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Does cardiovascular performance of modern fattening pigs obey allometric scaling laws?

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ABSTRACT: In view of the remarkable decrease of the relative heart weight and the relative blood volume in growing pigs, we investigated whether cardiac output (CO) and stroke volume (SV) of modern growing pigs are proportional to body mass (M), as predicted by allometric scaling laws: CO (or SV) = $a \cdot M^b$, in which b is a multitude of 0.25 (quarter power scaling law). Specifically, we tested the hypothesis that CO scales with M to the power of 0.75 ($CO = a \cdot M^{0.75}$) and SV scales with M to the power of 1.00 ($SV = a \cdot M^{1.0}$) and investigated whether these relations persisted during increased cardiac stress. For this purpose, 2 groups of pigs (group 1 of 57 ± 3 kg in Lelystad, and group 2 of 28 ± 1 kg in Rotterdam) were chronically instrumented with a flow probe to measure CO and SV; instrumented pigs were studied at rest and during strenuous exercise (at ~85% of maximum heart rate). Analysis of both groups of pigs (analyzed separately or combined) under resting conditions demonstrated that the 95% confidence intervals of power-coefficient b for CO encompassed 0.75 and for SV encompassed 1.0. During exercise, similar results were obtained, except for SV in group 2, in which the 95% confidence limits remained below 1.0, which may have been due to the relatively small range of BW in group 2. These observations indicate that CO and SV of growing pigs with M less than 75 kg are still proportional to M, even during strenuous exercise, and that CO and SV scale with M according to the quarter power scaling laws. In conclusion, the concerns about disproportional growth and development of modern growing pigs with BW up to 75 kg were not confirmed by the present study.

Key words: cardiac output, cardiovascular system, domestication, exercise, growing pig, scaling law

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INTRODUCTION

Domestication of pigs began approximately 9,000 yr ago, resulting in marked differences in anatomy and physiology with its ancestor, the wild boar (Darwin, 1868; Hemmer, 1990; Jones, 1998; Giuffra et al., 2000). During the last century in particular, pig breeding has been dominated by selection based on meat quantities and other economic aspects, which has yielded remarkable increases in skeletal muscularity as well as litter size (Müller et al., 1999). This economy-driven selection process has inadvertently resulted in alterations of anatomy and physiology of the cardiovascular system of the domesticated pig, including reduced relative heart weight (**RHW**), blood volume, and hemoglobin concentration (van Engelhardt, 1966; Huisman, 1969; Schürmann, 1984). Wachtel (1963) measured cardiac output (**CO**) of anesthetized pigs and wild boar and observed that CO of farm pigs reached a plateau above 50 kg, resulting in a marked decrease in relative CO per kilogram of BW. Van Engelhardt (1966) postulated that all these cardiovascular alterations could contribute to an unstable circulatory system in pigs, but emphasized that our understanding of cardiovascular physiology of domesticated pigs was fragmentary and that there was a serious lack of data, especially CO data, in conscious animals. Similar concern was raised more recently by Niewold et al. (2000) that the relatively small heart, blood volume, and decreased hemoglobin concentration could limit CO and hence cardiovascular adaptability to stress. The consequent increased risk of circulatory insufficiency or failure might even contribute to persistent pig diseases such as edema disease and transport-associated health problems (Niewold et al., 2000).

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In wild animals, heart weight and CO have been shown to scale with body mass (**M**) to the power of 0.75, blood volume scales with M to the power of 0.25, and stroke volume (**SV**) scales with the power of 1.00 (West et al., 1997; West and Brown, 2005). The present study was undertaken to test the hypothesis that CO and SV of modern growing pigs are proportional to their M as predicted by the quarter scaling laws (H_0: CO = $a{\cdot}M^{0.75}$; and H_0: SV = $a{\cdot}M^{1.0}$). For this purpose, we collected and analyzed CO data of 60 chronically instrumented, awake pigs with BW ranging from 22 to 75 kg. Because a deviation from the established scaling law would be most likely detected under conditions of increased physical load, animals were studied both at rest and during heavy treadmill exercise.

MATERIALS AND METHODS

All studies were performed in accordance with the Council of Europe Convention (ETS123)/Directive (86/609/EEC) for the protection of vertebrate animals used for experimental and other scientific purposes, and with approval of the Animal Care Committees of the Animal Science Group (**ASG**) of Wageningen University and Research Centre (group 1, studies 1 to 3) or Erasmus University Medical Center Rotterdam (group 2, study 4).

Experimental Design

The present report encompasses the results obtained in 4 studies in chronically instrumented, growing, conscious pigs performed at Lelystad, the Netherlands (group 1, studies 1, 2, and 3) and in Rotterdam, the Netherlands (group 2, study 4). The Lelystad studies were performed to investigate the influence of daily exercise training (study 1), husbandry system (study 2), and genetics (study 3) on cardiac performance during strenuous exercise. The Rotterdam data were obtained as part of ongoing studies pertaining to regulation of cardiac performance during strenuous exercise (study 4).

After arrival in Lelystad and at least 1 wk before surgery, all pigs were housed 3 pigs to a pen. After surgery, pigs were housed individually on 1.8-m^2 indoor space at the animal facility of ASG at Lelystad. After arrival in Rotterdam and at least 1 wk before surgery, all pigs were housed separately with 1 pig per pen at the animal facility of Erasmus University Medical Center. All pigs were given ad libitum access to regular dry pelleted food. Furthermore, all pigs were familiarized to run on a treadmill before surgery. Subsequently, pigs were instrumented for measurement of heart rate, SV, and CO at rest and during strenuous exercise testing.

Surgical Instrumentation

Group 1: Studies 1 to 3. Pigs received ampicillin (15 mg/kg, intramuscularly; AUV, Cuijk, the Netherlands) 24 h before surgery and were deprived of food for 16 h before surgery. Surgical instrumentation was carried out under general anesthesia. Pigs were sedated with ketamine (10 mg/kg, intramuscularly; AUV) combined with midazolam (0.75 mg/kg, intramuscularly; AUV). Anesthesia was deepened for induction with sufentanil (1 μg/kg, intravenously) and mivacurium (0.4 mg/kg, intravenously; OPG, Staphorst, the Netherlands). Pigs were intubated and mechanically ventilated (tidal volume 13 mL/kg and 13 breaths/min) with a mixture of air and O_2 (3:2) and 2.5% sevoflurane (OPG). Anesthesia was maintained with rocuroniumbromide (5 $mg{\cdot}kg^{-1}{\cdot}h^{-1}$, intravenously; OPG) and sufentanil (1 $\mu g{\cdot}kg^{-1}{\cdot}h^{-1}$, intravenously; OPG). The chest was opened via the fourth left intercostal space. The pericardial space was opened and the ultrasonic CO flow probe 20A (Transonic Systems Inc., Ithaca, NY) was placed around the pulmonary artery. The pericardial space and the thorax were closed with soluble sutures, and the probe wire was tunneled from the thorax wound under the skin to the dorsal region just between the shoulders. Ampicillin was repeated on d 1 and 3, and the pigs received the daily injections of the analgesic agent flunixine (2 mg/kg, intramuscularly; AUV), during the first 2 d after surgery.

Group 2: Study 4. Pigs were sedated with ketamine (30 mg/kg intramuscularly; AUV), anesthetized with thiopental (10 mg/kg intravenously; AUV), intubated, and ventilated with a mixture of O_2 and N_2O (1:2) to which 0.2 to 1% (vol/vol) isoflurane (AUV) was added (Stubenitsky et al., 1998; Duncker et al., 2001; Merkus et al., 2007). Anesthesia was maintained with midazolam (2 mg/kg followed by 1 $mg{\cdot}kg^{-1}{\cdot}h^{-1}$ intravenously) and fentanyl (10 $\mu g{\cdot}kg^{-1}{\cdot}h^{-1}$ intravenously). Under sterile conditions, the chest was opened via the fourth left intercostal space, and a fluid-filled polyvinylchloride catheter was inserted into the aortic arch for blood pressure measurement (Combitrans pressure transducers, Braun, Melsungen, Germany). An electromagnetic flow probe (14- to 15-mm, Skalar, Delft, the Netherlands) was positioned around the ascending aorta for measurement of CO. Catheters were tunnelled to the back, and animals were allowed to recover, receiving analgesia (0.3 mg of buprenorphine intramuscularly: AUV) for 2 d and antibiotic prophylaxis (25 mg/kg of amoxicillin and 5 mg/kg of gentamycin intravenously; AUV) for 5 d.

Experimental Groups

Group 1 Lelystad, Study 1: Daily Exercise Training. To investigate the influence of daily exercise training on cardiovascular performance, 9 female Dalland pigs from different litters with BW of 25.7 ± 1.4 kg (9.2 ± 0.5 wk) were obtained from the breeding farm of ASG of Wageningen University and Research Centre at Raalte, the Netherlands. During the second postsurgical week, pigs underwent treadmill running at ~2 km/h for 20 min on 3 d (Monday, Wednesday, and

Friday). Two weeks after surgery, all pigs were able to run a full exercise test. The training group (n = 5) was subsequently exercised on a treadmill at 0% grade during 4 wk for 5 consecutive days (Monday through Friday) each week. The training protocol consisted of 3 min of warming-up exercise at 1.2 km/h, followed by 4 min at 1.9 km/h, 5 min at 3 km/h, and 10 min at 3.6 km/h, followed by exercise at a maximal speed of 4.2 km/h, until exhaustion. Hemodynamic measurements were obtained once every week (Friday). The control group (n = 4) stayed in their pens for 4 wk and underwent hemodynamic measurements at the beginning and at the end of the 4-wk period. For this purpose, pigs were placed on the treadmill and flow probes were connected to the flow meter (Transonic Systems T 450) that was connected to a computer. The mean flow (L/min) and the treadmill speed were recorded every 20 s by the IOX data acquisition and analysis software (EMKA, Paris, France) on the computer. Heart rate was derived from the flow signal by the IOX software. After resting measurements (heart rate 80 to 120 beats/min) were obtained, a staged exercise protocol was performed, consisting of 3 min of warming-up exercise at 1.2 km/h, followed by 4 min at 1.9 km/h, 5 min at 3 km/h and 10 min at 3.6 km/h, followed by exercise at a maximal speed of 4.2 km/h until exhaustion during 12.3 ± 2.1 min. Pigs were considered to be exhausted when they stopped running and attempted to sit or lie down on the treadmill.

Group 1 Lelystad, Study 2: Zoo-Technical Influence: Organic Vs. Conventional Husbandry. To investigate the influence of environmental and or zoo-technical variables like food, feeding patterns, housing, and freedom of movement on cardiovascular performance, 8 female half sisters, 3/4 great Yorkshire and 1/4 Dutch Landrace pigs, who shared the same father, were obtained from the breeding center of ASG at Raalte and subjected to exhaustive treadmill exercise. Four pigs had been reared under organic conditions and the other 4 under conventional conditions. The organic group was continuously fed organic food (ingredients on as-fed basis: CP: 15.7%, Lys: 083%, crude fiber: 4.0%, ME: 13.47 MJ/kg) composed of ingredients cultivated without fertilizer, the conventional group was fed a regular food (ingredients on as-fed basis: CP: 16.3%, Lys: 0.96%, crude fiber: 4.4%, ME: 13.55 MJ/kg). Another important difference is that conventionally reared piglets were weaned at 28 d vs. organic piglets at 42 d. Finally, organic pigs had more freedom of movement at the breeding farm. Thus, conventional pigs had just 0.4 m^2 per piglet, whereas organic piglets had 0.6 m^2 inside room and 0.4 m^2 outside room. Upon arrival in Lelystad, BW were 36.3 ± 1.7 kg for conventional pigs and 42.6 ± 4.7 kg for organic pigs. Two weeks after surgery, pigs ran their final test on the treadmill, identical to the procedures described for study 1.

Group 1 Lelystad, Study 3: Influences of Genetics. To investigate the influence of genetic background on cardiovascular performance, 2 purebred strains (Piétrain and Duroc) and 1 crossbred strain (Dalland) were compared for cardiovascular performance during exhaustive treadmill exercise. The Duroc and Piétrain strains differ in growth phenotype; Duroc pigs and their offspring have been found to grow faster, but also have more backfat. Piétrain-sired pigs are leaner than Duroc-sired pigs (Edwards et al., 2008). Piétrain pigs have 5 to 10% more meat than comparable pigs of other breeds (Houba and te Pas, 2004). The Dalland pig was a synthetic line of Piétrain and Large White (de Vries and Loenen, 2007). After the Dalland breeding group merged into the TOPIGS group, the Dalland sow was renamed as the TOPIGS 40 sow, which shows excellent utility characteristics and economic piglet production. For this study, 6 Duroc, 6 Dalland, and 6 Piétrain gilts were all obtained from TOPIGS (Vught, the Netherlands). All 3 strains consisted of 2 BW groups each compassing 3 pigs: Duroc 24.7 ± 0.3 kg (8.0 ± 0.2 wk) and 34.8 ± 1.0 kg (11.9 ± 0.3 wk), Dalland 25 ± 0.4 kg (7.8 ± 0.4) and 35.1 ± 0.6 kg (11.9 ± 0.4 wk), and Piétrain 25.3 ± 0.3 kg (8.2 ± 0.5 wk) and 35.4 ± 0.5 kg (12.3 ± 0.5 wk). All 3 BW-matched pigs of each strain were kept in 1 pen until surgery, after which pigs were housed individually. Two weeks after surgery pigs ran 3 tests (as described under study 1) on Monday, Wednesday, and Friday within 1 wk.

Group 2 Rotterdam, Study 4: Cardiovascular Performance in Young Pigs. Twenty-eight Yorkshire × Landrace pigs, 8 to 12 wk old and 23 ± 1 kg at the time of surgery, of either sex were obtained from a commercial breeding farm and housed separately. After surgery, pigs performed exercise test at 10 ± 1 d (26 pigs) and 24 ± 1 d (16 pigs). Pigs were placed on the treadmill and aortic blood pressure, CO, heart rate, and SV were measured at rest and during a consecutive 5-stage exercise protocol with pigs exercising at 1, 2, 3, 4, and 5 km/h and each stage lasting 2 to 3 min.

Statistical Analyses

The different experiments have different number of observations per animal during rest and exercise at different BW. The CO of the animals was measured at rest and during exercise at each BW. Therefore a randomly selected BW of each animal was taken for the analysis with the corresponding CO observations at rest and during exercise.

Mean heart rate, mean CO, and mean SV were compared at rest vs. during maximal exercise using a linear mixed effects model (Pinheiro et al., 2007) with a normal distribution for the outcome with pig as random effect to model the correlation between the repeated observations within pig. The random effect was assumed to have a normal distribution.

To model the function $Y = a.M^b$, the data were analyzed using a linear mixed effects model (Pinheiro et al., 2007) with a normal distribution for the outcome with pig as random effect to model the correlation between the repeated observations within pig.

Table 1. Hemodynamics at rest and during strenuous exercise[1]

Group	n	BW, kg	CO, L/min Rest	CO, L/min Exercise	Heart rate, bpm Rest	Heart rate, bpm Exercise	SV, mL Rest	SV, mL Exercise
Group 1 Lelystad								
Study 1 Control	4	48 ± 6	9.2 ± 1.8	13.8 ± 1.3	157 ± 15	256 ± 15	56 ± 5	53 ± 4
Study 1 Trained	5	43 ± 4	8.1 ± 1.1	13.6 ± 1.3	131 ± 9	258 ± 11	62 ± 8	52 ± 5
Study 2 Regular	4	48 ± 1	6.8 ± 0.4	15.3 ± 0.6	118 ± 5	255 ± 3	57 ± 2	60 ± 3
Study 2 Organic	4	55 ± 3	7.1 ± 0.6	14.8 ± 1.1	105 ± 4	222 ± 4	69 ± 8	67 ± 6
Study 3 Dalland	5	67 ± 1	8.8 ± 0.3	18.5 ± 0.8	112 ± 3	255 ± 8	78 ± 3	72 ± 2
Study 3 Duroc	5	70 ± 1	11.9 ± 0.9	19.1 ± 1.1	133 ± 6	251 ± 7	89 ± 4	78 ± 5
Study 3 Pietrain	5	64 ± 2	10.7 ± 1.3	18.5 ± 1.1	118 ± 6	243 ± 13	90 ± 8	76 ± 2
Studies 1 to 3 pooled	32	57 ± 3	9.1 ± 0.5	16.4 ± 0.6*	125 ± 4	249 ± 4*	73 ± 3	66 ± 2*
Group 2 Rotterdam								
Study 4	28	28 ± 1	3.6 ± 0.1	8.0 ± 0.2*	120 ± 4	256 ± 1*	31 ± 1	32 ± 1

[1] All data are presented as means ± SE; *$P < 0.05$ versus corresponding Rest (statistical analysis for exercise effects was only performed for studies 1 to 3 pooled and for study 4); CO = cardiac output; SV = stroke volume.

This formula was e-log-transformed to estimate the constant a and regression coefficient b: log(Y) = log(a) + b·log(M). The random effect was assumed to have a normal distribution. This model was fitted with CO (Y) as the dependent variable and with M as the independent variable. Also, an interaction term between M and the physical performance level was added to the model to estimate the coefficients a and b for both performance levels separately. The same model was used with SV as dependent variable Y. The maximum likelihood method was used to estimate the variable effects. The best model per experiment was selected using the AIC criterion (Pawitan, 2001). The 95% confidence intervals were based on the degrees of freedom calculated by the analysis. The models were fit using the statistical program R (R Development Core Team, 2007). The Lelystad and Rotterdam data were analyzed separately and combined.

RESULTS

Table 1 shows average hemodynamic data at rest and during strenuous exercise of Lelystad pigs of group 1 (studies 1, 2, and 3) and Rotterdam pigs of group 2 (study 4). Exercise at 85% of maximum heart rate resulted in a near doubling of the CO in both groups of pigs. This was principally due to an increase in heart rate because SV was either unchanged (group 2) or even slightly decreased (group 1). Interestingly, it has been shown that whereas during prolonged exercise CO remains constant, heart rate increases slightly, which is accompanied by an equivalent decrease in SV (Coyle and González-Alonso, 2001). Thus, it is possible that the longer duration of exercise in the pigs of group 1 (total exercise time ~35 min) may have resulted in a small decrease in SV, whereas during the much shorter exercise test in group 2 (total exercise time < 15 min) such a decrease did not occur.

To test the hypothesis that CO and SV of modern growing pigs are proportional to its body size as predicted by the quarter scaling laws (H_0 of CO: b = 0.75; H_0 of SV: b = 1.0), we plotted CO and SV as a function of M for the Lelystad and Rotterdam pigs (Figure 1). Within group 1 there was no effect ($P > 0.05$) of exercise training (probably due to the relatively mild intensity and short duration of each training session and overall training period), husbandry or genetic strain on CO and SV. Therefore pigs from studies 1, 2, and 3 were pooled. Table 2 shows the expected exponent of CO of 0.75 falls within the 95% confidence interval of all the Lelystad and Rotterdam pigs at rest and during exercise. The expected exponent of SV of 1.00 falls also well within the 95% confidence interval of all the Lelystad and Rotterdam pigs at rest and during exercise except the exercising pigs of study 4 (95% confidence interval: 0.02 to 0.85).

DISCUSSION

Domestication of the pig has resulted in a dramatic increase of muscularity, litter size, and growth rate. At the beginning of the 19th century, pigs needed 2 to 3 yr to reach a BW of 40 kg (Huisman, 1969). Currently, fattening pigs reach their slaughter weight of 110 kg within one-half year. The RHW (heart weight normalized to BW) declines during growth. At 4 wk, the RHW of the piglet is 0.82%, and at 110 kg it is decreased to 0.25 to 0.30%, which is reduced in comparison with the adult wild boar (0.64%), horse (0.7 to 1.1%), and human (0.5%; Van Engelhardt, 1966). The RHW of domesticated pigs at the end of the 19th century was 0.45% (Huisman, 1969). Thus, the rate of RHW declined from 0.45 to 0.25% during the last century and is similar to the rate of RHW decline from 0.64 to 0.45% that occurred during the foregoing 9,000 yr of domestication. Modern growing pigs exhibit a significant decrease of blood volume during growth. The relative blood volume of a 20-kg growing pig was 117 mL/kg, decreasing to 68 mL/kg at around 110 kg of BW (Yang and Lin, 1997). Wild boar has a substantially greater hemoglobin concentration; the blood of wild boar is able to carry 25 to 40% more oxygen than that of modern pigs of the same

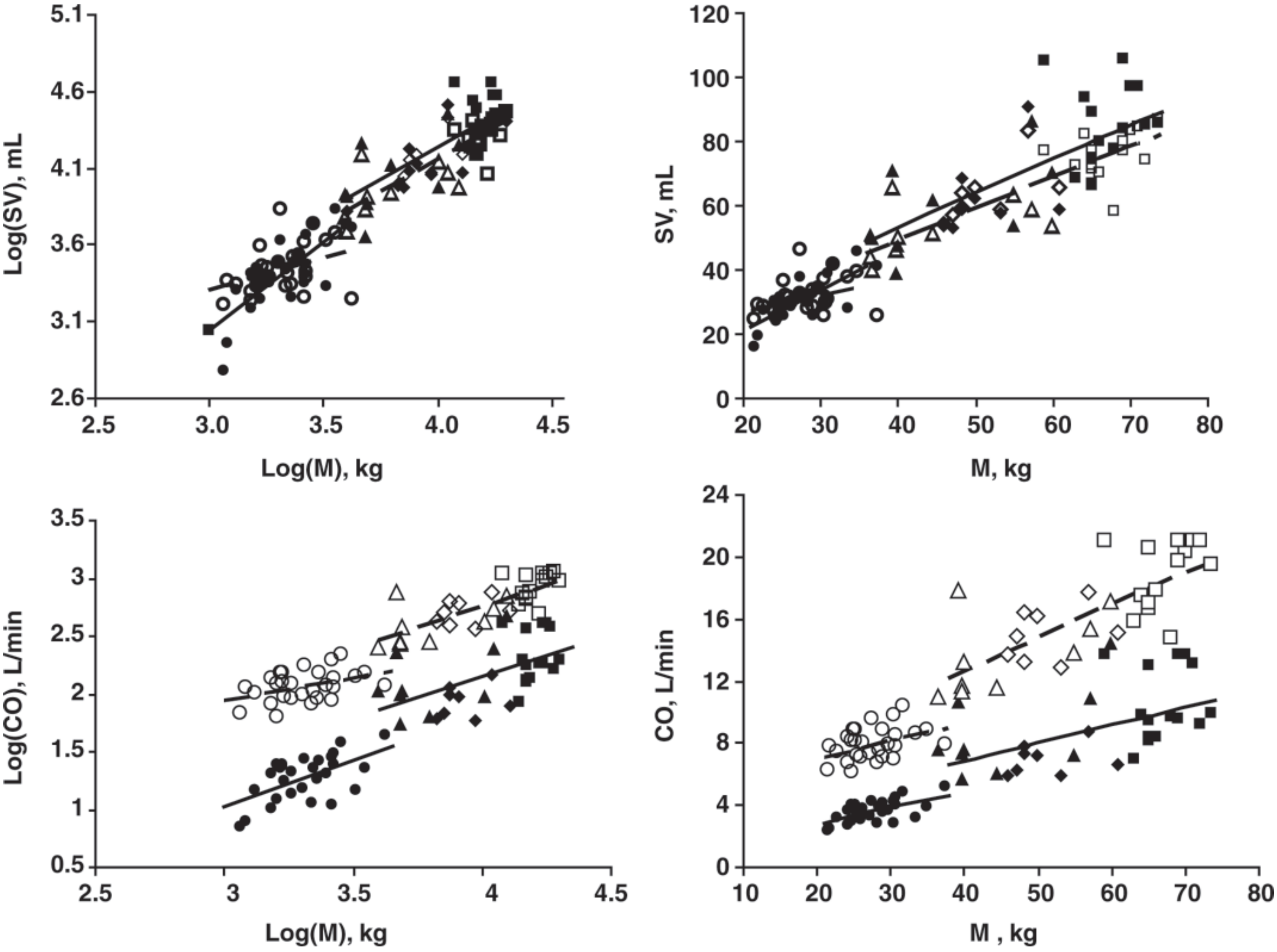

Figure 1. Relations between body mass (M) and stroke volume (SV; upper panels) and M and cardiac output (CO; lower panels) in resting (solid symbols and solid lines) and exercising (open symbols and dashed lines) from Lelystad studies 1 (triangles), 2 (diamonds), and 3 (squares) and from Rotterdam study 4 (circles). Data have been plotted on linear (right panels) and logarithmic (left panels) scales.

BW (Van Engelhardt, 1966). Wachtel (1963) measured CO of anesthetized pigs and wild boar and observed leveling off of the CO in growing fattening pigs with M above ~50 kg. Thus, the CO of the heaviest pigs with BW ranging from 91 to 96 kg was almost similar to the CO of the 43 to 53 kg group. All these observations raise concern regarding a loss of proportionality, scaling, and adaptability of the cardiovascular system of growing pigs at BW of up to 75 kg compared with their BW-matched wild counterparts.

Van Engelhardt (1966) and Niewold et al. (2000) reported the relatively small heart, decreased blood volume, and reduced hemoglobin concentrations of growing pigs and raised concern about their cardiovascular stability and adaptability. However, information regarding the cardiovascular system of the pig in relation to body size is fragmentary, and especially CO measurements in conscious growing pigs were lacking to date. Consequently, in the present study we addressed this question by collecting and analyzing CO and SV data of 60 con-

Table 2. Confidence intervals of coefficient b[1]

Location	Activity	CO	SV
Group 1 Lelystad	Rest	0.41 to 1.04	0.63 to 1.05
	Exercise	0.40 to 1.03	0.63 to 1.05
Group 2 Rotterdam	Rest	0.43 to 1.20	0.74 to 1.5
	Exercise	−0.01 to 0.76	0.02 to 0.85
Total	Rest	1.03 to 1.26	1.05 to 1.25
	Exercise	0.80 to 1.03	0.86 to 1.06

[1] Data shown are the 95% confidence intervals for coefficient b for CO ($CO = a{\cdot}M^b$) and SV ($SV = a{\cdot}M^b$); CO = cardiac output; SV = stroke volume; M = body mass.

scious growing pigs with BW ranging from 22 to 75 kg, both at rest and during strenuous exercise. The latter was done, in light of the concern that modern fattening pigs have a poor cardiac adaptability to stress. All pigs showed adaptation of the CO during strenuous exercise with an approximate doubling of CO. In both groups of pigs the increase in CO was mainly due an increase in heart rate, as SV was unchanged (group 2) or slightly decreased (group 1). An essentially unchanged SV is in accordance with other exercise studies in young farm pigs (Stubenitsky et al., 1998; Merkus et al., 2007) and adult miniature pigs (Hastings et al., 1982; Armstrong et al., 1987).

Many physiological processes scale with animal size in a surprisingly simple fashion. Indeed, the cardiovascular system and its components, like heart weight, CO, heart rate, and blood volume scale with quarter power of body mass. The observed scaling is typically a simple power law: $Y = aM^b$, where Y is some observable for example CO, a is a constant, M is the body mass of the animal, and the exponent b almost invariably approximates a multitude of 1/4 (West and Brown, 2005). We tested the hypothesis that CO and SV of modern growing pigs are proportional to their body size as predicted by the quarter scaling laws (H_0 of $CO_:$ $b = 0.75$; H_0 of $SV_:$ $b = 1.00$). The calculated 95% confidence range of the coefficient b for CO of all groups encompassed 0.75 and the 95% confidential range for SV encompassed 1.00 for all groups except the exercised pig of study 4 (0.02 to 0.85). The different confidence interval of SV of the last group is remarkable and difficult to explain, but may have been, at least in part, the result of the relatively narrow BW range within the Rotterdam study. Alternatively, it is possible that an increase in arteriovenous oxygen extraction may have compensated for the reduced SV in group 2 but, unfortunately, such measurements were not performed in both groups and can therefore not be resolved in the present study. Importantly, analysis of pigs from both Lelystad and Rotterdam groups combined yielded 95% confidence limits that stay well above 0.75. Therefore, we submit that our investigation indicates proportionality and scaling of the cardiovascular system of growing pigs with BW until 75 kg.

Methodological Considerations

Although our study of CO and SV in conscious pigs is somewhat limited by BW range (28 ± 1 kg, group 2; and 57 ± 3 kg, group 1), by different pig breeding, laboratories, and slight differences in pig instrumentation, all 60 pigs were modern growing fattening pigs and the CO for all pigs was measured by direct blood flow measurement on the pulmonary artery or ascending aorta. Consequently, any major aberration from the scaling law (i.e., for CO: $b \leq 0.50$ and for SV: $b \leq 0.75$) should have been revealed in the present study. Nevertheless, the results from this study cannot be extrapolated to make any meaningful statements regarding the proportionality of CO and SV with BW of heavier pigs (200 to 300 kg). Future studies in adult heavy modern fattening pigs are clearly warranted to identify important factors in the unexplained pathogenesis of severe multifactorial animal disease (Niewold et al., 2000). Furthermore, pigs are extremely useful as an animal model to study diseases like obesity, diabetes mellitus and cardiovascular disease (van Engelhardt, 1966; Verdouw et al., 1998). The supposed disproportional development of the cardiovascular system could be an advantage to study, in modern fattening pigs, the cardiovascular consequences of obesity in human beings.

Conclusions

There is growing concern that modern fattening pigs display circulatory insufficiency during stressful events like weaning, fighting, or transport due to impairments in cardiovascular performance. During stress, blood flow is redistributed away from the intestines toward active skeletal muscle groups (Duncker et al., 2001). Circulatory insufficiency will aggravate this redistribution of blood flow away from the intestines, thereby increasing the risk of intestinal ischemia (Krack et al., 2005). Intestinal ischemia may subsequently lead to impairment of the gut barrier and result in increased translocation of gut microbes into the bloodstream (Niewold et al., 2000), increasing the likelihood of circulatory disease, impairment of animal welfare, and also a greater risk of contamination of meat that will increase the risk of food poisoning of pork consumers. Confirmation of this concern may require reconsideration of adjustments in the current genetic selection process, the way in which pigs are raised, or both. These concerns about disproportional growth and development of modern fattening pigs and consequently insufficiency of the cardiovascular system during stressful circumstances were, notwithstanding the limitations, not confirmed by the present study in pigs with BW up to 75 kg. Future studies in adult heavy pigs of over 250 kg of BW are required to assess whether scaling proportionality of CO and SV with M are maintained at these extreme BW.

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