rock dove's natural environment. In this paragraph, information on the geographical distribution of the rock dove, on its breeding biology and ecology will be linked with data on mortality rates. With respect to mortality, the discussion will not only deal with rock doves and feral pigeons, but also with a literature record on the fate of racing pigeons stranded in a rock dove colony.

The geographic distribution of the rock dove includes cold, humid regions as well as hot, arid habitats. It ranges from Western Europe to China and the northern part of India, and extends in southern direction to Senegal, Sudan, Arabia and Sri Lanka (Glutz and Bauer, 1980). The literature cited in this chapter is limited to the European nominate, Columba l. livia, and to studies on feral pigeons in this region.

The natural habitat of the rock dove is linked with the nest-site on rock-faces, not only coastal (Cramp, 1985), but also deep inland (Géroudet, 1982). The nest-sites of the feral pigeon, living commensally with man, possess the same structural elements offered by the nest-sites of the rock dove: For man ill accessible nests in more or less darkened caves, in rock cavities or on ledges high above the ground (Glutz and Bauer, 1980). A pair bond is generally for life, during which the same nesting site is occupied, even in non-breeding periods (Glutz and Bauer, 1980). Feral pigeons have 7 to 9 clutches of 2 eggs pro year, of which only 3 to 6 are successful (Murton et al., 1972a). Both in rock doves (Murton and Clarke, 1968) and feral pigeons (Murton et al., 1972a), breeding success during the winter months is low due to a higher desertion percentage and a higher nest mortality in young from those eggs that did hatch. Annual mortality rates in rock doves in Yorkshire were estimated at 30% in adults, with a first-year mortality of 85% (Murton and Clarke, 1968). Feral pigeons in the Manchester docks had a yearly mortality rate of 33% in adults, with a juvenile mortality rate of 43% pro annum between leaving the nest and becoming adults (Murton et al., 1972a). Data on death causes are rare, especially in fledged birds. Prey samples from raptors, however, provide insight in the final destination of some of disappeared birds. In coastal regions of Northern Ireland, rock doves constitute 35.2% of the total prey of the peregrine falcon (Falco peregrinus). Inland, feral pigeons are also a popular prey for peregrines, as indicated by a prey share of 20.7 to 35.2% in Germany (Cramp, 1982), nicely illustrated by the pair of peregrine falcons breeding at the Dom of Cologne, in the heart of the city (unpublished personal observations). If present in the same habitat, also goshawks (Accipiter gentilis) and Lanner falcon (Falco biarmicus) are important predators (Cramp, 1982). Not only during daytime, but also at night pigeons are at risk of being preyed upon, as indicated by prey data of the eagle owl

(Bubo bubo), also inhabiting rocky inland habitats (Glutz and Bauer, 1980).

Lost racing pigeons, eager to socialize with either feral pigeons or rock doves, have poor survival opportunities, as indicated by the gradual disappearance of racing pigeons from the rock dove colony they had joined (Murton and Clarke, 1968). By means of the foot rings, the owners of four dead racing pigeons found dead in the colony could be traced back, thus providing one of the rare literature data on the fate of racing pigeons that do not return to their loft. Three out of four pigeons were young birds. One disappeared from the loft at the age of 10 weeks, a second did not return from a training flight, and the third got lost during its first race (Murton and Clarke, 1968).

As will have become clear, feral pigeons and rock doves live under harsh conditions, and are subject to a high selective pressure. The highest survival opportunities have those pigeons that are best fitted ecologically to occupy their respective niche. In this respect, adequate thermoregulatory effector mechanisms are essential. These are subject of the next paragraph.

TIME AND THERMOREGULATION

The importance of water availability

Backgrounds for heat tolerance

The original geodistribution of the rock dove is not known (Cramp, 1985). However, both historical and physiological indicators suggest that the ancestors of the contemporary birds evolved in a hot, arid region. From 4.500 B.C. onwards, domestication occurred in the Near East. In Central-Europe, the earliest relics date from about 100 A.D., probably following migration of the Romans (Glutz and Bauer, 1980). Furthermore, studies in heat stress revealed that heat-acclimated pigeons are outstanding in their thermoregulatory capacities (Arad et al., 1989). In hot and arid regions, where water evaporation is high but water resources are scarce, water intake is presumably associated with a number of costs: A transfer cost (energy, water, predation) due to the flight to and from water resources, and a higher risk of predation while drinking at the water source. Hence, a selection is likely in favor of those pigeons that adopt water economizing strategies and (or) can survive a considerable degree of dehydration, as the combined result of water deprivation and duration of heat exposure.

As demonstrated in this thesis (Chapter 1 to 4), also non-acclimated racing pigeons, show a remarkable tolerance to heat exposure during water deprivation, especially with respect to the ability to endure water loss. In Chapter 3, it was demonstrated that also the capacity to restore body water reserves within a short period is noteworthy, and comparable to research on heat-acclimated pigeons in Israel (Arad et al., 1987).

However, the environmental conditions under which the predecessors of the racing

pigeons used in our experiments were raised are quite opposite to the moderately cold and humid climate present in the Netherlands. Therefore, two hypotheses can be postulated to explain the heat tolerance present in Dutch racing pigeons, as demonstrated in our experiments:

1. The trait "heat tolerance" had a limited distribution in the original Dutch pigeon population from which the present racing pigeon population was bred. The higher flight losses in young birds during their first racing season may reflect a selection mechanism. In the transport procedures adopted prior to this research, continuous water supply was not compulsory. Combined with heat exposure, an environmental pressure was present in favour of pigeons tolerant to heat and dehydration. This way, the proportion of heat tolerant pigeons in the Dutch racing pigeon population may have been increased in the successive generations.

2. The original genetic capacity to endure heat and dehydration, present in the base population, was maintained when Columba livia occupied new, less arid and colder regions. The influence of a selective transport environment is small, compared to other selection agents such as problems in navigation or orientation, and culling by the pigeon fancier when the homing performance of the bird is not satisfactory.

Both hypotheses seem plausible, and they may be complementary in contributing information to a valid explanation. E.g., the homing performance of a pigeon, mentioned as a culling criterion in the second hypothesis, is defined by the flight speed and by the ability to orientate and navigate correctly. From Chapter 1 it seems plausible that the homing performance may also depend on the capacity to withstand adverse transport conditions, thus representing a link between both hypotheses. For selection on a trait, however, variation in that trait within the population is a prerequisite. As shown in the next paragraph, this prerequisite seems to be fulfilled for the trait "heat tolerance", assessed with a time-dependent combination of water deprivation and heat exposure.

Individual variation in thermoregulatory capacity

In Chapter 1, 4 and 5 of this thesis it was demonstrated that a considerable variation in heat tolerance, or, more general, "thermoregulatory capacity" was present between animals. E.g., the variation in body weight loss within groups increased at exposure temperatures above 32°C. In Chapter 1, it was demonstrated that the coefficient of variance in body weight loss within groups was not affected by temperature in water deprived pigeons. But expressing the within-group variation as the standard deviation revealed a significant increase in variation above the upper critical temperature. It should be noted, however, that body weight loss is a somewhat polluted indicator for thermoregulation, since it includes both droppings and evaporative water loss.
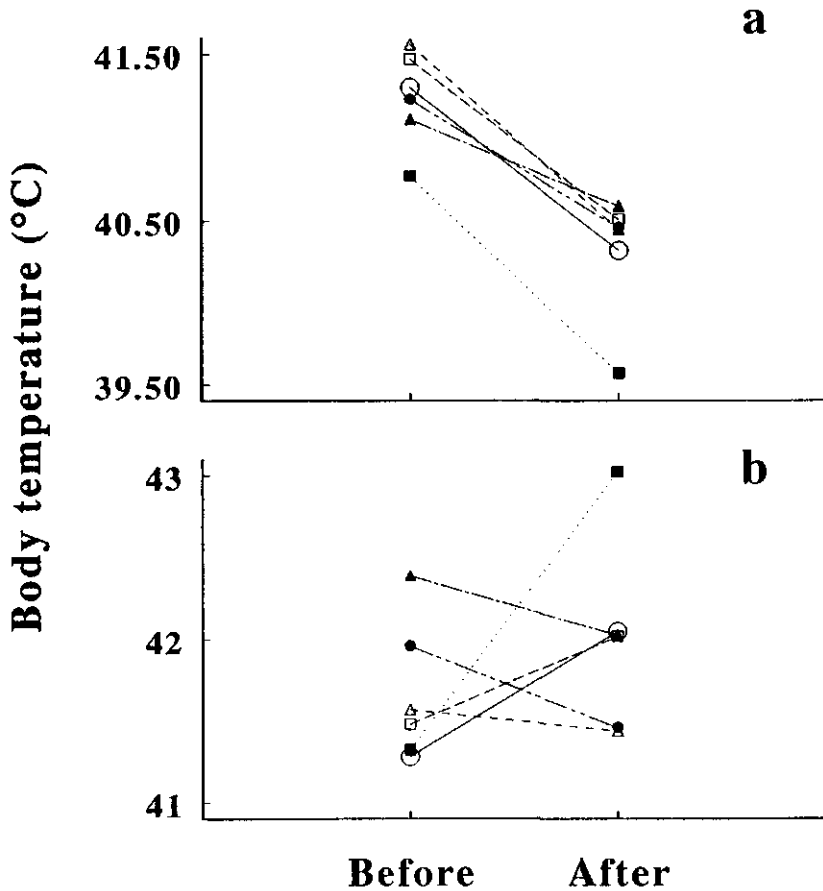
Figure 1. Mean body temperatures during "lights on" of six pigeons exposed to 37°C with access to water (part a) or deprived of water (part b) before and after the onset of hyperthermia. Each symbol represents one pigeon. See Chapter 3 for further detail.

Deep body temperature (T_b) data were presented as group means in Chapter 3. In Figure 1, all six individual observations per water availability level at 37°C are presented. In this figure, two intervals are compared: one "before" and one "after" the onset of hyperthermia observed during the dehydration period of this experiment (see Chapter 3). During both intervals, lights were on. Figure 1 confirms the deductions made from the findings on body weight loss: The variation in thermoregulatory capacity increases when both a thermal (temperature) and an osmotical (water deprivation) stressor are imposed upon the pigeons. Figure 1.a shows that the ranking of the pigeons according to T_b within treatments is relatively

stable between both intervals when the pigeons have access to water. The quantitative measure of this stability in rank, the Spearman rank correlations between the pigeon's rank in T_b "before" and "after" confirms this observation ($r = 0.94$, $p \leq 0.01$). For water deprived birds, however, there is no relation between the pigeon's rank in T_b "before" and "after" the onset of hyperthermia ($r = -0.54$, $p = 0.27$) (Figure 1.b). Indirectly, this indicates that indeed an individual variation is present in the pigeon's capacity to cope with a combined thermal and osmotical stressor.

However, it remains unclear to what extent this variation in thermoregulatory parameters truly reflects a genetic variation in thermoregulatory capacities. Although Chapter 1 showed that relative body weight loss is likely to be higher in birds with higher body weight, one can rightfully argue that body mass also depends on environmental factors. Furthermore, as indicated by rank correlations between body weight loss and behavior in Chapter 5, and by the generally observed variation in behavior between pigeons within a group, the variation in thermoregulatory capacities can at least partially be explained by individual differences in behavior.

But, irrespective of the genetic or environmental background of the variation in thermoregulatory capacity, the existence of individual variation within a group of pigeons has major practical implications for the construction of transport guidelines: Should they focus on the weakest link in the chain, or rather on the average strength of all links?

The perception of light: the predictive link between time and temperature

Thermoregulation is a dynamic process. Heat production and heat loss, hence also their end product body temperature, vary with time, not only within but also between days. Throughout this thesis, differences in thermoregulation and behavior between light and darkness has been stressed repeatedly. Thermoregulatory parameters in pigeons show a distinct day-night variation. Following the onset of darkness, a decrease in heat production, body temperature, heat loss and overall thermal conductance takes place. Also the temperature sensitivity of heat production is lower during the night (Aschoff and Pohl, 1970; Graf, 1980b).

For thermoregulation in homeotherms, heat production is the starting point. Heat production results from energy expenditure. Energy, or food, feeds the "Fire of life" (Kleiber, 1961). Ample evidence is found in literature concerning the major role of energy intake and energy utilization in evolution. Energy spent for thermoregulatory processes cannot be used for growth, reproduction or the deposition of body reserves. Selection will favor those organisms that succeed best in obtaining energy from the environment and that minimize energy loss to the environment, resulting in an energy surplus required for maintenance, for growth, and, above all, for reproduction.

As demonstrated in Chapter 2, both high and low temperatures may represent an energetic cost. The combination of heat exposure and water deprivation results in an increase

in the coefficient of heat strain. Under natural conditions, however, especially in regions with a moderate to cold climate, the energetic cost of low ambient temperatures is more important. For each downward deviation from a thermoneutral temperature, an energy cost has to be paid in terms of an increased heat production. An energetic cost that can be quantified. In Chapter 2, this cost was represented by the coefficient of cold strain (c_s), the increase in heat production for each °C decrease in temperature below thermoneutrality, or the slope of the line relating ambient temperature and heat production below the lower critical temperature.

Under natural conditions, the fluctuation in ambient temperature within a 24-h period is, on average, fairly predictable by means of light: Highest values are obtained in the afternoon, followed by a gradual decrease towards the end of the night and early morning. Besides variation in ambient temperature, Chapter 2 and 3 showed that a within-photoperiod variation is also present in body temperature, in heat production and in evaporative water loss. Furthermore, a within-photoperiod variation is also present in the coefficient of cold strain (see Chapter 2). Two distinct maxima in the coefficient of cold strain (c_s) were found, one immediately before and one immediately after the dark period, with a minimum during the dark. Also during the late part of the dark period, an increase in c_s was observed.

The question can be raised: What is the adaptive value of a within-photoperiod variation in c_s? The physiological significance and adaptive value of the within-photoperiod variation in c_s might be related to energy economy. However, the estimates in Chapter 2 were obtained under artificial conditions, not under free-ranging conditions. Also, the adaptation period of only one night to the 13 L: 11 D light scheme might have been too short. Therefore, there is ample reason to be cautious when concluding that a similar within-photoperiod variation in c_s is present in free living birds. It is, however, striking that Cramp (1985) explicitly mentions the habit of feral pigeons to sun (i.e., to gain heat by solar radiation) on cold, sunny early mornings. A time of day which, in our experiments, corresponded with a maximum in sensitivity to cold (Chapter 2), during which it is energetically most profitable to increase the effective temperature.
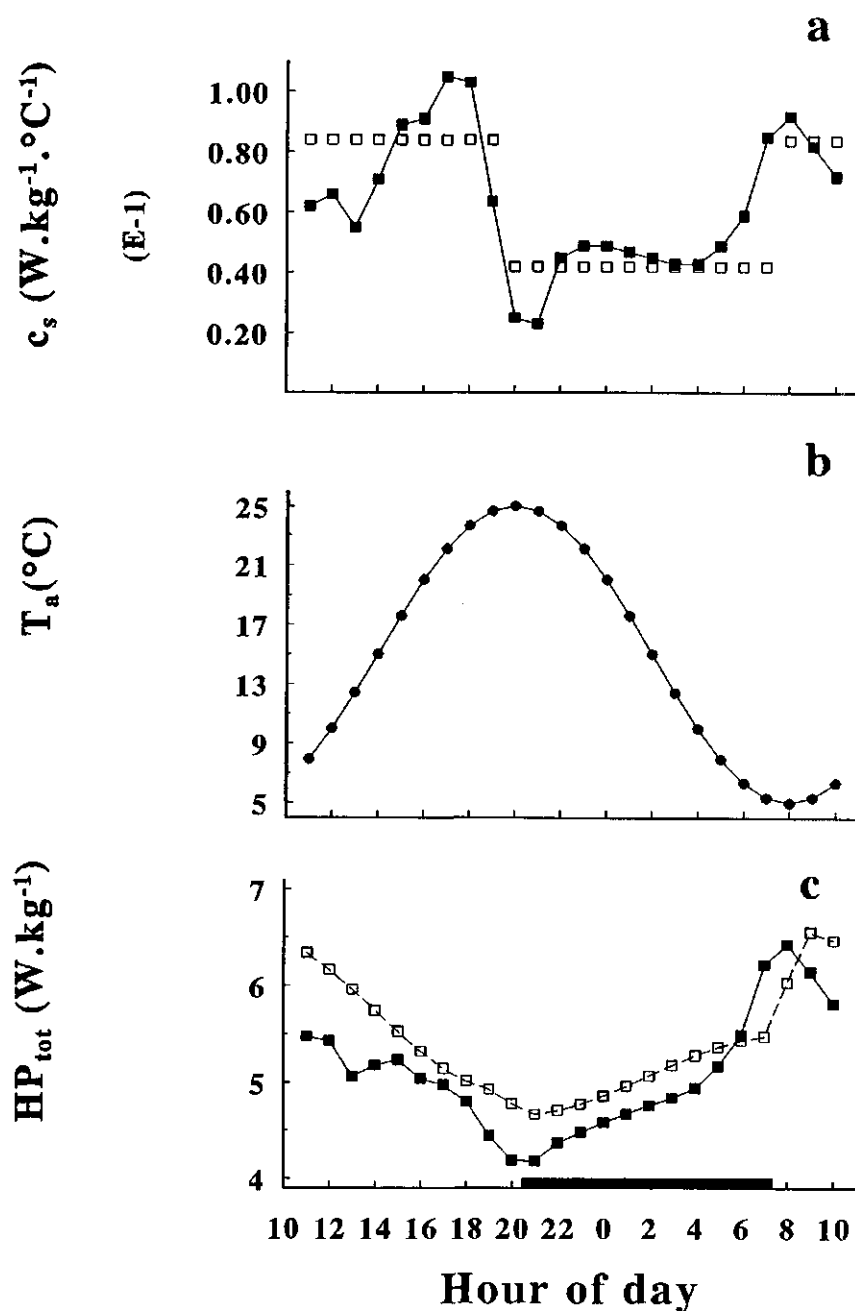
Figure 2. The coefficient of cold strain (c_s; part **a**), variable between and within photoperiods (■) or only variable between photoperiods (□) and ambient temperature (T_a; part **b**) used for the calculation of the corresponding total heat production (HP_{tot}; part **c**). "Lights off" (▬▬▬).

Table 1. Estimated mean daily heat production[1] from the temperature pattern presented in Figure 2 at two different variation patterns in c_s.

Value for c_s	Heat Production ($W \cdot kg^{-1}$)		
	Mean	Minimum	Maximum
Variable[2]	5.08	4.19	6.43
Li/Da[3]	5.41	4.67	6.56

[1] Heat production was estimated using a constant reference value of $4.4\ W \cdot kg^{-1}$. This represents the estimated heat production at $31\,°C$ using the regression equation for water deprived birds, presented in Chapter 1.

[2] Diurnal variation according to Figure 2.a.

[3] During "lights on" and "lights off", c_s was constant at $0.084\ W \cdot kg^{-1} \cdot °C^{-1}$ and $0.042\ W \cdot kg^{-1} \cdot °C^{-1}$, respectively.

The within-photoperiod estimates of c_s presented in Chapter 2 provide a tool to evaluate the adaptive value of a within-photoperiod variation in c_s by calculating the daily energy expenditure (or average heat production). In Figure 2, 2-h estimates for c_s from Chapter 2 are presented. These estimates resulted from the simple linear regression of heat production on ambient temperature levels between 15 and $31\,°C$ (see Chapter 2). Estimates of c_s in Figure 2.a are based on the heat production data pooled over both water treatments. A sinusoidal approximation of normal outside temperature fluctuations was used for calculating the impact of within-photoperiod variation in c_s on daily energy expenditure. The average temperature was $15\,°C$, with an amplitude of $10\,°C$ (Figure 2.b). The variation pattern in c_s, presented in Figure 2.b, was compared with the situation where only a between-photoperiod variation in c_s is present (Table 1). The calculated average daily heat production is $5.41\ W \cdot kg^{-1}$ for the situation where only a between-photoperiod variation in c_s is present. In the scenario involving a within-photoperiod variation in c_s, heat production is only $5.08\ W \cdot kg^{-1}$ (Figure 2, Table 1). For a pigeon of 450 g, this difference of $0.33\ W \cdot kg^{-1}$ represents a daily increase in energy expenditure of about 13 kJ.

In conclusion, a flexible c_s, involving both a between- and within-photoperiod variation, appears to have indeed an adaptive value for free living pigeons.

TIME AND BEHAVIOR

Aggression within a crate: An on-going conflict between birds

Pigeons readily learn to deal with new environments. Direct evidence for this well-developed ability to learn and to adapt is found in experimental psychology. Indirect, ecological proof is provided by the wide geographical distribution of <u>Columba livia</u>, both in man-made and in natural environments.

Starting from this typical property, also in the transport setting adopted in this thesis, behavioral adaptations were expected, aimed at a decrease in adverse effects of the physical (hyperthermia, dehydration, mortality) and the social (head injuries) environment. Specifically, a reduction in aggression related behavior would have made sense: Threatening, pecking, avoidance, etc., since these types of behavior increase locomotor activity, and are positively correlated with heat production and head injuries (Chapters 5 and 6). As shown in Chapter 5, aggressive behavior is well developed from the start of the experiment onwards, and does not extinguish in the course of the 23 h exposure period.

From Chapter 5 and 6, several conclusions can be drawn. First, since the pigeons used in our experiments all had racing (hence transport) experience, previous exposure to similar conditions did not lead to sufficient behavioral adaptations. Second, if aggression levels would decrease with time, our measurement period of 23 h was too short to record such a decrease. From a pilot experiment, however, it was derived that even after 4 days of confinement to a crate, aggression levels showed no sign of decrease. Third, all experiments were performed with groups of pigeons that had been housed in the same loft compartment prior to the experiment. So, pigeons confined to the same crate were familiar to each other. Fourth, even at less crowded conditions (630 cm^2), aggression still is well developed, although the physical repercussions in terms of head injuries are considerably less when compared to lower space allowance levels.

In addition, reduction in group size seemed to have no preventive effect on the occurrence of aggression: In Chapter 3, pigeons had to be removed from a group of only 6 pigeons due to severe head injuries. And extending the group size from 10 pigeons to 20 pigeons at a space allowance level of 280 cm^2 did not result in significant differences in neither aggression nor activity-related heat production (Gorssen and Koene, 1994).

From the preceding, it appears that group confinement of pigeons to a crate environment provides a social condition under which aggressive behavior overrules normal behavior patterns and learning mechanisms aimed at the avoidance of hyperthermia and physical damage. This may comply with early observations by Diebschlag (1941), who found no difference in learning ability between high and low ranking pigeons in a loft when the pigeons underwent the learning procedure alone, but a strongly reduced learning ability in low ranking birds in the presence of high ranking birds. But this correspondence with literature does not answer the basic question: Why is aggressive behavior so predominant within a crate?

A nesting site of one's own: Finders keepers, losers weepers

Messenger-pigeons and racing pigeons earn their name by their capacity to home. Rock doves and feral pigeons, however, are sedentary birds throughout the year, with a flight range of no more than 10 km, and usually less (Cramp, 1985). As mentioned before, pair bonds are generally for life, and the nesting site is occupied and defended year round, also during non-breeding periods (Glutz and Bauer, 1980). It is the male who selects and occupies a suitable nesting location (Heinroth and Heinroth, 1949). As indicated by the comparison of activity-related heat production and behavior, threatening behavior is more displayed by males than by females (Chapter 5 and Chapter 6). The bowing display, the major component of threatening behavior, is not only linked to territorial struggles within a group, but also to sexual behavior at the breeding colony, where it is more a kind of "showing off" for the partner's eye (Glutz and Bauer, 1980).

Keeping the strong territorial attitude of feral pigeons and rock doves in mind, it seems plausible that the predominance of aggressive behavior in group confined racing pigeons is linked to a high adaptive value of the occupation or the defense of a good roosting or nesting territory. In terms of increased survival and reproduction, it pays off to conquer and to defend a good roosting or nesting site, because in a natural or semi-natural habitat good spots are probably very scarce. For the qualification "good" nesting site, several criteria have to be met. In general, these criteria also pertain to roosting sites:

1.   not subject to competition from other species;
2.   attractive from a thermoregulatory point: Sheltered from wind, humidity and extreme temperature fluctuations;
3.   low risk of predation for the parents at the nest or during the flight route to and from the site;
4.   low risk of predation or loss of eggs or non-fledged young;
5.   sheltered from disturbance;
6.   low "fixed costs" pertaining to the transport of food and water: A short flight distance to food and water resources;
7.   good overview of the surrounding area (see also 3. and 5.).

It can be expected that selection will favor pigeons, in casu males, that succeed in conquering and defending sites that meet these criteria. From studies on feral pigeons, it appears that body weight is an important indicator for individual breeding success. Only 27% of the feral pigeon population in the Manchester docks was breeding (Murton et al., 1972a). Breeding males had a 12% higher body weight than non-breeding males, and breeding females had 5% higher body weight (Murton et al., 1974). The value of body weight as an indicator of social rank was already indicated by Murton et al. (1972b), who reported that heavy birds generally have a higher food intake at a lower activity cost. This was confirmed in Chapter 5 of this thesis, where it was demonstrated that relatively heavy birds are more successful in

maintaining a stable position in a transport crate.

In conclusion, the predominance of aggressive behavior among racing pigeons within a transport crate seems to result from a strongly developed and well preserved behavioral pattern aimed at the conquest and defense of a nesting or roosting site. The artificial crate environment, with no possibility of escape by flying away, and the persistence of aggressive interactions with time result in adverse effects on the pigeon. Since changing the pigeon's crate behavior is not possible, adaptations of the transport environment such as increasing space allowance are the sole alternative to reduce the adverse effects experienced by racing pigeons on transport.

IMPLICATIONS FOR PRACTICE - WITH PRACTICAL ASSUMPTIONS

Quantitative risk assessment: An objective tool...

In Chapter 6, the risk of having major injuries was quantified in relation to sex and space allowance. This association is expressed with the Odds Ratio (OR), which approximates how much more likely (or unlikely) it is for the outcome (e.g., having major injuries) to be present among those with exposure to a factor, than among those without exposure to that factor (e.g., high stocking density). The OR is a rough estimate of the Relative Risk and can be interpreted in the same way as the Relative Risk. Direct estimation of the RR is generally preferable, i.e., if it is in accordance to the study design. However, in logistic regression it is rather complicated to calculate confidence intervals for the RR's in contrast to those for the OR's. Since a confidence interval is needed in the statistical testing of a hypothesis, OR's are often presented as an indication for the Relative Risk.

Not only categorical data, such as lesion scores, can be used for risk quantification. With respect to continuous variables, such as body weight loss or body temperature, the same procedure can be adopted if a suitable decision criterion (cut-off value) is available. In Figure 3, odds ratios are presented for the risk of water deprived birds to be dehydrated after exposure using data from Chapter 1 (Figure 3.a) and Chapter 4 (Figure 3.b). In Chapter 1, dehydration at 31°C was chosen as a reference, being the experimental temperature level just below the upper critical temperature. A body weight loss of 10% was adopted as a decision criterion. In Chapter 4, body weight loss was measured during the second part of a 48 h period. Due to droppings, this resulted in higher basic body weight loss. A constant temperature exposure was adopted as a reference vs. the fluctuating temperature exposure.

As shown in Figure 3, odds ratio calculations confirm the results obtained by ANOVA and 2-phase linear regression. For Chapter 1, the odds ratio increased dramatically above the upper critical temperature, ranging from 4.9 at 33°C to 2080 at 37°C. Data at 39°C could not be used in the estimates, since all birds were dehydrated following exposure.
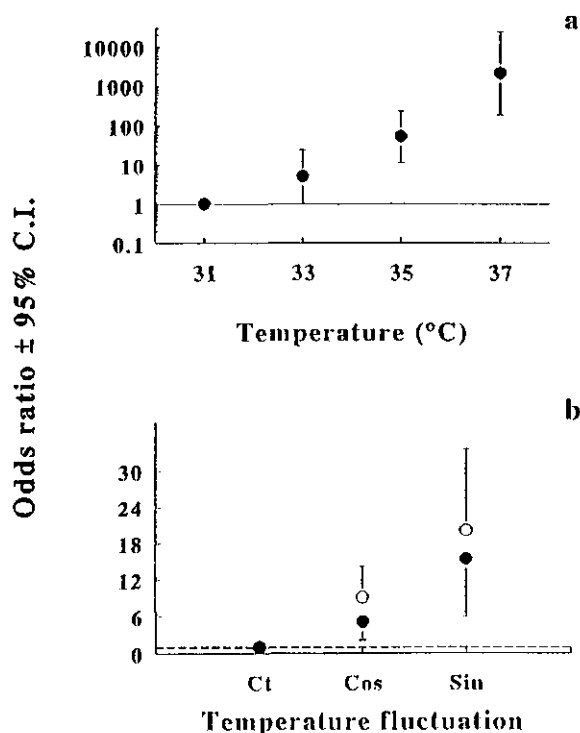
Figure 3. Odds ratio's with their 95% confidence intervals for losing body weight after exposure to temperatures above 31°C (part a) and after exposure to fluctuating temperatures compared with constant temperature exposure (average temperature of 35°C) (part b). Cut off-value of 13% (○) or 14% (●) of dehydration.

... but what about the decision criteria?

In Chapter 4, where also birds found dead were included as "dehydrated", the odds ratio for dehydration following exposure to a "Sine" pattern was 20.2, for a "Cosine" pattern it was only 9.1. At least when a cut off-value of 13% is adopted. When the tolerated degree of dehydration is increased by 1%, the crude OR's, not comprising terms of interaction or confounding, decrease to respectively 15.4 and 5.0 (Figure 3.b).

The former exercise illustrates a basic property of the adopted quantitative risk assessment procedure: The absolute importance of the outcomes is relative to the assumptions and decision criteria made.

Another illustration: The left side of Figure 4 represents the effect of space allowance on the odds ratios for having major injuries, already presented in Chapter 6. In this Chapter,

350 cm^2 was chosen as a reference value, departing from the situations presently encountered during transport. Practical (read: Financial) considerations underlie this choice of the reference value. Under the present regulations, it is unrealistic to expect that transporters will adopt the space allowance level of 630 cm^2. Although, as shown in Figure 4, increasing available space from 350 to 630 cm^2 significantly reduces the risk of having major injuries. At least, when considered at a confidence level of 95%, but this is no longer the case at a 99% confidence level.
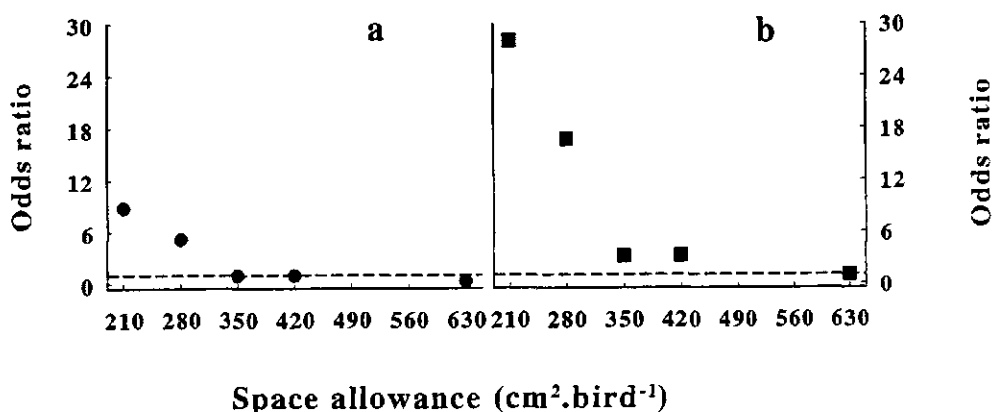
Figure 4. Odds ratio's for having major injuries at various space allowance levels with 350 cm^2 as reference (part **a**) or 630 cm^2 as reference (part **b**).

Furthermore, what deviation from normal is considered acceptable? Lesion score 1 or 2? A body weight loss of 10%? Or 15%? What is "normal"? As indicated in Chapter 1, expressing body weight loss relative to the weight at catch increases the weight loss after exposure by 9%. What parameter should be used? Body weight loss, or body temperature? When is the parameter measured? What is the diagnostic validity (sensitivity and specificity) of the test? E.g., at a high stocking density of $210 \text{ cm}^2 \cdot \text{bird}^{-1}$, major shifts in behavior patterns can be expected (Chapter 6). They will, however, not be detected by scoring eye and bill lesions only 1 h after confinement under light conditions, or after 12 h of enclosure in a dark container.

For monitoring transports in practice, analysis is even more complicated, because not only the measurement technique, but also the sampling procedure comes into play. How many birds should be sampled to provide a good estimate of the actual situation? For instance, when

comparing different truck types, each truck consists of a few hundred crates, each containing about 30 pigeons. Not all pigeons, even not all crates, can be sampled to obtain information on the specific problems associated with the different truck types. Which crates should be examined? How many birds should be taken from each crate?

As indicated by Willeberg (1991), quantitative epidemiology can be a useful tool to deal with important welfare questions. However, the premises underlying the epidemiological approach should be clear to, and agreed upon by, all players in the field. Research should provide information aimed at the construction of a scientific framework for the decisions to be made, clearly indicating the assumptions that were made and the blind spots in knowledge that still exist.

For a closely related reason, this thesis contains no "Recommendations to practice": The research performed in the course of this project provides information for all people involved in pigeon transport, ranging from small-scale pigeon fanciers to policy makers. The translation of the transport results into new or adapted transport guidelines, however, is beyond the project's scope: The investigated transport aspects were analyzed from (what we thought to be) the pigeon's perspective. And this perspective is not necessarily reconcilable with other view angles and interests (e.g., financial and practical).

These considerations, however, do not affect the informative value of this thesis for transport practice. Therefore, a summary of findings relevant for transport practice will conclude this chapter, whether they will be translated to transport guidelines or not.

RESEARCH FINDINGS RELEVANT FOR PIGEON TRANSPORT PRACTICE

1. Water intake is the primary defense mechanism for racing pigeons exposed to high ambient temperatures.

2. In case no water is supplied, 32°C is the upper border of the optimal temperature zone. Trespassing this threshold temperature results in dehydration. Dehydration is reflected in a higher energy expenditure, in hyperthermia, in a increased body weight loss, and in a reduced water content of the breast muscle. On-going water deprivation at temperatures above 32 °C may result in mortality.

3. Temperature fluctuations exceeding 35°C increase activity levels. During water deprivation, this may result in mortality.

4. The optimal temperature zone is similar for "First year" and "Old" pigeons.

5. "First year" pigeons have a higher heat production than "Old" pigeons. This difference can not be explained by differences in behavior.

6. Severe head injuries, resulting from aggressive social interactions, are more likely to be observed when the space allowance level is low. Increasing space allowance levels are associated with an increase in grooming behavior and a reduction in activity-related heat production, both for male and for female pigeons.

7. Aggressive behavior levels within a group of racing pigeons do not extinguish with time.

RECOMMENDED FURTHER RESEARCH: AN EPIDEMIOLOGICAL APPROACH OF FLIGHT LOSSES

The data on dehydration, hyperthermia and head injuries presented in this thesis provide both thermoregulatory and behavioral support for the hypothesis that flight losses may be increased by adverse conditions during transport. However, as shown in Figure 1 of the General Introduction, transport is only one element of the dynamic cycle in racing pigeon contests. In the occurrence of flight losses, the role of environmental factors before and after transport, at the home loft and during the flight respectively, can not be neglected.

The multitude of environmental factors, possibly contributing to the occurrence of flight losses, makes a continuation of the experimental approach followed so far difficult. When this conclusion is combined with the vast amount of available scientific literature on pigeon navigation and orientation, and added to the pile of field data and meterological observations that can be collected during a racing season, an observational-analytic epidemiological approach of the occurrence of flight losses may prove its use.

The main entrance gate for quantitative epidemiology in the field of racing pigeon contests is the fact that the occurrence of flight losses is highly variable between racing contests. A primary multivariate analysis of a sufficient quantity of field data should be carried out to identify the factors before, during and after transport that contribute significantly to an explanation of the variation in flight losses between racing contests. In a secondary step, risk analysis should be carried out on these factors to identify the magnitude and nature of the factor's effect (preventive or not) on the occurrence of flight losses. Based on the results of this risk analysis, controllable factors (e.g., the ventilation capacity of the transport truck) can be manipulated to decrease their contribution to the occurrence of flight losses. The risk assessment of uncontrollable but predictable factors, however (e.g., weather conditions), can be incorporated in decision models or checklists. By means of these checklists, the risks pertaining to the weather conditions that are forecasted for the planned racing contest can be quantified, and translated into a flight loss prediction. These flight loss predictions, based on quantitative risk assessment, can then be used to support decision making by transport officials on the issue whether or not a planned racing pigeon contest should be postponed, or even cancelled.

REFERENCES:

References

Arad, Z. Thermoregulation and acid-base status in the panting dehydrated fowl. Am. J. Physiol. 54:234-243; 1983.

Arad, Z.; Arnason, S.; Chadwick, A.; Skadhauge, E. Osmotic and hormonal responses to heat and dehydration in the fowl. J. Comp. Physiol. B. 155:227-234; 1985.

Arad, Z.; Gavrieli-Levin, I.; Eylath, U.; Marder, J. Effect of dehydration on cutaneous water evaporation in heat-exposed pigeons (Columba livia). Physiol. Zool. 60:623-630; 1987.

Arad, Z.; Horowitz, M.; Eylath, U.; Marder, J. Osmoregulation and body fluid compartmentalization in dehydrated heat-exposed pigeons. Am. J. Physiol. 257:R337-R382; 1989.

Aschoff, J.; Pohl, H. Der Ruheumzatz von Vögeln als Funktion der Tageszeit und der Körpergrösse. J. Ornith. 111: 38-47; 1970.

Aschoff, J. Der Tagesgang der Körpertemperatur und der Sauerstoffaufnahme bei Säugetieren als Funktion des Körpergewichtes. Z. Säugetierkunde 46: 201-216; 1981a.

Aschoff, J. Thermal conductance in mammals and birds: its dependence on body size and circadian phase. Comp. Biochem. Physiol. 69A: 611-619; 1981b.

Aschoff, J. The circadian rhythm of body temperature as a function of body size. In: Taylor, C.R. et al., eds. A companion to animal physiology. New York: Cambridge University Press; 1981c:173-188.

Bayliss, P.A.; Hinton, M.H. Transport of broilers with special reference to mortality rates. Appl. Anim. Behav. Sci. 28:93-118; 1990.

Biesel, W.; Nachtigall, W. Pigeon flight in a wind tunnel. IV. Thermoregulation and water homeostasis. J. Comp. Physiol. B. 157:117-128; 1987.

Blaxter, K.L. Energy metabolism in animals and man. Cambridge: Cambridge University Press; 1989:336 pp.

Bordel, R.; Haase, E. Effect of flight on blood parameters in homing pigeons. J. Comp. Physiol. B 163:219-224; 1993.

Brown, C.R.; Foster, G.G. The thermal and energetic significance of clustering in the speckled mousebird, Colius striatus. J. Comp. Physiol. B. 162:658-664; 1992.

Brummermann, M.; Rautenberg, W. Interaction of autonomic and behavioral thermoregulation in osmotically stressed pigeons (Columba livia). Physiol. Zool. 62:1102-1116; 1989.

Calder, W.A.; Schmidt-Nielsen K. Temperature regulation and evaporation in the pigeon and the roadrunner. Am. J. Physiol. 213:883-889; 1967.

Cramp, S. Handbook of the birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic. Volume IV. Terns to woodpeckers. Oxford: Oxford University Press; 1985.

Cross, J.D.; Goodman, I.J. Attack-target attributes and pigeon aggression: accessibility, vocalization, and body movements. Aggressive Behavior 14:265-273; 1988.

De Vries, H.; Netto, W.J.; Hanegraaf, P.L.H. Matman: a program for the analysis of sociometric matrices and behavioural transition matrices. Behaviour 125(3-4):157-175; 1993.

Diebschlag, E. Psychologische beobachtungen über die Rangordnung bei der Haustaube. Zeitschrift für Tierpsychology 4:173-188; 1941.

Fabricius, E.; Jansson, A.-M. Laboratory observations on the reproductive behaviour of the pigeon (Columba livia) during the pre-incubation phase of the breeding cycle. Animal Behaviour 11:534-547; 1963.

Fagen, R.M.; Mankovich, N.J. Two-act transitions, Partitioned contiongency tables, and the 'significant cells' problem. Animal Behaviour 28:1017-1023; 1980.

Géroudet, P. Limicoles: gangas et pigeons d'europe. Paris: Delachaux et Niestlé; 1983.

Glutz von Blotzheim, U.N; Bauer, K.M. Handbuch der Vögel Mitteleuropas. Band 9, Columbiformes -Piciformes. Wiesbaden: Akademische Verlagsgesellschaft; 1980.

Goodwin, D. Behaviour. In: Abs, M., ed. Physiology and behaviour of the pigeon. London: Academic Press; 1983:285-308.

Gorssen, J.; van der Hel, W. Climatic requirements of racing pigeons during transport, phase 1. Research report (in Dutch), available from author; 1993:72 pp.

Gorssen, J.; Schrama, J.W.; Heetkamp, M.J.W. The effect of water availability on metabolic heat production of heat exposed, group housed, unfed pigeons in relation to duration of exposure. In: Collins, E.; Boon, C., eds. Livestock Environment IV. St. Joseph, Michigan: ASAE publication 03-93; 1993:560-569.

Graf, R. Diurnal changes of thermoregulatory functions in pigeons. I. Effector mechanisms. Pfluegers Arch. 386:173-179; 1980a.

Graf, R. Diurnal changes of thermoregulatory functions in pigeons. II. Spinal sensitivity. Pfluegers Arch. 386:181-185; 1980b.

Graf, R.; Krishna, S.; Heller, H.C. Regulated nocturnal hypothermia induced in pigeons by food deprivation. Am. J. Phys. 256:R733-R738; 1989.

Griminger, P. Digestive system and nutrition. In: Physiology and behaviour of the pigeon. Academic press; 1983:19-39.

Heinroth, O.; Heinroth, K. Verhaltensweisen der Felsentaube (Haustaube) Columba livia livia l.. Zeitschrift für Tierpsychologie 6:153-201; 1949.

Henken, A.M.; van der Hel, W.; Smits, M.C.J. Heat tolerance of one-day old chickens. In: Environment and animal health. Skara, Sweden: Swedish University of Agricultural Sciences; 1988:570-574.

Hirth, K.D.; Biesel, W.; Nachtigall, W. Pigeon flight in a wind tunnel. III. Regulation of body temperature. J. Comp. Physiol. B. 157:111-116; 1987.

Hodgson, D.R.; Davis, R.E.; McConaghy F.F. Thermoregulation in the horse in response to exercise. Br. Vet. J. 150:219-235; 1994.

Hohtola, E.; Rintamäki, H.; Hissa, R. Shivering and ptiloerection as complementary cold defense responses in the pigeon during sleep and wakefulness. J. Comp. Physiol. B. 136:77-81; 1980.

Hosmer, D.W.; Lemeshow, S. Applied logistic regression. New York: Wiley; 1989.

Kettlewell, P.J.; Moran P. A study of heat production and heat loss in crated broiler chickens: a mathematical model for a single bird. Br. Poult. Sci. 33:239-252; 1992.

Kettlewell, P.J.; Mitchell, M.A. The thermal environment on poultry transport vehicles. In: Collins, E.; Boon, C., eds. Livestock Environment IV. St. Joseph, Michigan: ASAE publication 03-93; 1993:552-559.

Korine, C.; Arad, Z. Effect of water restriction on temperature regulation of the fruit-bat Rousetuus aegyptiacus. J. Therm. Biol. 18:61-69; 1993.

Kleiber, M. The fire of life. New York: Wiley; 1961.

Krauth, J. Experimental design and data analysis in behavioral pharmacology. In: Van Haaren, F., ed. Methods in behavioral pharmacology. Amsterdam: Elsevier Science Publishers B.V.; 1993:623-650.

Marder, J. Cutaneous water evaporation. II. Survival of birds under extreme thermal stress. Comp. Biochem. Physiol. 75A:433-439; 1983./Chapter 4 + 5

Marder, J.; Gavrieli-Levin, I. Body and egg temperature regulation in incubating pigeons exposed to heat stress: the role of skin evaporation. Physiol. Zool. 59:532-538; 1986./Chapter 4

Martin, S.W.; Meek, A.H.; Willeberg, P. Veterinary epidemiology: principles and methods. Ames Iowa: Iowa State University Press; 1987.

McNabb, F.M.A.; McNabb, R.A.; Ward, J.M. Jr. The effect of dietary protein content on water requirements and ammonia excretion in pigeons, Columba livia. Comp. Biochem. Physiol. 43A:181-185; 1972.

McNab, ,B.K. On estimating thermal conductance in endotherms. Physiol. Zool. 53:145-156; 1980.

Moon, R.D.; Zeigler, H.P. Food preferences in the pigeon (Columba livia). Physiol. Behav. 22:1171-1182; 1979.

Mount, L.E. 1974. The concept of thermoneutrality. In: Monteith, J.L.; Mount, L.E., eds. Heat loss from animals and man. London: Butterworths; 1974:425-439.

Murton, R.K.; Thearle, R.J.P.; Thompson, J. Ecological studies of the feral pigeon Columba livia var.. I. Population, breeding biology and methods of control. Journal of Applied Ecology 9:835-874; 1972a.

Murton, R.K.; Coombs, C.F.B.; Thearle, R.J.P. Ecological studies of the feral pigeon Columba livia var. II. Flock behavior and social organization. Journal of Applied Ecology 9:875-889; 1972b.

Murton, R.K.; Thearle, R.J.P.; Coombs, C.F.B. Ecological studies of the feral pigeon Columba livia var.. III. Reproduction and plumage polymorphism. Journal of Applied Ecology 11:841-854; 1974.

Nichelmann, M. Some characteristics of the biological optimum temperature. J. Therm. Biol. 8:69-71; 1983.

Nickerson, D.M.; Facey, D.E.; Grossman, G.D. Estimating physiological thresholds with continuous two-phase regression. Physiol. Zool. 62:866-887; 1989.

Noldus Information Technology. The Observer, Base Package for DOS. Sample Applications Manual, Version 3.0 Edition. Wageningen, The Netherlands; 1993.

Oshima, I.; Yamada, H.; Goto, M.; Sato, K.; Ebihara, S. Pineal and retinal melatonin is involved in the control of circadian locomotor activity and body temperature rhythms in the pigeon. J. Comp. Physiol. A. 166:217-226; 1989.

Phillips, D.L.; Rashotte, M.E.; Henderson, R.P. Energetic responses of pigeons during food deprivation and restricted feeding. Physiol. Behav. 50:195-203; 1991.

Prinzinger, R. The energy costs of temperature regulation in birds: the influence of quick sinusoidal temperature fluctuations on the gaseous metabolism of the Japanese quail (Coturnix coturnix japonica). Comp. Biochem. Physiol. 71A:469-472; 1982.

Robinson, E.L.; Demaria-Pesce, V.H.; Fuller, C.A. Circadian rhythms of thermoregulation in the squirrel monkey (Saimiri sciureus). Am. J. Physiol. 265:R781-R785; 1993.

Romijn, C.; Lokhorst, W. Some aspects of energy metabolism in birds. In: Brouwer, E.; Van Es, A.J.H., eds. Proceedings of the 2nd Symposium on Energy Metabolism of Farm Animals. Wageningen, The Netherlands: EAAP Publication (10); 1961:49-59.

Saarelaa, S.; Vakkuri, O. Photo-period induced changes in temperature-metabolism curve, shivering threshold and body temperature in the pigeon. Experientia 38 373-375; 1982.

SAS Institute Inc. SAS/STAT User's Guide, Version 6. 4th ed. Cary, NC; 1989:846 pp.

Schrama, J.W.; Arieli, A.; Brandsma, H.A.; Luiting, P.; Verstegen, M.W.A. Thermal Requirements of young calves during standing and lying. J. Anim. Sc. 71:3285-3292; 1993.

Smith, R.M. Circulation, respiratory volumes and temperature regulation of the pigeon in dry and humid heat. Comp. Biochem. Physiol. 43A:477-490; 1972.

Stewart, C.A.; McClure, P.A. Diurnal variation in thermal and metabolic parameters of the golden hamster (Mesocricetus auratus). J. Comp. Physiol. B. 163:234-238; 1993.

Thomas, S.P.; Follette, D.B.; Farabaugh, A.T. Influence of air temperature on ventilation rates and thermoregulation of a flying bat. Am. J. Physiol. 260:R960-R968; 1991.

Thornton, S.N. Drinking in the pigeon (Columba livia) in response to water deprivation and the influence of intracerebroventricular infusions of NaCl or sucrose solutions. Physiol. Behav. 38:719-724; 1986.

Torre-Bueno, J.R. Temperature regulation and heat dissipation during flight in birds. J. Exp. Biol. 75:231-236; 1976.

Van der Hel, W.; Verstegen, M.W.A.; Pijls, L.; Van Kampen, M. Effect of two-day temperature exposure of neonatal broiler chicks on growth performance and body composition during two weeks at normal conditions. Poultry Sci. 71:2014-2021; 1992.

Van Kampen, M.; Mitchell, B.W.; Siegel, H.S. Thermoneutral zone of chickens as determined by measuring heat production, respiration rate and electromyographic and electroencephalographic activity in light and dark environments and changing ambient temperatures. J. Agric. Sci., Camb., 92 219-226; 1979.

Verstegen, M.W.A.; van der Hel, W.; Brandsma, H.A.; Henken, A.M.; Bransen, A.M. The Wageningen respiration unit for animal production research: a description of the equipment and its possibilities. In: Verstegen, M.W.A.; Henken, A.M., eds. Energy metabolism in farm animals. Dordrecht: Martinus Nijhoff Publishers; 1987:21-47.

Walraff, H.G. To be the first in pigeon homing: championship or luck? Anim. Behav. 47:833-846; 1994.

Warriss, P.D.; Bevis, E.A.; Brown, S.N.; Edwards, J.E. Longer journeys to processing plants are associated with higher mortality in broiler chickens. Br. Poultry Sci. 33:201-206; 1992.

Weathers, W.W. Physiological thermoregulation in heat-stressed birds: consequences of body size. Physiol. Zool. 54:345-361; 1981.

Webster, M.D.; Campbell, G.S.; King, J.R. Cutaneous resistance to water-vapor diffusion in pigeons and the role of the plumage. Physiol. Zool. 58:58-70; 1985.

Webster, A.F.J.; Tuddenham, A.; Saville, C.A.; Scott, G.B. Thermal stress on chickens in transit. Br. Poultry Sci. 34:267-277; 1993.

Wenk, C.; Van Es, A.J.H. Eine Methode zur Bestimmung des Energieaufwandes für die Körperliche Aktivität von wachsenden Küken. Schweiz. Landwirtsch. Monatsh. 54:232; 1976.

Willeberg, P. Animal welfare studies: Epidemiological considerations. In: Thrusfield, M.V., ed. Proceedings of a meeting held in London on 17-19th of April 1991. London: Society for Veterinary Epidemiology and Preventive Medicine; 1991:76 -82.

Yamada, H.; Oshima, I.; Sato, K.; Ebihara, S. Loss of the circadian rhythms of locomotor activity, food intake, and circadian plasma melatonin concentration induced by constant bright light in the pigeon (Columba livia). J. Comp. Physiol. A. 163:459-463; 1988.

Zerba, E.; Walsberg, G.E. Exercise generated heat contributes to thermoregulation by Gambel's quail in the cold. J. Exp. Biol. 171:409-422; 1992.

SUMMARY:

Summary

In the Netherlands, the awareness of possible animal welfare problems during transport is growing. Transport of animals is an essential component of racing pigeon (Columba livia) contests. The occurrence of flight losses during racing contests is a continuous source of concern for pigeon fanciers and animal welfare organisations. The background of these flight losses, defined as the number of racing pigeons which does not return to the home loft, is difficult to pinpoint. However, research on poultry transport and preliminary field studies during pigeon transport suggested that adverse conditions during transport may contribute significantly to the occurrence of flight losses. This is a clear break with earlier views, where mainly problems with orientation and navigation combined with adverse weather conditions during the flight home were invoked to explain for the pigeons lost during a racing contest.

In 1990, a research project was started, funded by the Dutch Racing Pigeon Fanciers Organisation (NPO), and financially supported by the Dutch Veterinary Service (Ministry of Agriculture, Nature Conservation and Fisheries). The project was aimed to provide answers to basic questions concerning thermoregulation and behavior of racing pigeons housed under transport conditions: Group confined to a transport crate for at least 23 hours. The experiments described in this thesis all were carried out in the course of this research project.

During the first series of experiments, ambient temperature and water availability were the main factors of interest (Chapter 1 to 4). Insight in the effect of temperature and water availability on thermoregulation of pigeons housed under transport conditions was needed.

In Chapter 1, the effect of water availability and age on the optimal temperature levels was studied. The upper critical temperature of the optimal temperature zone was estimated based on the heat production of the pigeons, on the alterations in body weight, and on body composition measurements. Age did not affect the optimal temperature zone, whereas water availability had a strong impact. In birds with access to water, no upper critical temperature was found for heat production, body weight loss and dry matter content. Variation in weight loss within groups increased above 32.1°C. Water deprivation caused dehydration, and resulted in mortality at 39°C. Heat production increased by 0.16 $W\cdot kg^{-1}\cdot{}^\circ C^{-1}$ above the upper critical temperature of 32.7°C. Above 32.1°C, body weight loss and dry matter content increased by respectively 1.3%$\cdot{}^\circ C^{-1}$ and 0.83%$\cdot{}^\circ C^{-1}$.

The relation between heat production and ambient temperature, as described in Chapter 1 for heat production data collected during a 23 h period, showed a diurnal variation. In Chapter 2, the possible effect of water deprivation and locomotor activity levels on the diurnal variation in the effect of ambient temperature on heat production was studied. No diurnal variation in the upper critical temperature was evident, and the upper critical temperature was not affected by the on-going dehydration due to prolonged heat exposure without access to water. For birds with access to water, the estimated threshold temperature

corresponded with the lower critical temperature, which ranged between 20 and 26°C. The coefficient of cold strain, the slope relating heat production and ambient temperature below the lower critical temperature, was not affected by water deprivation. On average, the coefficient of cold strain was 50% lower during "lights off" compared with a value during "lights on" of 0.10 W·kg^{-1}·°C^{-1}. The diurnal variation in the coefficient of cold strain was unaffected by differences in locomotor activity levels. A clear within photoperiod variation was present, both during "lights on" and "lights off". The coefficient of heat strain, the slope relating heat production and ambient temperature above the upper critical temperature, indicated that the combination of water deprivation and exposure to high ambient temperature levels only resulted in a significant increase in heat production after about 10 h of exposure. This increase from 0.06 to 0.32 W·kg^{-1}·°C^{-1} was not observed in groups with access to water, where the coefficient of heat strain approached zero. The rise in the coefficient of heat strain was photoperiod-dependent, showing an increase immediately after onset of darkness and prior to "lights on".

Also in Chapter 3, the diurnal variation in thermoregulatory parameters was studied. For this purpose, individual body temperature data were linked with group measurement of heat production and evaporative heat loss in order to assess the pigeon's capacity to recover from dehydration at three different temperature levels. Also, the effect of water deprivation and ambient temperature on dry thermal conductance was studied. During a 24-h dehydration period and an appending 24-h recovery period, heat production and body temperature (Experiment 1) and evaporative water loss (Experiment 2) were measured. Results of both experiments were combined to estimate dry thermal conductance during "lights on" and "lights off" periods. At 23 and 31°C, water deprivation did not affect body temperature, evaporative water loss and heat production. At 37°C, water deprivation increased body temperature and reduced evaporative water loss from 8 h after start of exposure onwards, whereas heat production was not affected. Within 30 min after rehydration the effects of previous dehydration disappeared. Dry thermal conductance increased with ambient temperature. At 37°C, conductance of dehydrated birds was lowered. Compared with "lights on", "lights off" values for dry thermal conductance were lower at 23°C and higher at 37°C, whereas no diurnal variation was found at 31°C. The lower dry thermal conductance found during "lights on" at 37°C may have been caused by increased locomotor activity during "lights on" compared to "lights off".

Chapters 1 to 3 dealt with exposure to constant temperature levels, which is, from a transport perspective, a highly artificial situation. Chapter 4, however, concentrated on locomotor activity patterns, heat production and body weight loss during exposure to fluctuating temperature levels both in a cold (15°C) and warm (35°C) reference situation.

For both reference temperature situations, responses in activity and heat production to one of three temperature fluctuation patterns were studied. At "35°C", activity patterns were

affected by temperature fluctuations, but not at "15°C". For both "Sine" and "Cosine" at "35°C", activity increased with temperature at levels exceeding 35°C. Mean heat production was 5.87 $W \cdot kg^{-1}$ at "15°C" and 5.30 $W \cdot kg^{-1}$ at "35°C", but was not affected by temperature fluctuations. For "Sine" and "Cosine" at "15°C", the heat production pattern differed from the activity pattern. At "35°C", however, activity and heat production patterns were similar for all temperature patterns. Body weight loss at "15°C" was about 9% and was not affected by temperature fluctuation patterns. At "35°C", body weight loss depended on the temperature fluctuation pattern, being 11.8% for "Constant", 14.3% for "Cosine" and 15.0% for "Sine". Data on heat production and body weight loss showed that at "15°C" the pigeon's thermoregulatory capacity is sufficient to cope with fluctuating temperatures. At "35°C", however, fluctuating temperatures increased the risk of exceeding the pigeon's thermoregulatory capacity.

Chapter 4 also constituted a bridge between Chapters 1 to 3, where emphasis was placed on the physical environment during transport, and Chapters 5 and 6, where the social environment within a crate and its effect on the behavior of the pigeons were the main points of interest.

In Chapter 5, the behavior of pigeons and the resulting heat production and injuries were studied at a high stocking density in the crate. In a first experiment - using "old" males - different heat exposures (26 vs. 36°C) and water deprivation ("access" vs. "deprived") during one day had no specific significant effects on behavior or heat production measurements. However, the frequency of threatening behavior and the proportion of activity related heat production in the total heat production increased during the experimental period. Behavior patterns differed between pecked and non-pecked birds but remained rather constant during the period. Pecked birds showed more cyclic transitions between immobility and retreat, indicating their subordinate position. No extinction of pecking behavior was found. In a second experiment - using "young" and "old" male and female pigeons under 36°C conditions and with access to water - "young" birds were more immobile than "old" pigeons, whereas heat production was lower in "old" pigeons. Male groups had a higher activity related heat production, pecked relatively more with contact and had more head injuries at the bill base and around the eye than females. Again, no extinction of aggressive behavior or changes in behavior patterns with time were found. Individual variation in body weight was consistent with variation in behavior patterns and head injuries: Higher body weight coincided with more threatening behavior, lower mobility, and less head injuries. The consistent pattern of behavior of pecked and non-pecked birds without obvious adaptation in time causing consistent predictable injuries indicates that a ceiling effect in adaptation is reached under these transport conditions, in which expected effects of the experimental conditions are overruled.

Chapter 6 concentrated on the effect of stocking density, or space allowance, as such. Groups of male or female pigeons were observed at space allowance levels at and above those applied during transport to date. Behavior and heat production of racing pigeons were studied in relation to space allowance and sex. The time pigeons spent immobile decreased from 85% at 210 cm² to 37% at 630 cm². This was compensated by an increase in autonomous and grooming behavior. An increase in space allowance was accompanied by a decreased activity-related heat production, and by a decrease in head injuries. Compared to the reference level of 350 cm² per pigeon, a space allowance of 630 cm² had a sparing effect on the occurrence of injuries. The risk of having major injuries was increased 9-fold for pigeons at 210 cm², and 5-fold at 280 cm². A level of 420 cm² was risk-neutral. The effects of space allowance levels on activity-related heat production, behavior and lesion scores were present in both male and female pigeons. Male pigeons, however, had a higher activity-related heat production, which was probably related to threatening behavior. Males were 3 times more at risk of having major injuries than females.

In conclusion, this thesis demonstrates that water availability is crucial for the maintenance of the thermoregulatory capacity of pigeons housed under transport conditions. A combination of water deprivation and continuous exposure to heat results in dehydration-induced hyperthermia, and may lead to mortality. Also temperature fluctuations exceeding 35°C of a short duration increase body weight loss, and may result in mortality due to an increase in activity levels. The present research also reveals that locomotor activity under crowded conditions consists mainly of aggressive social interactions. Typically, the frequency at which aggressive behavior is displayed persists with time. At low space allowance levels, these aggressive interactions often result in severe head injuries. Based on the experiments described in this thesis, the available space levels actually prevailing in Dutch transport practice are too low, and must increase considerably.

The present results from both the thermoregulation-oriented experiments (Chapter 1 to 4) and the behavior-oriented experiments (Chapter 5 and 6) provide circumstantial evidence for the hypothesis that adverse conditions during transport may increase the risk of flight losses. Further research aimed at the reduction of flight losses should focus on the present variation in flight loss rates between contests. Identification of the environmental factors responsible for the present variation through analysis of field data can be used to reduce flight losses in the future. After identification, controllable environmental factors (e.g., ventilation rate in the transport truck) can be manipulated to reduce their contribution to the occurrence of flight losses. On the other hand, information on the risk associated with uncontrollable but predictable environmental factors (e.g., weather conditions) can be included in a preliminary evaluation of the flight loss risk in a planned racing contest. Depending on the outcome of the evaluation, expected high flight losses can be avoided by postponing, or even cancelling, the planned racing pigeon contest.

SAMENVATTING:

Samenvatting

De publieke opinie in Nederland wordt er zich steeds meer van bewust dat het transport van dieren gepaard kan gaan met een verminderd welzijn. Het transport van dieren is een essentieel onderdeel van wedvluchten met postduiven (Columba livia). De transportduur is aanzienlijk: deze varieert tussen enkele uren voor de korte wedvluchten tot drie dagen voor de lange wedvluchten. Het optreden van vluchtverliezen is een voortdurende bron van zorg voor duivenliefhebbers en dierwelzijnsorganisaties. De oorzaak van deze vluchtverliezen, gedefinieerd als het aantal postduiven dat niet terugkeert op het hok, is niet duidelijk. Onderzoek bij pluimvee en oriënterend veldwerk tijdens duiventransporten deed echter vermoeden dat ongunstige omstandigheden tijdens duiventransporten een belangrijke verklaring kunnen vormen voor het optreden van vluchtverliezen. Dit inzicht is een vrij nieuwe invalshoek: tot dusver werden immers vooral problemen met oriëntatie en navigatie, al dan niet gecombineerd met slechte weersomstandigheden tijdens de vlucht, ingeroepen om de dierverliezen tijdens een wedvlucht te verklaren.

In 1990 werd een onderzoeksproject opgestart onder impuls van de Nederlandse Postduivenhouders Organisatie (NPO), met co-financiering door de Veterinaire Dienst (Ministerie van Landbouw, Natuurbeheer en Visserij). Het project had tot doel een aantal fundamentele vragen te beantwoorden betreffende de warmtehuishouding en het gedrag van postduiven gehuisvest onder transportcondities, i.e., groepen duiven gehuisvest in een transportmand gedurende minstens 23 uur. Alle experimenten beschreven in dit proefschrift werden uitgevoerd binnen het kader van dit onderzoeksproject.

Tijdens de eerste reeks experimenten stonden de omgevingstemperatuur en waterbeschikbaarheid centraal (Hoofdstuk 1 tot 4). Het was immers noodzakelijk om eerst inzicht te verkrijgen in het effect van de omgevingstemperatuur en de waterbeschikbaarheid op de warmtehuishouding van postduiven gehuisvest onder transportomstandigheden.

In Hoofdstuk 1 werd het effect van waterbeschikbaarheid en leeftijd op de optimale omgevingstemperatuur bestudeerd. De bovenste kritieke temperatuur, de bovengrens van het optimale temperatuurgebied, werd berekend op basis van de warmteproduktie, de gewichtsveranderingen en de lichaamssamenstelling. Deze bovenste kritieke temperatuur komt overeen met een knik- of breekpunt in het effect van de omgevingstemperatuur op een bepaald kenmerk, zoals bijv. de warmteproduktie. Leeftijd had geen invloed op het optimale temperatuurgebied. Waterbeschikbaarheid daarentegen bleek van doorslaggevend belang. Bij duiven met de beschikking over water kon immers geen bovenste kritieke temperatuur aangetoond worden op basis van de warmteproduktie, het gewichtsverlies en het percentage droge stof van het borststuk. Wel nam de binnen-groep variatie in gewichtsverlies toe bij temperaturen boven 32.1°C. Water onthouding leidde tot uitdroging: boven 32.1°C nam het

gewichtsverlies met $1.3\%\cdot{}^\circ C^{-1}$ toe, terwijl het percentage droge stof van het borststuk steeg met $0.8\%\cdot{}^\circ C^{-1}$. Bij $39^\circ C$ leidde dit uiteindelijk tot sterfte. Boven de bovenste kritieke temperatuur van $32.7^\circ C$ nam de warmteproduktie toe met 0.16 $W\cdot kg^{-1}\cdot{}^\circ C^{-1}$. Boven $32.1^\circ C$ namen zowel het gewichtsverlies als het percentage droge stof toe, en dit met respectievelijk $1.3\%\cdot{}^\circ C^{-1}$ and $0.83\%\cdot{}^\circ C^{-1}$.

Het verband tussen de warmteproduktie en de omgevingstemperatuur is beschreven in Hoofdstuk 1 voor warmteproduktiegegevens verzameld gedurende een periode van 23 uur. Deze relatie wordt echter gekenmerkt door een dag-nacht variatie. In Hoofdstuk 2 werd de mogelijke rol van water onthouding en bewegingsactiviteit in deze dag-nacht variatie bestudeerd. De bovenste kritieke temperatuur was nauwelijks onderhevig aan dag-nacht variatie, en ook de steeds sterkere uitdroging ten gevolge van een combinatie van hitteblootstelling en water onthouding had geen invloed op de bovenste kritieke temperatuur. Voor duiven met de beschikking over water kwam het geschatte knik- of breekpunt niet overeen met de bovenste kritieke temperatuur: bij temperaturen boven het knikpunt werd immers geen toename in warmteproduktie vastgesteld. Beneden het breekpunt nam de warmteproduktie wel toe bij een afnemende omgevingstemperatuur, zodat deze knikpunt-temperatuur overeen stemde met de onderste kritieke temperatuur. Deze varieerde tussen 20 and $26^\circ C$. De koudebelastingscoëfficiënt, de helling die het verband beschrijft tussen de warmteproduktie en de omgevingstemperatuur bij temperaturen beneden de onderste kritieke temperatuur, werd niet beïnvloed door waterbeschikbaarheid. Gemiddeld was de koude-belastingscoëfficiënt 50% lager tijdens de nacht, dit in vergelijking met een waarde van 0.10 $W\cdot kg^{-1}\cdot{}^\circ C^{-1}$ tijdens de dag. Bewegingsactiviteit bleek geen rol van betekenis te spelen in de dag-nacht variatie vertoond door de koudebelastingscoëfficiënt. Een duidelijke variatie was aanwezig binnen zowel licht- als donkerperiodes. De hittebelastingscoëfficiënt, de helling die het verband beschrijft tussen de warmteproduktie en de omgevingstemperatuur bij temperaturen boven de bovenste kritieke temperatuur, vertoonde een toename over de blootstellingsperiode van 0.06 tot 0.32 $W\cdot kg^{-1}\cdot{}^\circ C^{-1}$. Deze toename was afwezig bij duiven die wel de beschikking hadden over water: hier was de hittebelastingscoëfficiënt praktisch gelijk aan nul. De stijging van de hittebelastingscoëfficiënt was lichtafhankelijk. Een duidelijke toename werd gevonden direct na het doven van het licht, en tegen het einde van de donkerperiode, omstreeks het opnieuw ontsteken van de lampen.

Ook in Hoofdstuk 3 werd de dag-nacht variatie in de warmtehuishouding bestudeerd. Hiervoor werden individueel gemeten lichaamstemperatuurdata gekoppeld aan groepsmetingen van warmteproduktie en warmteverliezen via verdamping. Het vermogen van de duif om te herstellen van uitdroging werd bestudeerd bij drie verschillende omgevingstemperaturen. Ook werd het effect van water onthouding en omgevingstemperatuur op de droge thermische geleidbaarheid onderzocht. Gedurende een 24-u uitdrogingsperiode en een daaropvolgende 24-u herstelperiode werden warmteproduktie en lichaamstemperatuur (Experiment 1) en

warmteverliezen via verdamping (Experiment 2) gemeten. De resultaten van beide experimenten werden gecombineerd, om aldus de droge thermische geleidbaarheid te schatten tijdens de licht-en donkerperiode. Bij 23 en 31°C had water onthouding geen invloed op de lichaamstemperatuur, de warmteverliezen via verdamping en de warmteproduktie. Bij 37°C resulteerde water onthouding in een stijging van de lichaamstemperatuur en een daling van de warmteverliezen via verdamping; deze effecten traden echter slechts op 8 uur na de start van de meting. Warmteproduktie werd ook bij 37°C niet beïnvloed door water onthouding. Binnen 30 minuten na het beschikbaar stellen van water verdwenen de hierboven genoemde effecten waargenomen tijdens de voorafgaande uitdroging. De droge thermische geleidbaarheid is een maat voor het gemak waarmee de duif warmte afstaat aan de omgeving. Deze geleidbaarheid nam toe met een stijgende omgevingstemperatuur. Bij 37°C werd de geleidbaarheid beïnvloed door water onthouding: de droge thermische geleidbaarheid was lager bij duiven zonder water die reeds veel vocht hadden verloren.

De droge thermische geleidbaarheid was bij 23°C lager tijdens de donkerperiode dan tijdens de lichtperiode, maar bij 37°C was de geleidbaarheid het hoogst tijdens de donkerperiode. Bij het tussenliggende temperatuurniveau van 31°C was geen dag-nacht variatie in geleidbaarheid aanwezig. De lagere droge thermische geleidbaarheid aanwezig gedurende de lichtperiode bij 37°C werd misschien veroorzaakt door het feit de bewegingsactiviteit van de duiven hoger is tijdens de lichtperiode dan tijdens de donkerperiode.

De Hoofdstukken 1 tot 3 concentreerden zich op de effecten van een blootstelling aan een constante omgevingstemperatuur op de temperatuurregulatie. Vanuit het oogpunt van de transportpraktijk vormen constante omgevingstemperaturen echter een hoogst kunstmatige situatie. Hoofdstuk 4 legde dan ook de nadruk op de invloed van wisselende omgevingstemperaturen op de warmteproduktie en de bewegingsactiviteit van duiven gehuisvest onder transportcondities. Hiervoor werden een koude (15°C) en een warme (35°C) als uitgangssituatie gehanteerd. In beide uitgangssituaties werden de effecten van drie temperatuurcurves op de bewegingsactiviteit en de warmteproduktie met elkaar vergeleken. Voor iedere temperatuurcurve was de gemiddelde temperatuur over de blootstellingsperiode gelijk aan de referentietemperatuur. Alleen bij "35°C", en dus niet bij "15°C", werden de activiteitspatronen beïnvloed door de temperatuurschommelingen. Bij zowel de "Sinus" als de "Cosinus" temperatuurbehandeling nam de activiteit toe wanneer de omgevingstemperatuur uitsteeg boven 35°C. De gemiddelde warmteproduktie was 5.87 W·kg^{-1} bij "15°C" en 5.30 W·kg^{-1} bij "35°C", maar het gemiddelde werd niet beïnvloed door de temperatuurschommelingen. Bij "35°C" vertoonden de patronen van de warmteproduktie en de bewegingsactiviteit een grote mate overeenkomst, wat erop duidt dat de invloed van de omgevingstemperatuur op de warmteproduktie vooral indirect gebeurde, nl. via de bewegingsactiviteit. Dit was niet het geval bij "15°C", waar de directe invloed van de omgevingstemperatuur op de warmteproduktie sterker was dan bij "35°C". Het gewichtsverlies

bij "15°C" was ongeveer 9%, en dit werd niet beïnvloed door de temperatuurschommelingen. Bij "35°C" hing het gewichtsverlies wel af van de gevolgde temperatuurcurve. Het gewichtsverlies was 11.8% bij de "Constante" temperatuurbehandeling, 14.3% voor de "Cosinus" behandeling, en 15.0% voor de "Sinus" curve. De gegevens betreffende de warmteproduktie en het gewichtsverlies toonden aan dat de warmtehuishouding van de duiven, of beter, hun temperatuurregelend vermogen, bij "15°C" volstaat om om te gaan met temperatuurschommelingen. Bij "35°C" daarentegen betekenen wisselende omgevingstemperaturen een zware belasting voor het temperatuurregelend vermogen van de duiven, met hieraan gekoppeld het risico dat dit vermogen ontoereikend kan blijken.

Hoofdstuk 4 vormde ook de overgang tussen de fysische aspecten van de transportomgeving (Hoofdstukken 1 tot 3) en de sociale omgeving tijdens transport (Hoofdstukken 5 en 6).

In Hoofdstuk 5 werd het gedrag van duiven, en de daarmee samenhangende warmteproduktie en kopbeschadigingen, bestudeerd bij een hoge mandbezetting. Dit houdt in dat de oppervlakte waarover een duif kon beschikken in de mand laag was, nl. 280 cm^2. Uit een eerste experiment - waarbij "oude" doffers van minimaal één jaar oud werden gebruikt - bleek dat het gedrag en de warmteproduktie niet verschilden tussen een omgevingstemperatuur van 26 of 36°C. Ook water beschikbaarheid ("water onthouding" vs. "water beschikbaar") had geen invloed. In de loop van de meetperiode nam echter de frequentie toe waarmee dreiggedrag werd vertoond. Ook was er een toename in de tijd van het aandeel van de activiteitsgebonden warmteproduktie in de totale warmteproduktie. Verschillende gedragspatronen werden gevonden tussen bepikte en niet-bepikte duiven. Deze verschillen waren echter vrij constant in de tijd. Het gedrag van bepikte duiven vertoonde meer cyclische overgangen tussen stilzitten en wijken, wat een ondergeschikte positie in de groep doet vermoeden. Pikgedrag vertoonde geen afname in de tijd. In een tweede experiment werden metingen verricht aan "jonge" en "oude" doffers en duivinnen gehuisvest bij 36°C met de beschikking over water. "Jonge" duiven zaten vaker stil dan "oude" dieren, terwijl de warmteproduktie lager was in "oude" duiven. Mannelijke groepen hadden een hogere activiteitsgebonden warmteproduktie, ze pikten relatief vaker raak, en vertoonden meer letsels aan de neusdoppen en oogranden dan duivinnen. Ook in het tweede experiment werd geen afname in de tijd van agressief gedrag waargenomen. De individuele variatie in gewichtsverlies was consistent met de variatie in gedragspatronen en opgelopen beschadigingen: een hoger lichaamsgewicht ging samen met meer dreiggedrag, een stabielere positie in de mand, en minder letsels. Het consistente gedragspatroon van bepikte en niet-bepikte duiven, waaruit de afwezigheid van een adaptatie in de tijd blijkt, geeft aan dat bij hoge mandbezettingen het adaptatievermogen van de duiven de bovengrens bereikt. Hierdoor worden de verwachte effecten van de experimentele behandelingen op het gedrag van de duiven onderdrukt.

In Hoofdstuk 6 stond de mandbezetting, of de beschikbare oppervlakte, zelf centraal. Groepen doffers en duivinnen werden geobserveerd bij verschillende beschikbare oppervlakte niveaus. Deze stemden gedeeltelijk overeen met waarden die momenteel courant in de praktijk worden gehanteerd (210, 280 en 350 cm^2 per duif), maar ze werden aangevuld met oppervlakte niveaus die ruimer zijn dan in de praktijk gangbaar is (420 en 630 cm^2 per duif). Het gedrag en de warmteproduktie van postduiven werd bestudeerd in relatie tot beschikbare oppervlakte en geslacht. Het percentage van de geobserveerde tijd dat de duiven stil zaten nam af van 85% bij 210 cm^2 tot 37% bij 630 cm^2. Deze afname werd gecompenseerd door een toename in autonoom gedrag (rondkijken, liggen) en poetsgedrag. Een toename in beschikbare oppervlakte ging gepaard met een afname van zowel de activiteitsgebonden warmteproduktie als de kopbeschadigingen. Het risico op zware kopbeschadigingen bij de verschillende oppervlakteniveaus werd vergeleken met de beschadigingen waargenomen bij 350 cm^2 per duif: dit oppervlakteniveau komt overeen met de ruimste oppervlakteniveau wat momenteel in de praktijk wordt toegepast. Vergeleken met de referentie-oppervlakte van 350 cm^2 per duif had een beschikbare oppervlakte van 630 cm^2 een preventief effect op het voorkomen van zware kopbeschadigingen. Het risico op zware kopbeschadigingen door bepikking was negen maal hoger bij 210 cm^2, en vijf maal hogere bij 280 cm^2. Een beschikbare oppervlakte van 420 cm^2 was risico-neutraal. De effecten van de beschikbare oppervlakte op de activiteitsgebonden warmteproduktie, het gedrag en de kopbeschadigingen was zowel bij doffers als bij duivinnen aanwezig. Doffers hadden echter een hogere activiteitsgebonden warmteproduktie dan duivinnen. Dit hing waarschijnlijk samen met verschillen in dreiggedrag. Het risico om zware kopbeschadigingen op te lopen was voor doffers drie maal hoger dan voor duivinnen.

Samenvattend blijkt uit dit proefschrift dat water beschikbaarheid van cruciaal belang is voor het in stand houden van de thermoregulatoire capaciteit (handhaving van de lichaamstemperatuur bij een minimaal waterverlies) van postduiven gehuisvest onder transportcondities. Een combinatie van water onthouding en aanhoudende blootstelling aan hoge omgevingstemperaturen leidt tot het oplopen van de lichaamstemperatuur ten gevolge van uitdroging. Uiteindelijk kan dit leiden tot sterfte. Ook kortdurende temperatuurpieken boven 35°C veroorzaken een toename in gewichtsverlies en bewegingsactiviteit. Ook dit kan aanleiding geven tot sterfte. Dit onderzoek toont ook aan dat bewegingsactiviteit bij een hoge mandbezetting vooral bestaat uit agressieve sociale interacties. Het is kenmerkend dat de frequentie waarmee agressief gedrag wordt vertoond nauwelijks verandert in de tijd. Bij een lage beschikbare oppervlakte kunnen deze agressieve interacties leiden tot ernstige kop-beschadigingen. Uit de experimenten beschreven in dit proefschrift blijkt dat de beschikbare oppervlakte niveaus die momenteel worden toegepast in de Nederlands transportpraktijk te laag zijn, en dat ze aanzienlijk verhoogd moeten worden.

De gepresenteerde resultaten van de experimenten gericht op de warmtehuishouding (Hoofdstuk 1 tot 4) en van de meer gedragsgerichte experimenten (Hoofdstuk 5 en 6) leveren

een indirecte onderbouwing voor de stelling dat ongunstige transportcondities mee aan de basis kunnen liggen van het optreden van vluchtverliezen. Toekomstig onderzoek gericht op het verminderen van vluchtverliezen zou zich moeten concentreren op de variatie in vluchtverliezen die aanwezig is tussen wedvluchten. Middels een analyse van praktijkgegevens kunnen omgevingsfactoren geïdentificeerd worden die de aanwezige variatie helpen verklaren. Deze informatie kan vervolgens gebruikt worden bij het terugdringen van vluchtverliezen. Na identificatie kunnen immers controleerbare omgevingsfactoren, zoals de ventilatie in een transportcontainer, gewijzigd worden zodat hun aandeel in het optreden van vluchtverliezen wordt geminimaliseerd. Anderzijds kan informatie over oncontroleerbare maar voorspelbare omgevingsfactoren (bijv. weersomstandigheden) opgenomen worden in een voorafgaande evaluatie van het risico op vluchtverliezen bij een geplande wedvlucht. Afhankelijk van de uitkomst van deze evaluatie kan vervolgens beslist worden om de verwachte vluchtverliezen te vermijden door de wedstrijd uit te stellen, of zelfs te schrappen.

CURRICULUM VITAE:

Curriculum Vitae

Jos Gorssen (geb. 27 september 1967) groeide op te Kaulille, in Belgisch Noord-Limburg. Na een vorming Latijn-Wiskunde aan het Sint-Hubertuscollege te Neerpelt vervolgde hij in 1985 zijn opleiding aan de Faculteit der Landbouwwetenschappen van de KU Leuven. Op 10 juli 1990 studeerde hij met grote onderscheiding af als landbouwkundig ingenieur, specialisatie Veeteelt. Van 1 augustus daaropvolgend tot 31 juli 1991 was hij als gastmedewerker werkzaam bij de klimaat-respiratiecellen van de vakgroep Veehouderij, Landbouwuniversiteit Wageningen. Bij dezelfde vakgroep volgde op 1 augustus 1991 de aanstelling tot toegevoegd onderzoeker, verbonden aan het onderzoeksproject "Klimaatsbehoeften van postduiven tijdens transport".

De eerste fase van dit onderzoeksproject, gekenmerkt door een sterk fysiologische invalshoek, werd in het voorjaar van 1993 gevolgd door een tweede onderzoeksfase waarin met name gedrags- en voedingsaspecten centraal stonden. Een deel van de experimenten kaderend binnen dit onderzoeksproject staan beschreven in dit proefschrift. Het geheel van de onderzoeksresultaten is op een toegankelijke wijze vertaald in 3 onderzoeksrapporten, verkrijgbaar via de Nederlandse Postduivenhouders Organisatie. De promovendus woont en werkt met ingang van 1 april 1995 in België.

Jos Gorssen (born on September 27, 1967) grew up in Kaulille, a small village in the north-eastern part of Belgium. After a secondary education with emphasis on Latin and mathematics, he enrolled at the Faculty of Agricultural Sciences, Catholic University Leuven. In 1990, he obtained his MSc in Animal Production, and in August of that year he started as a guest researcher at the climate-respiration unit of the Department of Animal Husbandry, Wageningen Agricultural University. In August 1991, the Department appointed him as project researcher, responsible for a project aimed at the improvement of the climatic conditions for racing pigeons during transport.

The framework for the first part of this project was mainly physiological, with emphasis on thermal physiology. The second project phase started off during spring 1993, and concentrated on behavior and feeding. The experiments covered by this thesis were all carried out within the framework of the research project. From April 1995 onwards, Jos Gorssen lives and works in Belgium.