

High-throughput phenotyping to characterise range use behaviour in broiler chickens

Julie Collet, Claire Bonnefous, K. Germain, Laure Ravon, Ludovic Calandreau, Vanessa Guesdon, Anne Collin, Elisabeth Le Bihan-Duval, Sandrine Mignon-Grasteau

▶ To cite this version:

Julie Collet, Claire Bonnefous, K. Germain, Laure Ravon, Ludovic Calandreau, et al.. High-throughput phenotyping to characterise range use behaviour in broiler chickens. Animal, 2024, 18 (3), pp.101099. 10.1016/j.animal.2024.101099. hal-04588500

HAL Id: hal-04588500

https://hal.science/hal-04588500

Submitted on 27 May 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.





Contents lists available at ScienceDirect

Animal

The international journal of animal biosciences



High-throughput phenotyping to characterise range use behaviour in broiler chickens



Julie M. Collet ^{a,*}, Claire Bonnefous ^a, Karine Germain ^b, Laure Ravon ^b, Ludovic Calandreau ^c, Vanessa Guesdon ^d, Anne Collin ^a, Elisabeth Le Bihan-Duval ^a, Sandrine Mignon-Grasteau ^a

- ^a INRAE, Université de Tours, BOA, 37380 Nouzilly, France
- ^b INRAE, UE EASM, Le Magneraud, CS 40052, 17700 Surgères, France
- c INRAE, CNRS, IFCE, Université de Tours, PRC, 37380 Nouzilly, France
- ^d Junia, Comportement Animal et Systèmes d'Elevage, F-59000 Lille, France

ARTICLE INFO

Article history: Received 24 August 2023 Revised 19 January 2024 Accepted 25 January 2024 Available online 1 February 2024

Keywords:
Exploration
Free-range chickens
Gregariousness
Outdoor production
Radio Frequency Identification

ABSTRACT

A key characteristic of free-range chicken farming is to enable chickens to spend time outdoors. However, each chicken may use the available areas for roaming in variable ways. To check if, and how, broilers use their outdoor range at an individual level, we need to reliably characterise range use behaviour. Traditional methods relying on visual scans require significant time investment and only provide discontinuous information. Passive RFID (Radio Frequency Identification) systems enable tracking individually tagged chickens' when they go through pop-holes; hence, they only provide partial information on the movements of individual chickens. Here, we describe a new method to measure chickens' range use and test its reliability on three ranges each containing a different breed. We used an active RFID system to localise chickens in their barn, or in one of nine zones of their range, every 30 seconds and assessed range-use behaviour in 600 chickens belonging to three breeds of slow- or medium-growing broilers used for outdoor production (all <40 g daily weight gain). From those real-time locations, we determined five measures to describe daily range use: time spent in the barn, number of outdoor accesses, number of zones visited in a day, gregariousness (an index that increases when birds spend time in zones where other birds are), and numbers of zone changes. Principal Component Analyses (PCAs) were performed on those measures, in each production system, to create two synthetic indicators of chickens' range use behaviour. The first two PCA axes represented over 90% of the variance of the five measures and were both consistent over time and correlated with independent visual scans. Contributions of the five measures to the PCAs were similar among breeds, except for the correlation between the number of outdoor accesses and the four other measures. PC1 correlated with time spent inside the barn and zone changes frequency, whilst PC2 was explained by exploration of the range. Taken together, PC1 and PC2 indicators showed that range use increased with age, outdoor temperature (in spring), and did not differ between males and females. Importantly, daily scores for both indicators were repeatable among individuals - particularly in PC1 - showing inter-individual variability on range-use. The characterisation of broiler behaviour around their range with these reliable and repeatable indicators provides novel tools to help understand individual variations of range-use in free-range farming.

© 2024 The Authors. Published by Elsevier B.V. on behalf of The Animal Consortium. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

Implications

Characterising individual range use in free-range chickens is limited with traditional methods. We propose a new method based on active Radio Frequency Identification technology, to evaluate range use *in situ*, minimising any disturbance to chickens' natural behaviour. We used Radio Frequency Identification technology in

three broiler breeds used for outdoor production and provided two reliable and repeatable indicators to individually characterise range-use. From our precise individual characterisation of such complex behaviour as range-use, we will be able to investigate the origin, in particular genetic, of birds' variation in range use.

Introduction

Access to a free-range in farming is a key request from consumers in Europe (Harper and Makatouni, 2002; Van Loo et al.,

^{*} Corresponding author.

E-mail address: julie.collet@inrae.fr (J.M. Collet).

2014; Delanoue et al., 2017) who associate it with better animal welfare, especially in poultry. Several studies have shown that chickens who use the range more have improved levels of welfare indicators compared to low rangers. In broilers, chickens who visited the range more often and went farther on the range had improved gait scores, breast plumage, and other health indicators, as well as reduced stress responses to handling and confinement (Taylor et al., 2018; Taylor et al., 2020). Results are more ambiguous in laying hens, as several studies noticed a better plumage in high rangers (Rodriguez-Aurrekoetxea and Estevez, 2016; Bari et al., 2020) and that high ranger hens were less fearful towards novel objects than low rangers (Larsen et al., 2018). However, other clinical welfare indicators did not vary across high and low rangers (Wurtz et al., 2023) and even higher corticosterone was observed in higher rangers (Larsen et al., 2018). Laying hens raised in enriched environments and at lower stocking densities used the range for longer than non-enriched birds (Campbell et al., 2017: Campbell et al., 2020) and visited the range more after stressful events (Campbell et al., 2018a). If extensive poultry rearing guarantees an access to a range, there are still large discrepancies in the use of the range among flocks and among individuals within a flock, suggesting that both environmental and animal factors are involved in this behaviour.

Environmental conditions have dramatic effects on range-use. Flocks of broiler chickens use the range more frequently in spring and summer than in winter, and more generally in moderately warm weather, low rainfall, and low wind (Stadig et al., 2017b; Taylor et al., 2017a). Weather conditions have been shown to explain up to 35% of the variability in range use in slow-growing broiler chickens (Sztandarski et al., 2021), although animals' sensitivity to weather varied, even within a genotype. The presence and disposition of trees on the range can also double the number of chickens on the range (Lubac et al., 2003). Additionally, rangeuse increases with age in both broilers and laying hens (de Almeida et al., 2012; Rodriguez-Aurrekoetxea et al., 2014; Stadig et al., 2017b; Taylor et al., 2017a; Campbell et al., 2020). Beyond flock trends, a large portion of range-use behaviour varies among individuals. Using fast-growing broilers, Taylor et al. (2017b) found that 3-9% of the tagged population accounted for 33-50% of all range visits. It is therefore crucial to understand individual chicken behaviour related to range-use.

Within a flock, how individual chickens explore and exploit their range is a complex behaviour that can be associated with their morphology, personality traits, or other behaviours. Specifically, in a fast-growing broiler breed, the lightest animals prior to accessing the range are those individuals that go farthest on the range (Taylor et al., 2020). Range-use can also be associated with foraging behaviours. In broilers, high-rangers preferred to make efforts to obtain feed whilst low-rangers preferred easily accessible feed (Ferreira et al., 2021). Exploration behaviour was also associated with bold personalities in a wild bird species (Patrick et al., 2017); movement to the furthest extents of the range, where fewer birds have been, requires taking risks. In chickens, more fearful hens spent less time outside in the range (Hartcher et al., 2016; Bari et al., 2021) although this was not observed in broilers (Stadig et al., 2017b). Finally, the interaction between social motivation and range-use is not yet clear, although low-ranger broilers seem to prefer staying near conspecifics compared to high-rangers (Ferreira et al., 2020; Bonnefous et al., 2023).

To measure individual range-use accurately requires consistent tracking of a large number of individuals, inside the barn and outside on the range, during the lifetime of a chicken. Observational scans, where birds carry an individual (colour) tag, can track chicken movements on the range without any technological investments, but they are time-consuming, limited to small populations, and to behaviours occurring during the observers' presence

(de Almeida et al., 2012; Rodriguez-Aurrekoetxea et al., 2014; Stadig et al., 2017b; Stadig et al., 2017a). Camera recordings can extend the time-of-record and give access to the entire duration of outdoor access, although video coding can be time consuming, and still limits the studied population size. Passive Radio Frequency Identification tags (RFID) greatly advanced our understanding of range-use by automatically recording information on individual tagged chickens. Passive RFID systems measure the chicken's identity when they go through pop-holes equipped with antennae (Richards et al., 2011; Hartcher et al., 2016; Campbell et al., 2017; Campbell et al., 2018b; Bari et al., 2020; Campbell et al., 2020). Passive RFID is often used at barn doors to record when chickens enter and exit the barn, or can be placed on the range, to distinguish animals that travel far across the range from those that stay near (Larsen et al., 2017; Taylor et al., 2020). The tracking data provide insights into the time animals spent outside or the number of times they went out. The main limitation of this technology is that information on chicken movements is limited to the number of pop-holes and their location on the range, and, thus this method is unable to capture information on the various ways chickens use their range or how likely they are to visit different zones in their range.

To overcome the limitations of currently used technologies, we propose in this study an active RFID system to precisely track individual birds, both in the barn and on the range. We tested the system across three breeds of broilers used for outdoor production. This precise real-time system enabled us to describe individual behaviours on the range and to combine them into indicators of chicken range-use that could be associated with a time budget dedicated to ranging, locomotory activity, boldness or social motivation, and how a chicken perceives its ranging environment. First, we described these behaviours in the three breeds of broilers tested in different ranges. Second, we combined all indices to create two indicators of variation in chicken range use behaviours and tested their reliability. Finally, we used these indicators to understand how chickens use their range according to intrinsic factors, such as age and sex, as well as environmental conditions, such as temperatures and rainfall, throughout the day.

Material and methods

Animals, housing and active radio frequency identification system

Details of the population used and methods can be found in Bonnefous et al. (2023). Briefly, three breeds of slow to medium-growing broilers were raised: (i) Hubbard S757N, thereafter named Label, a naked-neck breed used for Label Rouge production, with a growth rate of 26 g/day; (ii) Hubbard JA757, thereafter named Certified, a breed used for outdoor production, with a growth rate of 36 g/d; and (iii) Dual-purpose, an experimental dual-purpose breed developed from a crossing between meat and egg type breeds with a 16 g/d growth rate (Dual-Purpose). Rearing durations of those breeds were 85, 71, and 99 days, respectively. Importantly, we do not directly compare these three breeds as they were each raised on a different range with distinct tree cover (Fig. 1).

Chicks of all breeds arrived at 1 day old, when they were vaccinated against Marek's and Gumboro diseases, and infectious bronchitis. Chicks from each breed were housed in separate but similar barns housing 734 Certified, 735 Label and 771 Dual-Purpose birds, of a balanced sex ratio. Barns were all 12.5×6 m to achieve an inside stocking density of 16.8-24.5 kg/m². Label birds arrived 14 days before both other breeds. Up to day 7 of growth, males and females were separated by cardboard within barns. On day 7, all birds were identified with a wing tag. Onwards from 36 days of age, all chickens had 24-hour free access to a 50×50 m range

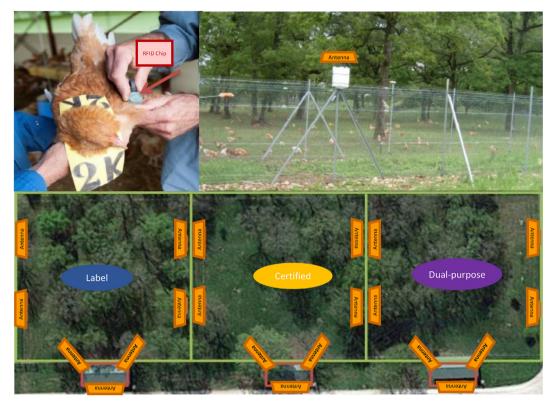


Fig. 1. Experimental set up. Top left: Radio Frequency Identification chip on a chicken wing. Top right: antennae placed on the range. Bottom: aerial view of the ranges.

with unevenly distributed trees (Fig. 1). All breeds had *ad libitum* access to water and a commercial organic feed, formulated for the Label breed, commonly used in French organic rearing (including three diets based on soya meal, maize, wheat and sunflower meal with barley, alfalfa and triticale in addition from day 29 to day 57 or with faba beans and triticale in addition from day 57 to the end of the rearing period) and with energy and CP contents of 15.8 MJ/kg and 20.8% (day 1 to day 28), 15.6 MJ/kg and 18.7% (day 29 to day 57), and 15.3 MJ/kg and 17.4% (day 57 to the end of the rearing period). Mortality was low in all breeds, four chickens (< 1% of the population) died in the Label breed during the course of the experiment, 3 (< 1%) in the Certified, and 26 (3%) in Dual-Purpose chickens.

On their 29th day of age, seven days before they got free access to the outdoors, 100 male and 100 female chickens per breed were chosen randomly and equipped with a RFID chip on their wing (Fig. 1). Chips sent 433 MHz signals every 10 seconds, which could be caught by the seven antennae located around the range and in the barn (Fig. 1). Range use was also measured directly on all the tagged males, who all wore a poncho with a unique code (Fig. 1) by visual scans carried out seven times a day over 11-15 days (depending on the breed's slaughter age), regularly spread over the outdoor access period (Bonnefous et al., 2023). From individual range position, the authors of that previous study (Bonnefous et al., 2023) obtained an individual distance index combining occurrences of outdoor access and distance between the observation zone and the barn. RFID signals were constantly measured from the day chickens gained access to the range, until the day before slaughter, corresponding to day 84 (Label), day 70 (Certified), and day 98 (dual-purpose) days of age.

Quality control of data

We first created a model that enabled chickens to be located on the range every 30 seconds in nine zones of different sizes (Fig. 2,

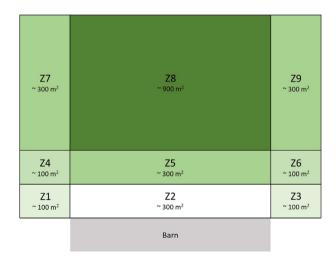


Fig. 2. Schematic representation of the position and surface of the nine range zones detected by the active Radio Frequency Identification system used for tracking chickens.

Supplementary Materials S1 for details on the calibration of the system and its error rate, Table S1). We disregarded data from animals on the (i) day(s) they were subjected to other tests that may disturb their behaviour (behavioural tests at D50-51 for Label and Certified chickens, D52-53 for dual-purpose chickens, weighing at D57 and blood sampling at D64 (Bonnefous et al., 2023)),when (ii) animals had very low numbers of detections on a day, specifically, when an animal was detected fewer times than 10% of the maximum number of times an animal was detected on that range), and (iii) from 10 min before and 30 min after visual scans were taken where an experimenter was going around the range as chickens had the tendency to follow the human.

Range use measures

We created five daily measures from raw data that could be associated with range-use behaviour, following the definition from Ontology ATOL ATOL_0000831: any measurable or observable characteristic related to the behaviour of the animals to use their physical environment according to the social or physical stimuli within this environment (Table 1, Golik et al., 2012). Barn time represented the proportion of tags coming from the barn on a given 24-hour day. As total number of times a chip was tagged on a specific day varied (although a low number of detections were removed, see quality control), outs measured the number of times a bird went out divided by the total number of times a bird was tagged on that day. The total number of outside zones used that day corresponded to range, which was thus an integer between 0 and 9. The gregariousness index measured daily individual visits to the most popular zones. Hence, gregariousness was a proxy of the capacity of birds to spend time in zones more visited by conspecifics and was lower when birds spent a long time in zones less visited by other birds (following the definition from Ontology ATOL_0000900: any measurable or observable characteristic related to the propensity of an animal to stay close to its peers, or to react to social separation). For animal j, this index was calculated according to the formula:

$$Gregariousness_j = -1 \times \sum_{i=1}^9 \frac{\textit{Time spent in zone i by bird } j}{\textit{Overall time spent in zone i by all birds}}$$

Finally, *zone changes*, a proxy for locomotor activity, scored the number of times a bird was recorded changing zone, divided by the total number of times the bird was recorded on that day.

We calculated the repeatability of all daily measures as the ratio of among-individual variance over the sum of among- and within-individual variance with the rpt function (package rptR, Stoffel et al., 2017), using 1 000 boots per repeatability score. Although we could not disentangle whether differences among ranges were due to a flock effect, the differences in tree cover among ranges, or the difference in breeds placed on each range, we calculated differences among ranges for all daily measures with an ANOVA on the average index score per bird overall recorded days.

Two indicators to synthesize information on range use behaviour

To understand how range-use measures were correlated with each other and whether they were redundant, we performed a Principal Component Analysis (**PCA**, function prcomp, Venables and Ripley, 2002) on the standardised average measures of all birds on a range. We also performed PCA on daily standardised data to

observe how the relationships among range use measures changed over time. As the first two PCA axes explained a very large portion of the variance, and were both similar across breeds and ranges and repeatable across days, we further described range-use with these two indicators. We finally checked the reliability of both indicators by testing Spearman correlations between individual scores of both PCs and the distance index independently obtained by visual observations (Bonnefous et al., 2023).

Biological analyses of range use indicators

Coordinates on both indicators PC1 and PC2 were calculated individually by multiplying the values of the five daily measures (standardised per range) with the eigenvectors of respective PCs. We analysed how the range use indicators were affected by sex, age, and outside temperatures and rainfall (as measured on site by a weather station) by performing multivariate mixed models (Pinheiro and Bates, 2000):

$$y_{jk} = \beta_0 + \beta_1 \ day + \beta_2 \ min \ temp + \beta_3 \ max \ temp + \beta_4 \ rain + u_j + \varepsilon_{jk}$$

where y_{jk} is the daily individual scores of either PC1 or PC2, β_0 the sex-specific intercept, day the number of days since chickens had access to the range, min temp the minimum temperature, max temp the maximum temperature, rain is rainfall, u_j the random intercept for individual j and ε_{jk} the error term for individual j on day k. We did this first in an overall model, then within each range with a different breed.

As activity on the range is known to vary depending on the period of the day (Taylor et al., 2017a), we finally tested how range-use varied within a day by applying to our individual PCs the same model as above, but separating the individual scores in five daily periods: dawn (from first light till sunrise), morning (from sunrise until midday), afternoon (until Sunset), dusk (until sunlight disappeared), and night. In both cases, we accounted for *P*-value overestimation from multiple testing with an fdr correction (Benjamini and Hochberg, 1995).

Results

Range use varies across the three ranges

The individuals from the different breeds, raised on the different ranges, considerably varied in their range use (Table 1, Fig. S1). Label birds used the range more than other birds on all measures. Birds' preferred areas varied among ranges and breeds: Label and dual-purpose chickens had a similar share of their time

Table 1Definitions of daily measures for range-use in chickens, their mean \pm SD, repeatability (R) and their associated confidence intervals [CI] within each population, along with breed effects. Mean values were calculated for 24-hour periods. All measures were significantly repeatable (P < 0.001) and P-values are not reported here. Range effect shows the result of an ANOVA testing for a difference of the index among ranges.

		Label		Certified		Dual-Purpose		Range effect	
Item	Description	Mean ± SD	R [CI]	Mean ± SD	R [CI]	Mean ± SD	R [CI]	F _(3, 134)	p
Barn time	Proportion of time spent in the barn	0.75 ± 0.04	0.75 [0.71, 0.79]	0.88 ± 0.03	0.57 [0.50, 0.62]	0.88 ± 0.06	0.68 [0.63, 0.72]	6 538	<0.001
Outs	Number of times a bird went out	0.10 ± 0.01	0.64 [0.58, 0.69]	0.03 ± 0.01	0.46 [0.40, 0.52]	0.02 ± 0.01	0.41 [0.35, 0.46]	2 557	<0.001
Range	Number of zones explored [0-9]	8.1 ± 0.6	0.35 [0.30, 0.41]	7.7 ± 0.04	0.41 [0.35, 0.47]	6.6 ± 0.05	0.38 [0.32, 0.43]	12 673	<0.001
Gregariousness	Measure that increases with a bird's time spent close to its peers	9.3 ± 2.6	0.93 [0.91, 0.95]	8.1 ± 2.1	0.53 [0.46, 0.59]	7.4 ± 3.8	0.88 [0.85, 0.90]	38	<0.001
Zone changes	Number of zone changes	0.29 ± 0.02	0.61 [0.55, 0.66]	0.11 ± 0.03	0.54 [0.48, 0.60]	0.08 ± 0.03	0.58 [0.52, 0.63]	1 658	<0.001

outside, spending respectively 52 and 46% of their time outside in the area just outside the barn (Z2, Fig. S1), and 23 and 29% in the farthest zone (Z8). By contrast, Certified chickens spent most of their time outside in zone 9 (37% of the time), which corresponded to the corner of the field with the most trees (Fig. 1), hence showing that the cause of this variation may be range based as well genetic or random flock variation.

All range-use measures were consistent over time in individuals raised on the three ranges. *Gregariousness*, as measured in our experiment, was the most repeatable trait, and up to 90% of its variance was due to among-individual variance in the Label range (Table 1). The least repeatable trait, *range*, still had 35–41% of its variance due to among-bird variation. It must be noted that, by construction, *range* has a lower variance as its value can only be integers between 0 and 9.

Principal component axes are reliable indicators of range use

For all ranges, the first two axes of the total PCA represented over 89% of the variance in the five measures (Fig. 3). The first PC accounted for between 54 and 84% of the variance and the second between 12 and 23%. Further, PC1 correlated positively with zones changes and gregariousness, and negatively with barn time, whilst PC2 was mainly correlated with range. The main difference between flocks was how outs correlated with the other measures. In Label chickens, outs was positively correlated with barn time, whilst this correlation was negative in the Certified chickens in which birds that changed zones more often, and were less gregarious, went in and out more often. In Dual-Purpose chickens, outs was independent from barn time and mostly correlated with range. The variance explained by PC2 was associated with the value of the correlation between PC2 and outs (Fig. 3).

As for the five daily measures, the two PCA axes were consistent over time. Contributions to the first two axes were repeatable across days in all flocks (Label: PC1, R = 0.70 [0.19, 0.88], PC2, R = 0.72 [0.22, 0.88]; Certified: PC1, R = 0.99 [0.94, 1.00], PC2, R = 0.95 [0.72, 0.99]; Dual-Purpose, PC1, R = 0.93 [0.59, 0.98], PC2, R = 0.75 [0.25, 0.90], all P-values < 0.001).

Individual chicken performances in PC1 and PC2 were repeatable, although scores varied among flocks (Label: PC1, R = 0.77 [0.73, 0.81], PC2, R = 0.34 [0.32, 0.43]; Certified: PC1, R = 0.56 [0.50, 0.61], PC2, R = 0.35 [0.29, 0.41]; Dual-Purpose, PC1, R = 0.72 [0.66, 0.76], PC2, R = 0.60 [0.55, 0.66], all *P*-values < 0.001). Both axes were correlated to the distance index independently obtained from visual scans (PC1: ρ = 0.76, P < 0.001, PC2: ρ = 0.41, P < 0.001, (Bonnefous et al., 2023)), con-

firming that PC1 and PC2 were reliable indicators of range use behaviour.

Range use indicators vary with age and environmental conditions, but not across sexes

The PC1 indicator increased during the growth of the broilers and the estimate of the mixed model was twice as high in Certified chickens as in Label chickens, with dual-purpose showing intermediate values (Table 2, Fig. 4). For PC2, the overall positive association between age and range-use was mostly due to Label chickens, as the coefficient of regression was very low in dual-purpose and null in Certified chickens.

Minimum and maximum temperatures affected range-use although their effect varied among flocks (Table 2). Maximum temperature (in the spring) tended to increase range use along PC1. The relationship between minimum temperatures and PC1 varied across flocks, as the mixed model estimate between minimum temperature and PC1 was positive in Label chicken but negative in Certified and dual-purpose chickens. Both minimum and maximum temperatures had a null or negative regression coefficient with PC2 (Table 2), meaning that as temperatures increased, animals moved between fewer zones. Rainfall decreased range use indicators in all situations but for PC2 in the Certified breed (Table 2). While males had lower values of PC1 overall, there was no significant effect of sex on range-use, but the most extreme values of range use on PC1 were observed in females (Fig. 5).

We further described range-use according to the time of the day, splitting the 24-h period of range access into five time periods according to the Sun's position each day (night-dawn-morning-af ternoon-dusk). General trends were similar at all times of the day but some daily pattern differences could be noted between the Label and the two other breeds. First, although range-use increased with age, night range-use decreased with age for Certified and dual-purpose chickens, and stayed stable in Label chickens. Second, minimum temperatures increased range-use at dawn, in the afternoon, and at dusk for Label chickens, but decreased or did not change range use for the other two breeds on the other two ranges. In parallel, maximum temperatures increased range-use in the afternoon for both Certified and dualpurpose birds but decreased it for the Label birds (Table S2). Finally, even if males and females used the range equally overall, daily patterns of range use sometimes changed during the day for each sex. When all animals were analysed together, males used the range less than females at dusk (Table S2). Effects of sex depended on the range and the breed at other times of the day;

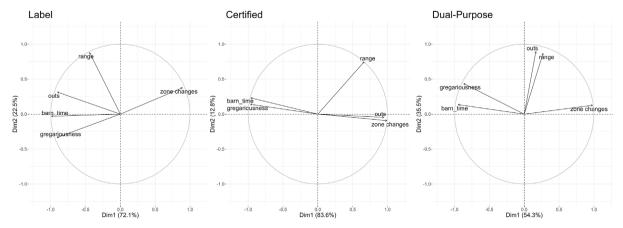


Fig. 3. Range-specific Principal Components on standardised values of range-use behaviours in chickens.

Table 2Results from mixed models of several factors that could affect range use in chickens, as defined by our two Principal Components (PC1 and PC2). Estimates are reported ± SE. Indicative *P*-values are adjusted for multiple testing (fdr). Sex effect describes the male sex effect.

item	Principal Components	Age	Minimum temperature	Maximum temperature	Rainfall	Sex
Overall	PC1	0.027 ± 0.001 P < 0.001	0.005 ± 0.003 P = 0.097	0.028 ± 0.002 P < 0.001	-0.033 ± 0.002 P < 0.001	-0.232 ± 0.111 P = 0.160
	PC2	0.012 ± 0.001 P < 0.001	-0.016 ± 0.002 P < 0.001	-0.017 ± 0.002 P < 0.001	-0.006 ± 0.002 P < 0.001	0.062 ± 0.055 P = 0.445
Label	PC1	0.020 ± 0.001 P < 0.001	0.024 ± 0.003 P < 0.001	0.005 ± 0.003 P = 0.061	-0.014 ± 0.003 P < 0.001	-0.252 ± 0.205 P = 0.392
	PC2	0.028 ± 0.001 P < 0.001	0.003 ± 0.003 P = 0.482	-0.030 ± 0.003 P < 0.001	-0.024 ± 0.003 P < 0.001	-0.027 ± 0.095 P = 0.849
Certified	PC1	0.041 ± 0.003 P < 0.001	-0.019 ± 0.008 P = 0.028	0.087 ± 0.007 P < 0.001	-0.071 ± 0.006 P < 0.001	-0.577 ± 0.227 P = 0.083
	PC2	0.000 ± 0.002 P = 0.772	-0.015 ± 0.005 $P = 0.002$	0.006 ± 0.004 P = 0.147	0.002 ± 0.004 P = 0.683	0.079 ± 0.085 P = 0.545
Dual-Purpose	PC1	0.033 ± 0.001 P < 0.001	-0.016 ± 0.004 P < 0.001	0.023 ± 0.003 P < 0.001	-0.021 ± 0.003 P < 0.001	-0.091 ± 0.155 P = 0.688
	PC2	0.003 ± 0.001 P < 0.001	-0.017 ± 0.004 P < 0.001	-0.007 ± 0.003 P = 0.014	-0.010 ± 0.003 P < 0.001	0.142 ± 0.108 P = 0.373

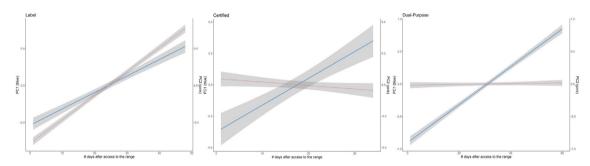


Fig. 4. Principal Component 1 (PC1, blue, left axis) and Principal Component 2 (PC2, pink, right axis) variation with chicken age in each production system. The line corresponds to a linear model and its associated SE (geom_smooth method "lm" in ggplot2 (Wickham, 2016)).

Certified male chickens used the range less than females during afternoon and dusk based on PC1, whereas Label males used the range less than females at dawn and dusk based on PC2 (Table S2).

Discussion

We used an active RFID technology to measure range use *in situ*, minimising any disturbance to chickens' natural behaviour. From these measures, we provided two reliable and repeatable composite indicators, which simply characterised this complex behaviour. The first indicator varied with chickens' daily time spent outside, the time they spend in popular places, and how often they changed zones, while the second indicator was associated with the extent of animal exploration of the range on a given day. Both indicators revealed similar range-use patterns among three chicken breeds used for outdoor production tested on three different ranges. Additionally, this study demonstrated the impact of intrinsic and extrinsic factors such as age and weather conditions on these indicators.

Reliable indicators of range use in two dimensions: towards personality traits?

Here, we demonstrated the validity of two independent composite indicators to describe range-use among individual chickens. These indicators were reliable, consistent over time, and accounted for most of the daily variance observed in range-use (89.6–96.4%, depending on the range). Moreover, the indicators were correlated with scores of range-use that were independently obtained

through visual scans. Compared to observational scans, the method used to obtain these indicators was less labour-intensive and provided more information. Indeed, with RFID, we collected individual information on more animals than with visual scans and were able to obtain continuous and complete data over the course of the day for the entire period of outdoor access. It was therefore possible to estimate more precisely the effect of age or of period-of-the-day on range-use. Moreover, the continuity of information provided a more comprehensive understanding of the individual chicken's range-use by recording more daily measures than would have been possible with scans or with passive RFID (e.g., gregariousness, zone changes, etc.).

It has been suggested previously that range-use could be characterised as a personality trait (Ferreira et al., 2019; Ferreira et al., 2022; Bonnefous et al., 2023). Personality traits are defined as "behavioural differences between individuals that are consistent over time and across situations" (Réale et al., 2010). Here, consistency over time is shown by the repeatability of individual performances on PC1 and PC2. While this study did not directly assess whether the range-use indicators are consistent across situations, the repeatability scores were obtained during spring, over a long period of time (between 34–62 days) and covering a large variety of environmental conditions and animal growth stages. This suggests that range-use scores are also consistent between environmental conditions and developmental stages. Range-use behaviour, as described by these indicators, may thus be considered as a personality trait.

The two indicators identified in this study were found to be associated with distinct behavioural traits. PC2 was primarily associated with the number of zones visited by the chickens on a given

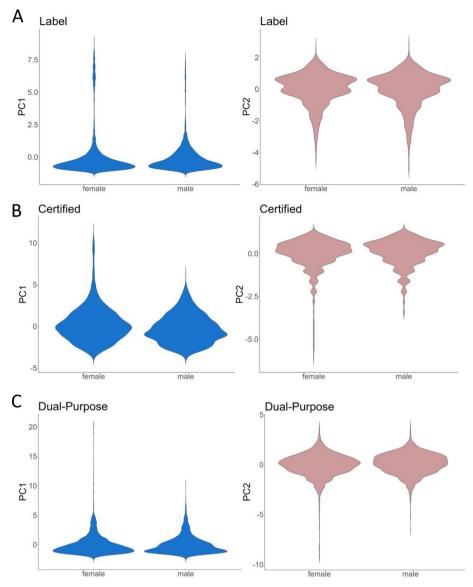


Fig. 5. Distribution of Principal Component 1 (PC1) and Principal Component 2 (PC2) in female and male chickens in the a. Label, b. certified, and c. dual-purpose production systems.

day, indicating an emphasis on the exploration of the range. In contrast, PC1 was correlated with the amount of time spent outside, particularly in zones less used by other birds, and with zone changes, a proxy for locomotor activity. Chickens have to decide whether to invest their time exploring new patches (exploration) or exploiting known resources (exploitation), forming an exploration–exploitation trade-off (Kramer and Weary, 1991; Mehlhorn et al., 2015). PC2, associated with the number of patches visited on a given day, can be interpreted as an exploration axis. PC1 however, had components that can be interpreted as exploitation (e.g., *Barn time* as the main source of feed is available in the barn) and as exploration (e.g., *Zone changes* as birds that often change zones are more likely to be exploring new resources). In this regard, PC1 could be interpreted as a representation of the exploration–exploitation trade-off.

High and low rangers did not have the same behaviour in different flocks

There were striking differences in the overall level of range-use among breeds. However, given that only one flock was tested per

breed, and that each population was on a range with variable levels of tree cover, it is challenging to draw a definitive conclusion as to whether these differences are due to genetic or environmental factors. We can nevertheless hypothesise that genetic differences partly caused those results, as dual-purpose birds - which used the range the least - were also more fearful in tests performed before range access (Bonnefous et al., 2023). A comparison of the relationships between the five measures of range-use among breeds yielded some interesting insights. Notably, the correlations between four of the five measures of daily range-use exhibited a high degree of similarity across the three ranges, while outs was the only trait that demonstrated distinct correlations with the other traits among breeds (Fig. 3). In Label chickens, outs was negatively associated with PC1, indicating that high rangers on PC1 did not frequently enter and exit the barn, but stayed on the range. Conversely, in Certified birds, outs was positively correlated with zone changes and negatively with barn time and gregariousness, meaning that high rangers frequently entered and exited the barn. Finally, in the dual-purpose breed, outs was positively associated with PC2 and was independent of PC1, suggesting that birds that frequently entered and exited the barn explored more zones of the range each day.

These findings suggest that the relationship between entering and exiting the barn and overall range-use is complex and varies across breeds or ranges. Specifically, entering and exiting the barn is not an accurate predictor of overall range-use since this behaviour can be associated with both high and low rangers, depending on the population's activity level and inquisitiveness. In flocks that spent more time outside, like the Label chickens, the birds that entered and exited the barn the most tended to be the lowest rangers, whereas in populations that spent a higher proportion of their time inside, like Certified and Dual-purpose, the most active and inquisitive birds tended to enter and exit the barn the most. These findings underscore the importance of considering multiple indices of range-use and their interactions when investigating the factors that influence the behaviour of birds in a range environment.

Extrinsic and intrinsic effects on range use behaviour

Similar to previous studies conducted on broilers (de Almeida et al., 2012; Rodriguez-Aurrekoetxea et al., 2014; Stadig et al., 2017b) and laying hens (Campbell et al., 2020), our investigation found that range-use increased with age, as observed in both PC1 and PC2; however, we observed a slight difference in the behaviour of Certified chickens over time. Specifically, PC2 did not increase with age, whereas PC1 exhibited an increase in the first 12 days of outdoor access, followed by a plateau in range-use (Fig. S2). This stabilisation of range-use after one to two weeks aligns with the findings from a previous study on fast-growing broilers (Ross 308, Taylor et al., 2017a), suggesting that faster-growing breeds may be more constrained in their ability to increase range-use with age.

Our analysis did not reveal any overall effect of sex on the mean range use indicators, although females exhibited more extreme behaviours than males (Fig. 5). Previous studies showed that males may be more active than females when kept indoors (Kjaer, 2017), but no sex-based differences were found in range visits in broilers (Taylor et al., 2017b). Our female chickens, however, displayed higher levels of activity during the evening (Table S2). Circadian rhythms often vary between sexes, although little is known about those rhythms in developing vertebrates such as broilers, or birds in general (Walton et al., 2022). Another study reported that males tended to use the range more than females during winter (Chapuis et al., 2011), suggesting that differences in temperature preference may not account for this sex difference.

Our results showed that higher temperatures tended to increase range-use as measured by PC1, but decreased it on PC2 (Table 2). This is consistent with the literature results showing that broiler chickens are more likely to go outside when weather is dry and moderately warm (Stadig et al., 2017b; Taylor et al., 2017a). The temperature during the outdoor access period corresponded to the spring season in a temperate zone, with mean temperature ranging from 15 to 25 °C. The distinct responses of the two indicators to higher temperatures are intriguing and highlight the advantages of using multidimensional indicators of range behaviour over simple descriptors. A possible explanation for this observation is that warmer temperatures increased the number of insects available in all zones, leading to increased foraging activity in a smaller area, while in colder temperatures, chickens needed to explore the entire range to locate this supplementary source of feed. Despite an overall effect, all breeds did not react consistently to warmer maximum or minimum temperatures. As the tree cover varied among ranges, the temperature may also not have been consistent among breeds or ranges, nor in different areas of the range, potentially leading to this contrast.

We observed that Label chickens had higher responses to minimum temperatures on PC1, while breeds primarily increased PC1 according to maximum temperatures. Notably, birds from the

Label breed accessed the range earlier in the season than the others, and consequently, these chickens were allowed outdoor access during periods of negative minimum temperatures, while the other breeds were not.

Caveats and how to overcome them

Despite their precision and reliability, our newly developed range-use indicators still suffered from some limitations. First, it is not necessarily straightforward to interpret our measures with common personality traits from the literature. For example, our measure of gregariousness could reflect social motivation (more socially motivated birds spend more time where other birds are), boldness (chickens with lower scores of gregariousness are less fearful to spend time away from their conspecifics), or simply the attractiveness of a given zone. This limitation arises as we only have localisation data for those chickens, while a more complete behavioural study would be interesting to fully interpret our results.

Additionally, technical limitations of the system include that one of the ranges showed an error rate of 15% in determining whether chickens were inside or outside the barn (see Supplementary Information). In addition, the precision of the positioning on the range limited the subdivision of the range into only nine zones, covering an area of over 2 500 m². To overcome this limitation, a more precise gridding of the range is needed in order to improve indicators such as the distance covered by animals or a description of non-random social interactions as was done in laying-hens (Gómez et al., 2022). A more precise position on the range would also permit a better estimation of the effect of parameters such as tree distribution on range-use.

Conclusions

Despite those few limitations, our novel method of characterising range-use is precise, reliable, repeatable, and encapsulates a complex behaviour into two simple composite dimensions. The indicators we described here will be valuable for the detailed characterisation of range-use in broiler chickens at an individual level, and may facilitate the genetic characterisation of this behaviour in a more sophisticated manner than previously achieved (Chapuis et al., 2011; Kjaer, 2017). We also provided a first estimate of range-use for chickens from a dual-purpose breed, a type of breed bound to see their use expand in the next few years and they would ethically enable the use of males as meat in egg-laying breeds and prevent the killing of day-old chicks (Brümmer et al., 2018).

Supplementary material

Supplementary material to this article can be found online at https://doi.org/10.1016/j.animal.2024.101099.

Ethics approval

This study was conducted at the experimental unit UE 1206 EASM of INRAE, France (https://doi.org/10.15454/1. 5572418326133655E12), from February to June 2021. It received the Ethics committee approval (APAFIS#28675-20201202 15483186 v3) in agreement with the French and European legislation, and was carried out in accordance with relevant guidelines and regulations.

Data and model availability statement

Datasets generated and codes used in our study are available at: https://entrepot.recherche.data.gouv.fr/dataverse/inrae under the reference https://doi.org/10.57745/JUDHTG. Information can be made available from the authors upon request.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) did not use any AI and AI-assisted technologies.

Author ORCIDs

Julie M. Collet: https://orcid.org/0000-0002-6028-5234.
Claire Bonnefous: https://orcid.org/0000-0002-3522-5686.
Karine Germain: https://orcid.org/0009-0005-6638-9404.
Laure Ravon: https://orcid.org/0009-0009-7339-0875.
Ludovic Calandreau: https://orcid.org/0000-0002-7535-5733.
Vanessa Guesdon: https://orcid.org/0000-0003-3806-6163.
Anne Collin: https://orcid.org/0000-0002-3410-6108.
Elisabeth Le Bihan-Duval: https://orcid.org/0000-0002-0712-

5549.

Sandrine Mignon-Grasteau: https://orcid.org/0000-0002-0142-0109.

CRediT authorship contribution statement

Julie M. Collet: Writing - review & editing, Writing - original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. Claire Bonnefous: Writing - review & editing, Methodology, Investigation, Data curation, Conceptualization. Karine Germain: Writing - review & editing, Resources, Project administration, Methodology, Investigation, Data curation, Conceptualization. Laure Ravon: Writing - review & editing, Project administration, Methodology, Investigation, Data curation, Conceptualization. Ludovic Calandreau: Writing review & editing, Methodology, Investigation, Conceptualization. Vanessa Guesdon: Writing - review & editing, Methodology, Investigation, Conceptualization. Anne Collin: Writing - review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. Elisabeth Le Bihan-Duval: Writing - review & editing, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. Sandrine Mignon-Grasteau: Writing review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of interest

None

Acknowledgements

We thank all animal caretakers for their daily care to the chickens and Nina Kruger for their help setting up the RFID tags. We are grateful to the breeding companies and Maxime Reverchon for providing one-day-old chicks. Thanks to Vitor Hugo Bessa Ferreira's theoretical support and Scott C. Atkinson for his extremely useful copy editing.

Financial support statement

The project PPILOW has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement N°816172.

References

- Bari, M.S., Downing, J.A., Dyall, T.R., Lee, C., Campbell, D.L.M., 2020. Relationships between rearing enrichments, range use, and an environmental stressor for free-range laying hen welfare. Frontiers in Veterinary Science 7, 480. https:// doi.org/10.3389/fvets.2020.00480.
- Bari, M.S., Allen, S.S., Mesken, J., Cohen-Barnhouse, A.M., Campbell, D.L.M., 2021. Relationship between range use and fearfulness in free-range hens from different rearing enrichments. Animals (Basel) 11, 300. https://doi.org/10.3390/ ani11020300.
- Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society. Series B (Methodological) 57, 289–300.
- Bonnefous, C., Calandreau, L., Le Bihan-Duval, E., Ferreira, V.H.B., Barbin, A., Collin, A., Reverchon, M., Germain, K., Ravon, L., Kruger, N., Mignon-Grasteau, S., Guesdon, V., 2023. Behavioural indicators of range use in four broiler strains. Applied Animal Behaviour Science 260, https://doi.org/10.1016/j.applanim.2023.105870 105870.
- Brümmer, N., Christoph-Schulz, I., Rovers, A.-K., 2018. Consumers' perspective on dual-purpose chickens. International Journal on Food System Dynamics 9, 390– 398. https://doi.org/10.18461/ijfsd.v9i5.951.
- Campbell, D.L.M., Dyall, T.R., Downing, J.A., Cohen-Barnhouse, A.M., Lee, C., 2020.

 Rearing enrichments affected ranging behavior in free-range laying hens.

 Frontiers in Veterinary Science 7, 446. https://doi.org/10.3389/fvets.2020.00446.
- Campbell, D.L., Hinch, G.N., Dyall, T.R., Warin, L., Little, B.A., Lee, C., 2017. Outdoor stocking density in free-range laying hens: radio-frequency identification of impacts on range use. Animal 11, 121–130. https://doi.org/10.1017/ S1751731116001154.
- Campbell, D.L.M., Hinch, G.N., Downing, J.A., Lee, C., 2018a. Early enrichment in freerange laying hens: effects on ranging behaviour, welfare and response to stressors. Animal 12, 575–584. https://doi.org/10.1017/S1751731117001859.
- Campbell, D.L.M., Horton, B.J., Hinch, G.N., 2018b. Using Radio-Frequency Identification Technology to Measure Synchronised Ranging of Free-Range Laying Hens. Animals (Basel) 8, 210. https://doi.org/10.3390/ani8110210.
- Chapuis, H., Baudron, J., Germain, K., Pouget, R., Blanc, L., Juin, H., Guéméné, D., 2011. Caractérisation des déplacements et de l'adaptation des poulets de chair au cahier des charges BIO via la technologie RFID. Book of abstracts of the 9th Journées de la Recherche Avicole, 29-30 March 2011, Tours, France, p. 1–5.
- de Almeida, G.F., Hinrichsen, L.K., Horsted, K., Thamsborg, S.M., Hermansen, J.E., 2012. Feed intake and activity level of two broiler genotypes foraging different types of vegetation in the finishing period. Poultry Science 91, 2105–2113. https://doi.org/10.3382/ps.2012-02187.
- Delanoue, E., Dockes, A.-C., Chouteau, A., Philibert, A., Madgdelaine, P., Roguet, C., 2017. Points de vue et attentes des consommateurs et citoyens vis-à-vis de l'élevage. Journées Recherche Porcine 49, 295–300.
- Ferreira, V.H.B., Peuteman, B., Lormant, F., Valenchon, M., Germain, K., Brachet, M., Leterrier, C., Lansade, L., Calandreau, L., Guesdon, V., 2019. Relationship between ranging behavior and spatial memory of free-range chickens. Behavioural Processes 166, https://doi.org/10.1016/j.beproc.2019.103888 103888.
- Ferreira, V.H.B., Barbarat, M., Lormant, F., Germain, K., Brachet, M., Lovlie, H., Calandreau, L., Guesdon, V., 2020. Social motivation and the use of distal, but not local, featural cues are related to ranging behavior in free-range chickens (Gallus gallus domesticus). Animal Cognition 23, 769–780. https://doi.org/10.1007/s10071-020-01389-w.
- Ferreira, V.H.B., Simoni, A., Germain, K., Leterrier, C., Lansade, L., Collin, A., Mignon-Grasteau, S., Le Bihan-Duval, E., Guettier, E., Leruste, H., Calandreau, L., Guesdon, V., 2021. Working for food is related to range use in free-range broiler chickens. Scientific Reports 11, 6253. https://doi.org/10.1038/s41598-021-85867-2.
- Ferreira, V.H.B., Šimoni, A., Germain, K., Leterrier, C., Lansade, L., Collin, A., Mignon-Grasteau, S., Le Bihan-Duval, E., Guettier, E., Leruste, H., Lovlie, H., Calandreau, L., Guesdon, V., 2022. Foraging behavior shows individual-consistency over time, and predicts range use in slow-growing free-range male broiler chickens. Frontiers in Veterinary Science 9., https://doi.org/10.3389/fvets.2022.814054 814054.
- Golik, W., Dameron, O., Bugeon, J., Fatet, A., Hue, I., Hurtaud, C., Reichstadt, M., Meunier-Salaün, M.-C., Vernet, J., Joret, L., Papazian, F., Nédellec, C., Le Bail, P.-Y., 2012. ATOL: The Multi-species Livestock Trait Ontology. Proceedings of the 6th Metadata and Semantics Research Conference (MTSR 2012), 28-30 November 2012, Cadiz, Spain, p. 289–300.
- Gómez, Y., Berezowski, J., Jorge, Y.A., Gebhardt-Henrich, S.G., Vögeli, S., Stratmann, A., Toscano, M.J., Voelkl, B., 2022. Similarity in temporal movement patterns in laying hens increases with time and social association. Animals 12, 555.
- Harper, G.C., Makatouni, A., 2002. Consumer perception of organic food production and farm animal welfare. British Food Journal 104, 287–299.

- Hartcher, K.M., Hickey, K.A., Hemsworth, P.H., Cronin, G.M., Wilkinson, S.J., Singh, M., 2016. Relationships between range access as monitored by radio frequency identification technology, fearfulness, and plumage damage in free-range laying hens. Animal 10, 847–853. https://doi.org/10.1017/S1751731115002463.
- Kjaer, J.B., 2017. Divergent selection on home pen locomotor activity in a chicken model: Selection program, genetic parameters and direct response on activity and body weight. PLoS ONE 12, e0182103.
- Kramer, D.L., Weary, D.M., 1991. Exploration versus exploitation: a field study of time allocation to environmental tracking by foraging chipmunks. Animal Behaviour 41, 443–449. https://doi.org/10.1016/S0003-3472(05)80846-2.
- Larsen, H., Cronin, G.M., Gebhardt-Henrich, S.G., Smith, C.L., Hemsworth, P.H., Rault, J.L., 2017. Individual ranging behaviour patterns in commercial free-range layers as observed through RFID tracking. Animals (Basel) 7, 21. https://doi.org/10.3390/ani7030021.
- Larsen, H., Hemsworth, P.H., Cronin, G.M., Gebhardt-Henrich, S.G., Smith, C.L., Rault, J.L., 2018. Relationship between welfare and individual ranging behaviour in commercial free-range laying hens. Animal 12, 2356–2364. https://doi.org/10.1017/S1751731118000022.
- Lubac, S., Senecaille, M., Sperandio, D., Desquennes, A., Arnoult, C., Faure, J.M., Chauve, C., Barroux, D., Mirabito, L., 2003. Effet de la présence de taillis de saules à très courte rotation sur l'occupation des parcours par les poulets et sur les marqueurs minéraux et microbiologiques du sol. Sciences et Techniques Avicoles 45, 14–23.
- Mehlhorn, K., Newell, B.R., Todd, P.M., Lee, M.D., Morgan, K., Braithwaite, V.A., Hausmann, D., Fiedler, K., Gonzalez, C., 2015. Unpacking the exploration–exploitation tradeoff: a synthesis of human and animal literatures. Decision 2, 191–215. https://doi.org/10.1037/dec0000033.
- Patrick, S.C., Pinaud, D., Weimerskirch, H., 2017. Boldness predicts an individual's position along an exploration–exploitation foraging trade-off. Journal of Animal Ecology 86, 1257–1268. https://doi.org/10.1111/1365-2656.12724.
- Pinheiro, J.C., Bates, D.M., 2000. Mixed-effects models in S and S-PLUS. Springer, New York, NY, USA.
- Réale, D., Dingemanse, N.J., Kazem, A.J.N., Wright, J., 2010. Evolutionary and ecological approaches to the study of personality. Philosophical Transactions of the Royal Society B: Biological Sciences 365, 3937–3946. https://doi.org/ 10.1098/rstb.2010.0222.
- Richards, G.J., Wilkins, L.J., Knowles, T.G., Booth, F., Toscano, M.J., Nicol, C.J., Brown, S.N., 2011. Continuous monitoring of pop hole usage by commercially housed free-range hens throughout the production cycle. Veterinary Record 169, 338. https://doi.org/10.1136/vr.d4603.
- Rodriguez-Aurrekoetxea, A., Estevez, I., 2016. Use of space and its impact on the welfare of laying hens in a commercial free-range system. Poultry Science 95, 2503–2513. https://doi.org/10.3382/ps/pew238.
- Rodriguez-Aurrekoetxea, A., Leone, E.H., Estevez, I., 2014. Environmental complexity and use of space in slow growing free range chickens. Applied Animal Behaviour Science 161, 86–94. https://doi.org/10.1016/j.applanim.2014.09.014.

- Stadig, L.M., Rodenburg, T.B., Ampe, B., Reubens, B., Tuyttens, F.A.M., 2017a. Effect of free-range access, shelter type and weather conditions on free-range use and welfare of slow-growing broiler chickens. Applied Animal Behaviour Science 192, 15–23. https://doi.org/10.1016/j.applanim.2016.11.008.
- Stadig, L.M., Rodenburg, T.B., Ampe, B., Reubens, B., Tuyttens, F.A.M., 2017b. Effects of shelter type, early environmental enrichment and weather conditions on free-range behaviour of slow-growing broiler chickens. Animal 11, 1046–1053. https://doi.org/10.1017/S1751731116002172.
- Stoffel, M.A., Nakagawa, S., Schielzeth, H., 2017. rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. Methods in Ecology and Evolution 8, 1639–1644. https://doi.org/10.1111/2041-210X.12797.
- Sztandarski, P., Marchewka, J., Wojciechowski, F., Riber, A.B., Gunnarsson, S., Horbanczuk, J.O., 2021. Associations between weather conditions and individual range use by commercial and heritage chickens. Poultry Science 100., https://doi.org/10.1016/j.psj.2021.101265 101265.
- Taylor, P.S., Hemsworth, P.H., Groves, P.J., Gebhardt-Henrich, S.G., Rault, J.L., 2017a. Ranging behaviour of commercial free-range broiler chickens 1: factors related to flock variability. Animals (Basel) 7, 54. https://doi.org/10.3390/ani7070054.
- Taylor, P.S., Hemsworth, P.H., Groves, P.J., Gebhardt-Henrich, S.G., Rault, J.L., 2017b. Ranging behaviour of commercial free-range broiler chickens 2: individual variation. Animals (Basel) 7, 55. https://doi.org/10.3390/ani7070055.
- Taylor, P.S., Hemsworth, P.H., Groves, P.J., Gebhardt-Henrich, S.G., Rault, J.-L., 2018. Ranging behavior relates to welfare indicators pre- and post-range access in commercial free-range broilers. Poultry Science 97, 1861–1871. https://doi.org/ 10.3382/ps/pev060.
- Taylor, P.S., Hemsworth, P.H., Groves, P.J., Gebhardt-Henrich, S.G., Rault, J.L., 2020.
 Frequent range visits further from the shed relate positively to free-range broiler chicken welfare. Animal 14, 138–149. https://doi.org/10.1017/S1751731119001514.
- Van Loo, E.J., Caputo, V., Nayga, R.M., Verbeke, W., 2014. Consumers' valuation of sustainability labels on meat. Food Policy 49, 137–150. https://doi.org/10.1016/ j.foodpol.2014.07.002.
- Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S. Springer, New York, NY, USA.
- Walton, J.C., Bumgarner, J.R., Nelson, R.J., 2022. Sex differences in circadian rhythms. Cold Spring Harbor Perspectives in Biology 14, https://doi.org/10.1101/cshperspect.a039107 a039107.
- Wickham, H., 2016. Ggplot2: elegant graphics for data analysis. Springer-Verlag, New York, NY, USA.
- Wurtz, K.E., Tahamtani, F.M., Foldager, L., Thodberg, K., Riber, A.B., 2023. Associations of range use with individual behaviour, clinical welfare indicators, fear response and gastrointestinal characteristics of two laying hen hybrids. Applied Animal Behaviour Science 265, https://doi.org/10.1016/j. applanim.2023.105978 105978.