Measuring fluctuating asymmetry in fattening rabbits: A valid indicator of performance and housing quality?[1]

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ABSTRACT: Fluctuating asymmetry (FA) has been advocated as the preferred measure of developmental instability and a reliable indicator of the quality of an animal (performance/fitness) and of its environment during its growing life. Empirical studies, however, are too scant or equivocal to consider this assumption adequately validated, which is partly due to the lack of a robust methodological framework for collecting and analyzing FA data. Therefore, we conducted an experiment in which 306 weaned rabbits were housed either in welfare-friendly pens (n = 6) or barren pens (n = 6). The size of both types of pen was similar (1.91 m^2), but the welfare-friendly pens were equipped with suitable enrichment material (gnawing stick, elevated platform, and hiding box) and were stocked with one-half of the number of rabbits compared with the barren pens (17 vs. 34 rabbits per pen). Performance data (BW gain, ADFI, and G:F) were collected every 14 d. After slaughter (d 63 to 72), we measured twice the left- and right-hand side of 11 presumed bilateral traits on intact carcasses and 50 traits on fleshed bones. Using a stringent decision process, an optimal combination of morphological traits for estimating FA in fattening rabbits was determined. This combination consisted of five traits (fleshed bones) that showed no directional asymmetry or antisymmetry and showed a high level of FA relative to the measurement error; also, these traits were not correlated in their signed FA values. Measurements on intact carcasses seemed inappropriate for estimating FA. Using this robust FA measuring protocol, rabbits housed in the welfare-friendly pens were less asymmetric than were rabbits from the barren pens. Except for a greater daily BW gain in the welfare-friendly pens during the first 14 d after weaning, there were no effects of housing conditions on performance traits. The FA was negatively correlated with BW gain in rabbits from the barren pens, whereas in the welfare-friendly pens, there was no correlation. These results support the application of FA as an indicator of animal welfare and performance; however, FA seems to be a more reliable estimator of the underlying developmental instability when living conditions are suboptimal.

Key Words: Animal Welfare, Developmental Instability, Environmental Enrichment, Fluctuating Asymmetry, Production, Rabbits

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Introduction

Fluctuating asymmetry (**FA**) is the recommended index of developmental instability that reflects an individual's inability to develop the intended phenotype under given environmental conditions (Møller and Swaddle, 1997). Fluctuating asymmetry concerns small, randomly directed deviations from perfect symmetry in bilateral traits. If a growing individual fails to cope with perturbing factors, the development of such traits may be disrupted, resulting in non-identical development on both sides of the plane of symmetry.

Among populations, larger values of FA were interpreted to reflect worse environmental conditions and hence decreased welfare (Møller et al., 1995, 1999; but see Campo et al., 2000, 2002 for inconsistent relationships). Within populations, larger values of FA were interpreted to reflect lower individual quality in terms of fitness (natural populations) or productivity (farm animals; Møller, 1999; Møller and Manning, 2003). Oth-

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ers, however, reported that the relationship between FA and fitness/performance is generally weak and heterogeneous (Clarke, 1995, 1998).

Contradictory findings in the literature might be related to the lack of a standardized protocol for measuring and analyzing FA (Lens et al., 2002). Often no rationale is given for the selection of traits measured for FA or for the measuring method adopted. Research findings may depend crucially on such decisions. For example, empirical relationships between stress and FA based on single traits are, on average, weak and heterogeneous (Leung and Forbes, 1996), whereas analyses that combine information across traits provide greater power and are more reliable detectors of stress (Leung et al., 2000); however, selection of an optimal combination of traits for estimating FA has so far received little attention.

In this paper, we present a protocol for measuring FA in rabbits and investigate the effect of two different housing conditions on performance and FA.

Materials and Methods

Animals and Housing

At 4 wk of age, 306 broiler rabbits (line selected at the Agricultural Research Center, Belgium) were weaned, weighed, and transferred to a barn containing four rows of three pens. Apart from littermates being distributed homogeneously across treatments, rabbits were distributed randomly across these 12 pens. Each pen measured 200 cm × 100 cm and was equipped with a 90-cm × 10-cm feeder (11 feeding places) and four nipple drinkers. Each pen had a grid floor and walls (height = 65 cm) but no roof. The ventilation and heating system allowed ambient temperature to be maintained between 18 and 23°C throughout the experiment. Rabbits were fed a standard fattening diet containing 16.5% CP and 9.3 MJ of DE/kg (as-fed basis) ad libitum. This diet was based on alfalfa meal, wheat, wheat shorts, beet pulp, and sunflower meal and contained 66 mg/kg (as-fed basis) Robenidine as a coccidiostatic drug. During the first 3 wk of the experiment, rabbits were treated with Tiamutin (50 mg/L of drinking water) to protect them against enteropathy.

Six pens were enriched with a plastic platform (92 cm × 40 cm), a wooden hiding box (50 cm × 40 cm × 35 cm), and a gnawing stick. In these welfare-friendly pens, rabbits were stocked at low density (17 rabbits per pen or 8.9 rabbits/m^2). In the six remaining pens (barren pens), no enrichment was provided, and rabbits were stocked at double density (34 rabbits per pen or 17.8 rabbits/m^2). Along each row, welfare-friendly pens were alternated with barren pens.

Production Traits

The BW gain (per individual), ADFI (per pen), and G:F (per pen, as-fed basis) were determined each 14 d until slaughter age. Slaughter age varied between d 63 and 72. The number of rabbits slaughtered per working day varied between six and 14 to allow sufficient time for all measurements. Care was taken, however, that slaughter age was similar for rabbits from the welfare-friendly (mean = 69.67 ± 0.28 d) and barren pens (mean = 70.23 ± 0.15 d). The ADFI was estimated as the quantity of feed given during the period of interest minus the quantity of feed left at the end of this period. To correct for mortality before slaughter age, production traits were expressed per animal-day. For the calculation of ADFI and G:F, three animal-days were subtracted for rabbits that had died before slaughter, as they were assumed not to have eaten or grown for the 3 d before death. For the calculation of BW gain, these animals were not taken into account

Treatment effects on daily BW gain during each 14-d period, as well as during the entire fattening period, were analyzed using mixed regression models with animal-days and treatment as fixed effects; pen and litter were random effects. Because sex did not affect any of the production traits, this variable was omitted from further analyses.

Treatment effects on G:F and ADFI were analyzed using the *t*-test or, if the data were not normally distributed or variances were not equal, using the Mann-Whitney U-test. Because the experimental unit for these production traits was the pen instead of the individual rabbit, however, the power of these tests was low. Therefore, negative findings should be treated cautiously.

FA: Measurements on Intact Carcasses

Eighty-four rabbits were selected randomly (seven rabbits per pen), slaughtered by cervical dislocation, and put in a ventral recumbency with the forelegs extended cranially to resemble a sphinx-like position. The following day, when rigor mortis had set in, the following 11 presumed bilaterally symmetrical morphological traits were measured twice (with an interval of approximately 1 h) on the right- and left-hand sides: length of ear, length from ear to eye, length from ear to upper incisor, length of nostril, length from eye to nostril, length of upper incisor, length of lower incisor, length of claw of first digit of front paw, width of wrist, length from knee to heel, and length from heel to toe. All measurements were taken with a digital caliper to the nearest 0.01 mm.

FA: Measurements on Fleshed Bones

Bones were extracted from the carcasses using the method described by McDonald and Vaughan (1999). The forelegs, hind legs, and skull were placed into beakers filled with a solution of 60 g of sodium perborate tetrahydrate ($NaBO_3 \cdot 4H_2O$) in 1 L of hot water and incubated in a water bath (65°C). Most of the flesh was removed after 1 d, and the bones were incubated again in the water bath (65°C). This time, a solution of 20 g of $NaBO_3{\cdot}4H_2O$ in 1 L of hot water was used. After 1 d, the remainder of the flesh was removed from the bones with a water jet pump, and the bones were oven-dried (70°C) for 1 d. Fifty different measurements (varying the start and end point) of nine presumed bilateral symmetric bones from 30 carcasses (equal number per treatment selected randomly) were measured twice (with an interval of >1 h) on the left- and right-hand sides using a digital caliper to the nearest 0.01 mm. On the basis of this data set of 30 animals, the five best traits for estimating FA were selected following the procedure described later. In the remaining 54 animals, only these five traits were measured. Details regarding all measurements can be found at http://www.clo.fgov.be/dvl (Research - Section I).

Statistical Analyses of FA Data

For both data sets separately (intact carcasses and fleshed bones), the most suitable combination of morphological traits for estimating the degree of FA was selected on the basis of the following criteria: 1) a high signal:noise (or FA: measurement error), 2) a significant amount of FA, 3) absence of directional asymmetry, 4) absence of antisymmetry, and 5) absence of correlations in the signed FA values. These were determined as follows.

We carried out mixed regression analysis with REML parameter estimation to separate real asymmetry (signed FA; left minus right trait length) from measurement error (Van Dongen et al., 1999). The significance of FA was obtained from a likelihood ratio test, whereas directional asymmetry was tested by an F-test, adjusting the denominator df by Satterthwaite's procedure (Van Dongen et al., 1999). Whereas FA and antisymmetry cannot be separated statistically with high power, distributions of FA with a negative kurtosis are generally considered indicative for the presence of antisymmetrical individuals in the population (Palmer and Strobeck, 1992; Van Dongen, 1998). Unlike FA, directional asymmetry and antisymmetry are considered inappropriate for the estimation of the underlying developmental instability because of their presumed heritable component (Palmer and Strobeck, 1992; Palmer, 1994; but see Leamy, 1999, for an example of low heritability of directional asymmetry). To examine whether signed trait asymmetries were correlated at the individual level, we calculated unbiased individual FA estimates (i.e., deviations of the random slopes from the fixed-effects slope in the mixed regression model; Van Dongen et al., 1999) and estimated individual-level association with Pearson's correlation coefficients. Between-trait correlation for signed FA values would suggest that these traits developed dependently during ontogeny, which may hamper proper interpretation of between-trait correlations in unsigned FA (Leamy et al., 1997).

Between-treatment heterogeneity in average unsigned FA was tested with a Levene's test with unsigned standardized FA as the dependent variable, treatment as fixed factor, and pen and litter as random effects (modeled as GLMM in Proc Mixed; SAS version 8; SAS Inst., Inc., Cary, NC; Littell et al., 1996). As the effect of sex was not significant, this variable was not retained in the model. Standardized FA allows for the combination of traits that differ in size (and hence possibly in FA), and it is calculated as x-mean/SD. Levene's tests are insensitive to departure from normality (Palmer and Strobeck, 1992).

The association between production traits and FA was analyzed with mixed regression models. We opted to study multiple-trait FA through mixed regression analysis with repeated measure structure (treating traits as repeated measures). This statistical routine produces results comparable with those obtained with composite indices of FA; however, because the df in multivariate models reflect the number of individuals rather than the number of traits by individuals, pseudoreplication is avoided (Lens et al., 2002).

Results

Effect of Treatment on Production Traits

At weaning, the mean BW of rabbits housed in the welfare-friendly pens was 681 g (SD = 87) and 668 g (SD = 82) in the barren pens. At slaughter, mean BW of rabbits housed in the welfare-friendly pens was 2,448 g (SD = 244, n = 97) and 2,414 g (SD = 243, n = 201) in the barren pens. Preslaughter mortality was low: five of 102 animals in the welfare-friendly pens and three of 204 animals in the barren pens.

For the duration of the entire fattening period (from weaning to slaughter), no differences in BW gain, ADFI, or G:F were found between rabbits housed in the welfare-friendly pens vs. barren pens (Table 1). The only significant difference found between treatments concerned the period immediately after weaning, in which BW gain was greater for rabbits in the welfare-friendly pens compared with rabbits in the barren pens during the first 14 d after weaning ($P < 0.05$). Although not statistically significant, there was a trend that during the same period the ADFI was greater for rabbits in the welfare-friendly vs. barren pens. Given the limited power of the latter test, this trend could be biologically meaningful. Overall, G:F was very similar between rabbits from the welfare-friendly and barren pens.

FA: Measurements on Intact Carcasses

Of the 11 traits that were measured on intact carcasses, only four were found not to be directionally asymmetrical (Table 2). Of these four, only the length of the upper incisors and the eye-to-nostril distance had a significant amount of FA. The former trait may not be considered suitable because its negative kurtosis

Table 1. Mean (± SE) production traits of rabbits housed in welfare-friendly vs. barren pens[a]

Production trait (per 2-wk period)	Welfare-friendly pens	Barren pens
BW gain, g/d		
d 29 to 43	46.25 ± 0.59	43.93 ± 0.52*
d 43 to 57	46.80 ± 0.85	46.53 ± 0.54
d 57 to slaughter[b]	36.74 ± 0.76	35.98 ± 0.56
d 29 to slaughter[b]	43.45 ± 0.48	42.34 ± 0.34
ADFI, g/d[c]		
d 29 to 43	96.07 ± 2.26	91.34 ± 1.11†
d 43 to 57	140.78 ± 2.50	139.21 ± 2.06
d 57 to slaughter[b]	147.83 ± 3.49	146.85 ± 2.86
d 29 to slaughter[b]	127.10 ± 2.30	125.24 ± 1.63
G:F[c]		
d 29 to 43	0.47 ± 0.004	0.48 ± 0.003
d 43 to 57	0.33 ± 0.005	0.33 ± 0.001
d 57 to slaughter[b]	0.25 ± 0.006	0.25 ± 0.003
d 29 to slaughter[b]	0.34 ± 0.004	0.34 ± 0.001

[a]n = 102 (welfare-friendly pens) and n = 204 (barren pens).
[b]Age at slaughter ranged from 63 to 72 d.
[c]As-fed basis, n = 6 per treatment.
†$P < 0.10$.
*$P < 0.05$.

value is indicative of antisymmetry, such that only one trait remains (eye-to-nostril distance); however, signal:noise indicates that the measurement error of this trait was almost as large as the amount of FA. Hence, the measurements on intact carcasses were judged unsuitable for estimating the degree of FA in rabbits and were consequently not used for further analyses.

FA: Measurements on Fleshed Bones

Fleshing bones allowed traits to be measured in many different ways, taking different end and start points. Of the 50 types of measurement, 41 had a significant amount of FA and no directional asymmetry (Tables 3 and 4; further details can be found at http://www.clo.fgov.be/dvl). If the threshold for signal:noise was set at 20, nine trait measurements remained (Table 3). None of these nine trait measurements had to be discarded because of antisymmetry; however, four trait measurements were discarded because they were correlated in their signed FA values with another trait with higher signal:noise. The remaining five trait measurements (coded mandibula 2, femur 1, scapula 7, pelvis 3, and cranium 1; Figure 1) were selected to yield an accurate estimation of the degree of FA in rabbits. Only these traits were measured in the remaining 54 individuals and used for further analyses.

Effect of Treatment on FA

Adjusting for variation because of pen and litter effects, the degree of FA differed between both treatments ($P < 0.05$). Rabbits from the welfare-friendly pens were more symmetrical than were rabbits from the barren pens.

Association between Production Traits and FA

Adjusting for effects because of pen, litter, and animal-days, the correlation between the degree of FA and total BW gain during the postweaning period depended

Table 2. Statistics used in the procedure for selecting morphological traits measured on intact carcasses that provide the best estimates of the degree of fluctuating asymmetry (FA)[a]

Trait (Cut-off level)	DA[b] ($P > 0.05$)	FA[b] ($P < 0.05$)	Signal to noise ratio (>20)[c]	AS[b] (kurtosis >0)[d]
Upper incisor	**0.223**	**0.027**	0.8	–1.0
Claw digit 1, front paw	<0.001	**0.019**		
Nostril	<0.001	**0.002**		
Eye – nostril	**0.466**	**0.009**	1.1	0.5
Lower incisor	<0.001	1.000		
Eye – ear	0.043	**<0.001**		
Ear	0.006	**0.014**		
Ear – upper incisor	0.003	0.290		
Wrist	<0.001	0.060		
Knee – heel	**0.199**	0.120		
Heel – toe	**0.565**	1.000		

[a]Values are probability of directional asymmetry (DA), probability of FA, signal to noise ratio, and kurtosis value as an index of antisymmetry (AS). Levels of acceptance are indicated between parentheses. Traits meeting these criteria are indicated in **bold**. Correlations between traits in their signed FA values are not indicated. Signal to noise ratio and kurtosis are given only for traits with a significant amount of FA, not DA.
[b]Fluctuating asymmetry is defined as the deviation from symmetry in bilateral morphological traits for which signed differences between right and left sides at the population level have a mean of zero and a near-normal distribution. Directional asymmetry occurs when the mean of asymmetry values differs significantly from zero, whereas antisymmetry is a pattern of bilateral variation in which statistically significant differences exist between sides, but the side that is larger varies randomly among individuals.
[c,d]These cut-off points are not stringent.

Table 3. Statistics used in the procedure for selecting morphological traits measured on fleshed bones that provide the best estimates of the degree of fluctuating asymmetry (FA)[a]

Trait (Cut-off level)	DA ($P > 0.05$)	FA ($P < 0.05$)	Signal to noise ratio (>20)[b]	AS (kurtosis >0)[b]
Mandibula 2	**0.366**	**<0.001**	**2138.2**	**29.8**
Femur 1	**0.076**	**<0.001**	**131.4**	**11.0**
Scapula 7	**0.980**	**<0.001**	**76.1**	**5.3**
Femur 5	**0.139**	**<0.001**	**51.0**	**15.1**
Pelvis 3	**0.232**	**<0.001**	**37.1**	**0.9**
Tibia/fibia 4	**0.545**	**<0.001**	**28.7**	**13.2**
Cranium 1	**0.292**	**<0.001**	**23.4**	**1.2**
Ulna 1	**0.098**	**<0.001**	**23.0**	**1.2**
Radius 1	**0.543**	**<0.001**	**21.4**	1.2

[a]Values indicate correlation with a trait with a higher signal to noise ratio, probability of directional asymmetry (DA), probability of FA, signal to noise ratio, and kurtosis value as an index of antisymmetry (AS). Levels of acceptance are indicated between parentheses. Traits meeting these selection criteria are indicated in **bold**. Data are given for traits with a signal to noise ratio >20 only (nine of 50 trait measurements). Signed FA values of the following traits were correlated ($P < 0.10$): femur 1 with femur 5 and radius 1, scapula 7 with tibia/fibia 4, femur 5 with pelvis 3, cranium 1 with ulna 1, and ulna 1 with radius 1.

[b]These cut-off points are not stringent.

on the treatment (BW gain × treatment; $P = 0.01$). In the welfare-friendly pens, there was no correlation between BW gain and degree of FA, whereas in the barren pens, this correlation was highly significant ($P < 0.01$). In the barren pens, rabbits that achieved the least BW were most asymmetrical (Figure 2).

Discussion

To estimate FA in rabbits reliably, results of this study indicate that measurements should to be carried out on fleshed bones rather than on intact carcasses. Only one trait measured on intact carcasses showed a significant amount of FA without indications of antisymmetry or directional asymmetry. Estimating the degree of FA of an individual based on this single measurement would not be reliable because the measurement error was found to be as large as the amount of FA detected in this trait. Moreover, analyses that combine information across traits are believed to be more powerful in detecting relationships among FA, stress, and fitness than single-trait analyses when organism-wide asymmetry is expected (Leary and Allendorf, 1989; Watson and Thornhill, 1994). When the flesh was removed, many more suitable trait measurements were found, of which five were selected for further analyses and can be recommended for estimating FA in rabbits. These traits are not correlated in their signed FA values and have a high signal-to-noise ratio.

Using this robust protocol for estimating FA in rabbits, individuals housed in enriched, low-density pens were found to be less asymmetric than those housed in barren, high-density pens. The types of environmental enrichment, as well as the lowering of stocking density in the welfare-friendly pens, were carefully selected to promote rabbit welfare. Indeed, crowding and the lack of environmental enrichment are key factors responsible for serious welfare problems in intensive husbandry of fattening rabbits (Stauffacher, 1992; Verga, 2000). Crowding and a barren environment have been associated with changes in locomotion, abnormal behaviors, aggression, restlessness, panic reactions, and space-time disorders (Stauffacher, 1992; Bigler and Oester, 1996; Morisse and Maurice, 1997). The welfare-friendly

Table 4. Comparison of measurements on intact carcasses vs. fleshed bones regarding meeting cumulative criteria of the procedure for selecting suitable traits for estimating fluctuating asymmetry (FA)

Item	Intact carcasses	Fleshed bones
No. of trait measurements	11	50
Trait measurements remaining without significant DA[a]	4	41
Trait measurements remaining with significant FA	2	41
Trait measurements remaining without indication for AS[ab]	1	34
Trait measurements remaining with signal:noise >20	0	9
Trait measurements remaining without correlation in signed FA†	0	5

[a]DA = directional asymmetry; AS = antisymmetry.

[b]Kurtosis <0.

†$P < 0.10$.

Figure 1. The five selected trait measurements for estimating fluctuating asymmetry in fattening rabbits (the left-hand side measurements only are indicated). From left to right: cranium 1 (most dorsal point of nasale—sutura interfrontalis), mandibula 2 (dens incisivus—processus angularis), scapula 7 (processus hamatus—processus suprahamatus), pelvis 3 (pecten ossis pubis—foramen nutricium ossis ilii), and femur 1 (transition from caput ossis femoris to trochanter major—distal side of cartilago trochleae ossis femoris).

pens were enriched with materials recommended by the 1991 Swiss Order on Animal Protection: a wooden gnawing stick (straw or hay were not chosen because of hygiene and performance concerns; Morisse et al., 1999; Maertens and Van Oeckel, 2001; Dal Bosco et al., 2002) and a dark hiding box for shelter and withdrawal. In addition, an elevated platform was provided to increase environmental complexity and floor surface (Finzi et al., 1996). Rabbits use raised heights as a look-out and resting place. Such enrichments have been reported to fulfill behavioral needs and increase rabbit welfare (Hansen and Berthelsen, 2000). The space allowance in the welfare-friendly pens (0.112 m^2 per subject) was well above the thresholds recommended by Maertens and De Groote (1984), Morisse and Maurice (1997), and various codes of welfare for the husbandry of rabbits (Verga, 2000). The space allowance in the barren pens (0.056 m^2 per rabbit), however, was below or approximated most of these minimum allowances. The welfare-friendly pens not only had lower stocking density but also had smaller group size than the barren pens. Bigler and Oester (1996) reported more injuries and aggressive behavior with increasing group size. Hence, we are quite confident that the combined effect of environmental enrichment, decreased stocking density, and decreased group size in the welfare-friendly pens was beneficial for rabbit welfare compared with the barren pens.

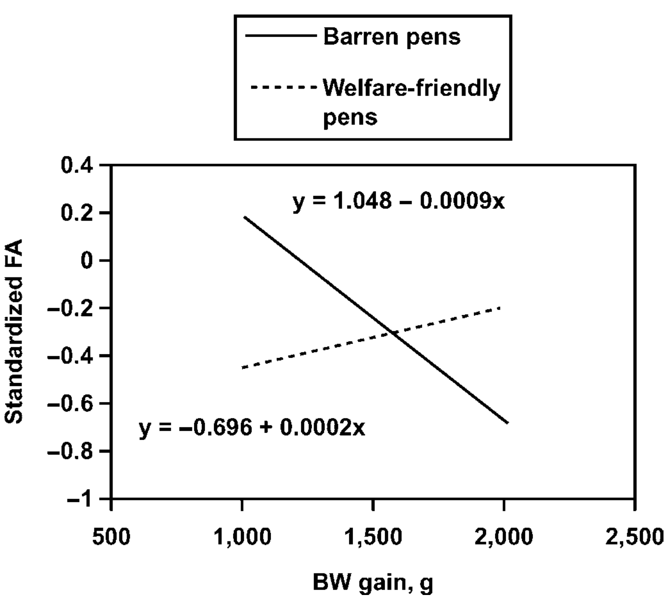

Figure 2. Estimated relationship between standardized fluctuating asymmetry (FA) and total BW gain (from weaning until slaughter) of rabbits housed in the barren pens vs. enriched pens.

Consequently, our findings agree with the hypothesis that FA is a useful and valid indicator of the quality of an animal's environment during its development and, thereby, of its welfare. Other evidence in support of this hypothesis is largely restricted to poultry (Tuyttens, 2003). Nevertheless, even in poultry, the use of FA as a general farm animal welfare measure cannot be considered to have been validated adequately because 1) Campo et al. (2000, 2002) reported that associations between FA and other welfare indicators are not general but are breed-, sex-, and trait-specific; 2) a robust methodology for selecting (as developed in the present study for rabbits) and analyzing (Lens et al., 2002) FA has rarely been used; 3) FA has been correlated only with single welfare indicators, but never with an overall welfare score; and 4) the majority of these welfare indicators concern biological fitness, whereas welfare has been argued to be primarily related to emotive states (Duncan, 1996).

Contrary to the level of FA, performance traits were hardly affected by improving the housing conditions of the rabbits. Daily BW gain was greater in the welfare-friendly pens than in barren pens, but this effect was restricted to the first 14 d after weaning. Neither feed intake nor G:F were affected by treatment. In the literature, the effect of stocking density and/or enrichment on production traits is equivocal. A negative correlation between density and growth rate or final live BW has been reported in many studies (Maertens and De Groote, 1984; Aubret and Duperray, 1992; Hamilton and Lukefahr, 1993), although others found no effect (Maertens and De Groote, 1985; Xiccato et al., 1999). Maertens and Van Oeckel (2001) found no effect of pen enrichment with a straw hopper or a wooden gnawing stick on performance traits. Mirabito et al. (2000) also found no effect of providing a wooden stick or hay on growth rate or feed intake. Within populations (i.e., at the level of the individual), BW gain was negatively correlated with the degree of FA in the barren pens. This finding confirms the general negative relationship between developmental instability and various fitness components such as growth, fecundity, and longevity reported by Møller (1997, 1999); however, BW gain was not correlated with FA in the enriched pens. Such a pattern agrees with the implicit, yet largely untested, hypothesis that FA is a more reliable estimator of the underlying developmental instability when living conditions are suboptimal (Palmer, 1994; Leung and Forbes, 1997; Lens et al., 2002). Under such conditions, "low-quality" individuals may face increasing difficulties in allocating sufficient energy to maintain high levels of developmental stability and thereby may become "unmasked" by their higher levels of FA. This extra complexity might explain why inconsistencies in the relationship between FA and fitness components have been noted (Clarke, 1995, 1998; Leung and Forbes, 1996).

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