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# Characterization of Swine Production Using Measurements Collected via Indoor Positioning System

Shaun Perisho

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CHARACTERIZATION OF SWINE PRODUCTION USING MEASUREMENTS

COLLECTED VIA INDOOR POSITIONING SYSTEM

by

Shaun Perisho

A Dissertation

Submitted to the Graduate School,  
the College of Education and Psychology,  
and the Department of Psychology  
at The University of Southern Mississippi  
in Partial Fulfillment of the Requirements  
for the Degree of Doctor of Philosophy

May 2018

CHARACTERIZATION OF SWINE PRODUCTION USING MEASUREMENTS

COLLECTED VIA INDOOR POSITIONING SYSTEM

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## ABSTRACT

Legislative and market initiatives are requiring that gestating sows move from individual housing to group settings. Little information is known about coping styles of individual sows in these more socially complex environments and thus the impact of different behavioral strategies on sow reproductive success and efficiency was investigated. The movements of 70 sows during periods of reintroduction into large pen gestational housing following insemination was measured with a commercially available system that tracked animal location and accelerations. Principle component analysis (PCA) was used to establish composite variables characterizing each animal's behavioral response to social reintroduction and revealed the presence of two new variables accounting for over 60% of the variance in behaviors: one pertaining to total movement and the other pertaining to social dominance/rapid movements. Component scores of total movement predicted measures of reproductive successes whereas social dominance/rapid movements predicted piglet birthweight. These findings suggest that different coping styles as measured by an automated, non-invasive, real time tracking system are correlated with the productivity of sows housing in socially complex settings.

## ACKNOWLEDGMENTS

Thank you to the staff at the Swine Teaching and Research Center of the University of Pennsylvania School of Veterinary Medicine. This wouldn't have made it off the ground without your help and guidance. I would also like to extend a special thank you to Mom, Dad, Christy, and Ryan for being my family and teammates at the same time. Finally, to Kristina and Devon – thank you for being there from the beginning.

## DEDICATION

This dissertation is dedicated to Annie Le.

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## CHAPTER I - INTRODUCTION

Behavioral flexibility is key to the survival of organisms faced with constantly changing environmental pressures throughout their lifespans (Dingemanse, Kazem, Réale, & Wright, 2010; Piersma & Drent, 2003; Réale & Dingemanse, 2010). In the same way that genetic diversity strengthens a population's overall fitness, behavioral diversity among conspecifics maximizes a group's ability to adapt to dynamic surroundings (Réale, Gallant, Leblanc, & Festa-Bianchet, 2000; Verbeek, Drent, & Wiepkema, 1994). In recent years, the theoretical and practical implications of these individual variations have become the focus of a growing body of research across a range of disciplines including biomedicine (Ginsburg & Willard 2009), ecology (Réale, Reader, Sol, McDougal, & Dingemanse., 2007; Sih et al., 2004; Wolf, Van Doorn, & Weissing, 2008), and developmental biology (Stamps & Groothuis, 2010). Although the exact evolutionary and ontogenetic origins of such variations are still an area of active investigation (Stamps et al., 2010), researchers have observed consistent and stable differences in the behavior of a variety of species including salamanders (Sih, Kats, & Maurer, 2003), fish (Wilson, Coleman, Clark, & Biederman, 1993), lizards (Cote & Clobert, 2007), birds (Groothuis & Carere, 2005), and mammals (Benus, Bohus, Koolhaas, & Van Oortmerssen, 1991; Hessing et al., 1993; Koolhaas et al., 1999). The current project specifically focuses on the methods and strategies used to cope with stress-inducing situations.

### Stress, coping, and coping strategies

Animals who fail to produce coping behavior in response to aversive situations are less fit from an evolutionary perspective and are therefore less likely to be represented in a population over time (Broom, 1991). In this sense, successful coping can be

characterized by its function – it is not simply a response to aversive stimuli, but a behavior that effectively removes or attenuates those aversive stimuli (Levine, Weinburg, & Ursin, 1978; Wechsler, 1995).

In a broad sense, stress occurs when an organism encounters a situation that approaches or exceeds its ability to adapt (Lazarus, 1966; Lazarus & Folkman, 1984). Early definitions of stress centered on elements in the environment that disrupt an organism's ability to maintain homeostasis (Seyle, 1936; McEwan & Wingfield, 2003). From this perspective, the stress response consists primarily of physiological changes aimed at restoring homeostatic functioning (e.g., changes in immune function, endocrine activity, heart rate, and blood pressure) that endure until the stressor is removed or neutralized (Koolhaas et al., 1999; Sapolsky, 1984; Von Holst, 1985). In more recent years, behavioral ecologists have characterized the stress response as being driven by a combination of genetic hard-coding and phenotypic plasticity, resulting in distinct suites of behavioral traits emerging over time in response to environmental pressures (Chapin III, Autumn, & Pugnaire, 1993; Kirkwood, Kapahi, & Shanley, 2000). Alternately, cognitive psychologists have explored models that conceptualize stress as a more internal process influenced by affect, personality traits, and cognitive self-regulation (Bandura, 1991; Folkman & Moskowitz, 2000; Mroczek & Almeida, 2004; Thoits, 1995).

Our study will define stress under a larger umbrella that attempts to unify each of these perspectives by recognizing not just the distinct physiological, psychological, and behavioral elements of the stress response, but the dynamic interactions that unfold between each of these components as well. The transactional model of stress emphasizes these interactions between environmental stressors, organism characteristics, and

behavioral responses (Lazarus, 1966; Lazarus, 1986; Schuler, 1982). It suggests that when an organism encounters a potential stressor it appraises the level of threat presented based on past experiences, personal abilities, and available resources. This suggests that, even within a given species, different conspecifics may perceive identical stimuli as either a threat or completely benign depending on their own individual interpretations. These interpretations are the result of what Lazarus et al. (1984) referred to as the primary appraisal of the stressor. Intraspecies variability in the outcome of these appraisals may have roots in the phenotypic plasticity described by behavioral ecologists as well as factors like personality and temperament described by psychologists (Lazarus et al., 1984; Mroczek et al., 2004; Chapin III et al., 1993).

Most importantly, the transactional model of stress paints a dynamic and reciprocal picture of the interactions between environmental stressor and organism behavior. The relationships between environmental stressor, organism characteristics, and behavioral response are not unidirectional – any one of the three can affect the others in a bidirectional and complex manner. This allows for a wide range of behavioral strategies and responses to the environment in a given population and suggests that the methods used to study these responses should be adequately dynamic and complex as well.

Once an organism identifies a stressor as a potential threat, it takes steps to mitigate bodily harm, loss of resources, and perceived level of threat (Lazarus, 1966; Lazarus et al., 1984). Some authors have made a point to distinguish between voluntary and involuntary stress responses, arguing that coping should refer only to those responses that the organism voluntarily controls and involve conscious effort (Compas, Connor-Smith, Saltzman, Thomsen, & Wadsworth, 2001; Connor-Smith, Compas, Wadsworth,

Thomsen, & Saltzman, 2000). Although this model considers involuntary responses such as emotional and physiological arousal part of the larger stress response, they are categorized separately. Other researchers have defined coping as any method of “regulation under stress” regardless of volitional control, arguing that it should include both automatic and deliberate processes (Eisenberg, Fabes, & Guthrie, 1997; Skinner & Zimmer-Gembeck, 2007). Proponents of this approach suggest that the line between voluntary and involuntary stress responses are often ambiguous and categorization of behavior into these categories requires a level of interpretation that may exceed the bounds of scientific objectivity (Carver, 2013). Interpretation of motivation and intention is especially difficult when dealing with non-human subjects, which is why this study will define coping broadly as any behavioral strategy employed in response to an environmental stressor, whether voluntary or involuntary.

When animals are continuously confronted with a stressor that cannot be removed or reduced through the use of coping strategies, severe behavioral and physiological effects can manifest in a relatively short period of time (Flügge, Kramer, & Fuchs, 2001; Von Holst, 1985). Environmental stressors that exceed an animal’s ability to cope can significantly compromise the animal’s health and can ultimately result in death (Koolhaas et al., 1999; Von Holst, 1985). For this reason, it is important that researchers gain a better understanding of the mechanisms responsible for the effects of stress and the strategies that animals employ to combat those effects.

Researchers have proposed a range of theoretical frameworks in an attempt to identify, categorize, and predict successful coping strategies. Some studies have emphasized the existence of two major strategic categories existing at opposite ends of

some behavioral continuum (Benus et al., 1991; Hessing et al., 1993; Sluyter, Bult, Lynch, van Oortmerssen, & Koolhaas, 1995; Jones & Satterlee, 1996). For example, observations of rodent populations have revealed several behavioral and physiological variables (e.g., aggression, nest-building behavior, and neuroendocrine behavior) that appear to produce bimodal distributions corresponding to two distinct and consistent coping strategies (Benus, Koolhaas, & Van Oortmerssen, 1987; Benus et al., 1991; Ebner, Wotjak, Landgraf, & Engelmann, 2005), which have been referred to as “active” and “passive” (Benus et al., 1991). Several studies have found evidence to support this theoretical framework and it has been extended to a range of non-rodent species including poultry (Blokhuis & Metz, 1992), pigs (Hessing et al., 1993), and humans (Bandler, Keay, Floyd, & Price, 2000; Brown & Nicassio, 1987; Snow-Turek, Norris, & Tan, 1996).

Animals who qualify as passive copers tend to react to aversive stimuli by “freezing”. For example, male tree shrews placed in a confined cage in the presence of a more dominant male will become unresponsive to external stimuli, produce elevated concentrations of glucocorticoids in the blood, cease autogrooming and scent-marking behavior, and gradually decrease in body weight (Von Holst, 1985). Passively coping rats (Benus, Bohus, Koolhaas, & Van Oortmerssen, 1991; Blanchard, Yudko, Dulloog, & Blanchard, 2001; Korte, Bouws, Koolhaas, & Bohus, 1992), mice (Benus et al., 1987; Benus et al., 1991), sows (Hessing et al., 1993; Hessing, Schouten, Wiepkema, & Tielen, 1994) and piglets (Hessing et al., 1993) have been shown to react to aversive stimuli with immobility and withdrawal as well. This passive behavior is typically sustained until the aversive stimulus spontaneously ceases or is removed.



Actively coping animals display a slightly more diverse range of behavior in the presence of aversive stimuli. These individuals take proactive measures to either remove the aversive stimuli via aggression and displacement, or distance themselves from it via flight and evasion (Benus et al., 1991; Wechsler, 1995). Actively coping animals are often more resistant to restraint (Bolhuis, Schouten, de Leeuw, Schrama, & Wiegant, 2004; Hessing et al., 1993), more resistant to change (Bolhuis et al., 2004), more aggressive with conspecifics (Benus et al., 1991; Bolhuis et al., 2004; Hessing et al., 1993) and quicker to develop behavioral routines (Bolhuis et al., 2004).

An illustrative example of this dichotomy can be found in studies of defensive burying behavior in rats. First introduced by Pinel & Treit (1978), defensive burying tests involve the placement of individual rats in a cage with some sort of bedding substrate and one or more electrical shock probes. Because the probes are novel, the animals eventually investigate and make physical contact with them. When this happens, the animal receives an aversive electrical shock. Pinel et al. (1978) observed that several rats reacted to this environmental stressor by burying the probe under a pile of substrate. When rats were shocked by only one of two identical prods, they responded by burying only the electrified prod. Thus, Pinel et al. (1978) concluded that the burying behavior was a direct reaction to the shocks received by the animal and were an active attempt to remove the aversive stimulus from their environment.

This behavior has been confirmed by several subsequent studies and defensive burying behavior has become a widely used paradigm for the investigation of active and passive coping strategies in rodents (see De Boer & Koolhaas, 2002 for review). Active individuals, initially identified as those exhibiting higher aggression levels and shorter

attack latencies, have been shown to be significantly more likely to respond to the task by burying the aversive probe or probes. Passive animals, characterized by lower aggression levels and longer attack latencies, tend to respond by withdrawing and avoiding the probes altogether (Sgoifo, De Boer, Haller, & Koolhaas, 1996; Koolhaas et al., 1999; De Boer et al., 2002). These findings were particularly important in the establishment of active and passive coping strategies as they show that the strategies extend beyond social competitive scenarios to non-social environmental stressors.

#### Evolutionary origins of differing coping strategies

If distinct behavioral phenotypes exist within several species, what are their origins? What are the mechanisms through which they influence the organism's survival? A particularly illustrative and well-known example of this process can be found in the phenotypic changes that occurred in the peppered moth, *Biston betularia*, during the industrial revolution (Majerus, 2009). Although the majority of moths exhibited white and speckled coloration patterns before the industrial revolution, accumulation of soot in their environment led to the proliferation of darker coloration patterns after industrialization (Kettlewell, 1958). This change was driven by the fact that, in any given generation, a range of phenotypic variations exist that can be alternatively advantageous or disadvantageous depending on the challenges presented by the environment. In the case of the peppered moth, a coloration pattern that had previously been disadvantageous became advantageous as it provided a superior level of camouflage in the face of rising pollution levels (Kettlewell, 1958; Majerus, 2009). These newly advantageous traits were passed on to successive generations, ultimately becoming the predominant coloration pattern of the species (Kettlewell, 1958; Marjerus, 2009). As pollution levels have

decreased in recent years, the original white speckled coloration pattern has once again become prevalent (Marjerus, 2009). This illustrates how, as environmental demands fluctuate, multiple distinct phenotypic variations can be alternately selected for. The end result is the emergence of multimodality in phenotypic variations among conspecifics.

Several studies have explored this process in a range of species, two additional examples of which we review in detail here. Both examples investigate correlations between individual behavioral strategies, survivability and reproductive success. Although each concerns very different species, their findings are aligned: fluctuating environmental pressures select for different behavioral strategies at different times. This alternating selection can result in the emergence of two distinct, but equally successful, behavioral phenotypes over a long period of time (Van Erp-van der Kooij, Kuijpers, Schrama, Ekkel, & Tielen, 2000). We emphasize the importance that natural environmental pressures play in this phenotypic divergence as we will later be addressing the question of how these patterns are affected when naturally occurring environmental pressures are removed (i.e., in managed care facilities).

Previous studies have shown that great tits (*Parus major*) differ in measures of exploration and boldness (Drent, van Oers, & van Noordwijk, 2003; Verbeek et al., 1994; Verbeek, Boon, & Drent, 1996). These variables are typically measured by releasing the animals into a novel environment that they are allowed to explore for a set period of time. Animals who spend a higher portion of their activity budget performing hopping and flying behaviors are considered fast explorers, while animals that react with relatively low mobility are considered slow explorers (Dingemanse et al., 2002; Verbeek et al., 1994). This exploratory behavior has been shown to be consistent and heritable

(Dingemanse et al., 2002), and longitudinal studies have shown these traits have complex interactions with environmental selection pressures. Dingemanse et al. (2004) found that propensity for exploratory behavior had alternating effects during successive years and that males and females experienced opposite effects. In years that coincided with beech tree masting, fast-exploring males and slow-exploring females had higher survival rates. This pattern was reversed in years without beech tree masting, when slow exploring-males and fast-exploring females exhibited the highest survival rates. Due to the fact that beech tree masts significantly relax competition for food resources (Perdeck, Visser, & Van Balen, 2000), the authors suggested that the observed trends were due to the effects of intra-sexual competition. Because female great tits are subordinate to males, they argued that food scarcity (i.e., years without a beech mast) would have a larger impact on their survival. In these years, animals that exhibited higher exploratory behavior would be more likely to encounter food resources.

During beech mast years, food resource pressures are removed but territorial competition (experienced exclusively by males) tends to increase (Perdeck et al., 2000). Under these conditions, males who exhibit higher levels of aggression toward conspecifics are more likely to be selected for. Levels of exploration have been shown to be positively correlated with aggressive behavior (Verbeek et al., 1996; Carere, Drent, Privitera, Koolhaas, & Groothuis, 2005), suggesting that high-exploration males are better suited for the selection pressures encountered during these years (Dingemanse & Réale, 2005).

Similar patterns have been observed in wild bighorn sheep (*Ovis canadensis*) populations (Réale et al., 2000; Réale & Fiesta-Bianchet, 2003). Réale et al. (2000) used

a series of corral traps to capture wild bighorn sheep in Alberta, Canada from 1998 to 1999. The authors treated the number of times each animal was caught (i.e., their willingness to approach the salt lick bait) as a measure of individual boldness. Each animal's behavior during subsequent human handling was coded as a measure of docility. The authors found that boldness and docility measures were both repeatable and negatively correlated: bold ewes tended to be non-docile, and shy ewes tended to be docile.

Réale et al. (2003) continued a longitudinal extension of this study to investigate the effects of these individual traits on annual survival rates. They found that boldness and docility did have a significant impact on survivability, but that the effect fluctuated from year to year. When cougar predation was relatively low, survivability seemed to be unrelated to these individual traits. However, in years of heavy cougar predation boldness and docility had a significant effect on survival rates; bold ewes, as well as docile ewes, were significantly more likely to survive during these periods. Due to the fact that these traits are negatively correlated (Réale et al., 2000), the authors suggested that this would result in the emergence of two distinct and consistent behavior patterns in the population: one consisting of animals who were bold and non-docile, and another consisting of animals who were shy and docile. Although the two groups apparently employed different strategies in coping with predation, each strategy was successful and therefore persisted in the larger population.

These studies illustrate the mechanisms through which varying and diverse environmental pressures might lead to the emergence of distinct bimodal coping mechanisms. Furthermore, the studies reviewed here are concerned with a relatively

limited range of behavioral characteristics and selection pressures. It is not hard to imagine more varied and rich collections of coping strategies emerging from the interaction between the countless environmental pressures encountered by species in the wild. It is the dynamic and multifaceted array of selection pressures in the wild that are responsible for shaping the variety of coping strategies observed in wild populations. One single strategy would lack the flexibility needed to carry an entire species successfully through the shifting challenges that natural environments present.

Given this relationship between diversity of coping strategies and environmental selection pressures, one must consider the effect that removal of these pressures would have on behavioral complexity. In agricultural settings, reproduction is often artificially controlled to select for highly productive animals (Ruis et al., 2000; van Erp-van der Kooij, Kuijpers, Schrama, Ekkel, & Tielen, 2000). This selection pressure is invariable and dominant: it does not fluctuate annually and it is the primary selection pressure that shapes the population. If the effect of widely varying selection pressures is the emergence of distinct coping strategies, does it follow that removal of these pressures through domestication would result in homogenization and convergence of coping strategies in captive populations over time? If so, we would expect to see the bi- or multimodal distributions of wild populations converge to continuous unimodal distributions as domestication progresses.

#### Coping strategies in domestic pigs

Hessing et al. (1993) investigated whether consistent individual behavior differences were observable in a sample of 218 piglets. The authors characterized each animal's level of aggression, and resistance in a series of experiments over the course of

three weeks. When piglets were one week old, they were placed in a small (1.6m x 1.6m x 0.78m) crate with three conspecifics of the same age. Two independent observers recorded instances of aggressive behavior in each animal and piglets were identified as either aggressive or non-aggressive. This experiment was replicated one week later to check for repeatability and consistency.

Resistance was measured via a widely used “backtest” method. In this test, a piglet is placed on its back and restrained in that position for sixty seconds. Researchers record the number of escape attempts exhibited by the animal and place the animal into resistant or non-resistant categories based on these observations. Animals that made less than two escape attempts were considered non-resistant while animals that made more than two escape attempts were considered resistant. When an animal made exactly two escape attempts it was classified as intermediate for that trial.

This backtest experiment was conducted five times for each animal over the course of three weeks. To be classified as resistant, the piglet must have recorded at least three resistant trials and no more than one non-resistant trial (the opposite criteria were used for the classification of non-resistant piglets). Animals who did not meet the criteria for either category were classified as doubtful. After data collection, the authors classified 44% (95 animals) of the sample as resistant, 35% (77 animals) as non-resistant, and 21% (46 animals) as doubtful.

The authors also investigated whether the classifications emerging from the backtests (resistant vs. non-resistant) were correlated with those emerging from the social confrontation tests (aggressive vs. non-aggressive). They found that 74.4% of the piglets classified as aggressive were also classified as resistant in the backtests. Similarly, 75.6%

of the animals classified as non-aggressive were also categorized as non-resistant in the backtests. These results were statistically significant (Kappa statistic;  $K=0.49$ ;  $P<0.01$ ). The authors then proceeded to state that these correlations between measures, along with the repeatability and consistency of each measure, suggest the existence of two distinct coping strategies in piglets. They argued that aggressive/resistant piglets reflect the previously mentioned active coping strategies observed in several species while the non-aggressive/non-resistant piglets reflect passive coping strategies (Benus et al., 1991; Hessing et al., 1993). The idea that pig coping strategies can be predicted by backtest results has been echoed by a range of studies on aggression (Hessing et al., 1994; Erhard & Mendl, 1999; Ruis, te Brake, Engel, Buist, Blokhuis, & Koolhaas, 2002; Ruis et al., 2000), immune function (Bolhuis, Parmentier, Schouten, Schrama, & Wiegant, 2003; Hessing, Coenen, Vaiman, & Renard, 1995; Schrama et al., 1997), HPA-axis reactivity (Geverink, Schouten, Gort, & Wiegant, 2002; Geverink, Schouten, Gort, & Wiegant, 2003; Ruis et al., 2001; Ruis, te Brake, Engel, Buist, Blokhuis, & Koolhaas, 2002), and behavioral flexibility (Bolhuis et al., 2004).

Hessing et al. (1994) replicated their initial findings using the same methodology to study an additional sample of 206 piglets. The authors found that 86 animals (42%) could be classified as resistant, 94 (46%) non-resistant, and 26 (12%) doubtful. Erhard et al. (1999) also used a slightly modified backtest to investigate behavioral responses of 219 piglets and found results similar to those of Hessing et al. (1993). They raised a similar hypothesis, suggesting that the animals could be divided into active and passive categories based on backtest responses, and that these classifications were consistent with behavior seen during later observations, suggesting behavioral stability. Their results and



methodology differed slightly from that of Hessing et al. (1993; 1994) in that all animals were split into one of two categories with 175 (80%) of the animals exhibiting active responses and 44 (20%) exhibiting passive responses.

It is worth noting that, while Hessing et al. (1993; 1994) and Erhard et al. (1999) were both able to split their animals into active (resistant) and passive (non-resistant) categories, the relative size of each category differed between the studies. Erhard et al. (1999) found that 80% of their animals exhibited active responses and 20% exhibited passive responses. However, the Hessing studies found that animals were split fairly evenly between the two categories. Because the species and ages of animals studied were similar across all studies, a likely cause for these variations lies in the methodology employed in each study. Hessing et al. (1993; 1994) set an upper time limit of sixty seconds on their backtest trials. Erhard et al. (1999) extended their backtest trials to three hundred seconds. This discrepancy in test duration is particularly important when dealing with binary categories (e.g., active versus passive), as was the case with these studies. When the criteria for classification into one group or another relies on whether a qualitative behavior was observed in a given time period, extending or shortening that time period will affect the proportion of the sample that are assigned to each category (Jensen, Rushen, & Forkman, 1995; Koolhaus et al., 1999). Extending the observation period increases the likelihood that the specified behavior is observed and decreases the likelihood that it will be absent. These arbitrary cutoffs turn what could be measured as a continuous variable (e.g., frequency or total duration of resistant behavior) into a categorical one (i.e., resistant behavior was observed or it wasn't). In this sense the

inclusion of these arbitrary cutoffs may make the data appear artificially binary, especially when coupled with a limited number (two to three) of available categories.

The existence of discrete categories suggest that the researchers decided a priori that piglet behavior would fall along active and passive lines. This resulted in theory shaping the data, as opposed to the opposite, and raises concerns about whether the possibility of unimodal distributions were sufficiently investigated and ruled out. Indeed, the authors performed no statistical tests to check whether the raw data was a better fit for bimodal versus unimodal distributions and the non-negligible proportion of “doubtful” classifications in Hessing et al. (1993; 1994) begs the question of how well this framework fits the data itself.

As a further illustration of the effect a priori determination of categories can have on apparent bimodal tendencies, we consider Ruis et al. (2000; 2001a; 2001b; 2002). The authors in these studies followed a piglet backtest protocol virtually identical to that outlined in Hessing et al. (1993; 1994). However, in this case the authors established different cutoffs for each category: passive animals were those exhibiting less than three escape attempts and the active animals were those exhibiting five or more escape attempts over the sixty second trial duration. Whereas the only unclassified (i.e., “doubtful”) animals in the Hessing et al. (1993; 1994) studies were those exhibiting exactly two escape attempts, that range was expanded to include everything from two to four attempts in the Ruis et al. (2000; 2001a; 2001b; 2002) studies. In both sets of studies, animals that did not fit into either active or passive categories were not included in the remaining experiments and analyses. This excluded between 40% (Ruis et al., 2000) and 49% (Ruis et al., 2001a; 2002) of the animals in the sample. However, Ruis et

al. (2000; 2001a; 2001b; 2002) do not make a claim of distinct behavioral categories (i.e., bimodality). Instead, the authors make a point of establishing the unimodal nature of the raw data (see Figure 1) and clarifying that the decision to limit their analysis to active and passive animals was a means of better characterizing a continuous behavioral spectrum by comparing the individuals that served as bookends to the distribution. Similar unimodal backtest distributions were reported by van Erp-van der Kooij et al. (2000), with the added finding that piglet performance appeared to be correlated with that of their mothers, suggesting trait heritability.

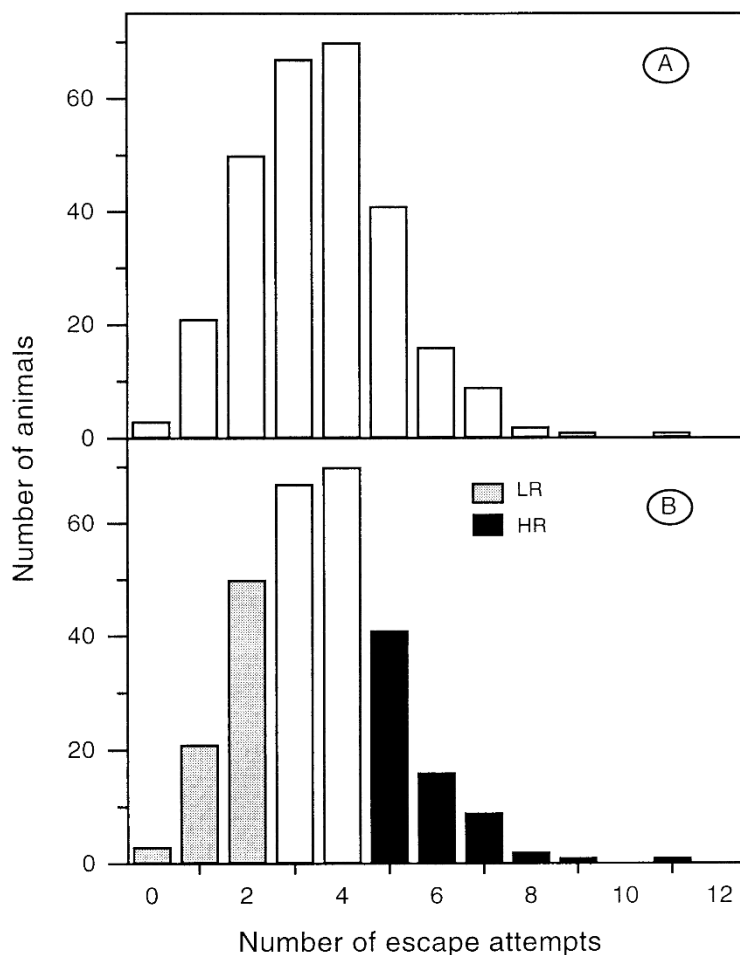


Figure 1. Backtest escape attempt frequency distribution.

A: The distribution of escape attempts during a sixty second backtest of two to four day old female piglets. B: The same data broken into discrete categories of low responding (LR), unclassified, and high responding (HR) animals. When data from all three groups are presented, the distribution shows a clear unimodal trend. Reprinted from Ruis et al. (2000). See Appendix B for reprint permissions.

Lawrence, Terlouw, & Illius (1991) presented further evidence refuting the bimodal model of pig coping with their study of 62 seven month old females. The authors observed behavior in both social and non-social contexts in an effort to determine whether the animals exhibited consistent responses across contexts corresponding to stable personality types. The first measure established was a “handling score” describing each animal’s performance in a series of tests in which humans either moved the animals between pens, approached them rapidly, or restrained them for a set period of time.

Animals who were more resistant to being moved, more aversive to human approach, and struggled more during restraints received a higher handling score and were referred to as high responders. Animals with low handling scores were referred to as low responders.

After handling scores were established, the authors chose 16 high responders and 16 low responders to undergo further testing in a novel object test and a social food competition task. The authors did find consistencies in behavior across these contexts (high responding animals were more likely to show interest in the novel object and win adversarial disputes with conspecifics) but they did not find evidence that the distribution of behavioral responses was bimodal in nature. As a result, the authors suggested a continuous approach to pig behavioral strategies. They argued that measures of the degree to which individual animals differed from each other on continuous scales of behavior would give a more accurate picture than attempting to bifurcate them into distinct and separate groups.

Unfortunately, the authors did just this when they chose 16 animals at each end of the behavioral spectrum (high and low responders) to complete the novel object and social competition battery of tests. Although the authors did not find statistically significant evidence of a bimodal distribution, this methodological decision did artificially augment the small amount of bimodality that appeared to be already present in their data before this selection was made (see Figure 2). Further studies including the subset of animals that fall between “high” and “low” responding behavioral categories would provide a better perspective on whether this behavioral middle ground truly does exhibit continuous unimodal characteristics.

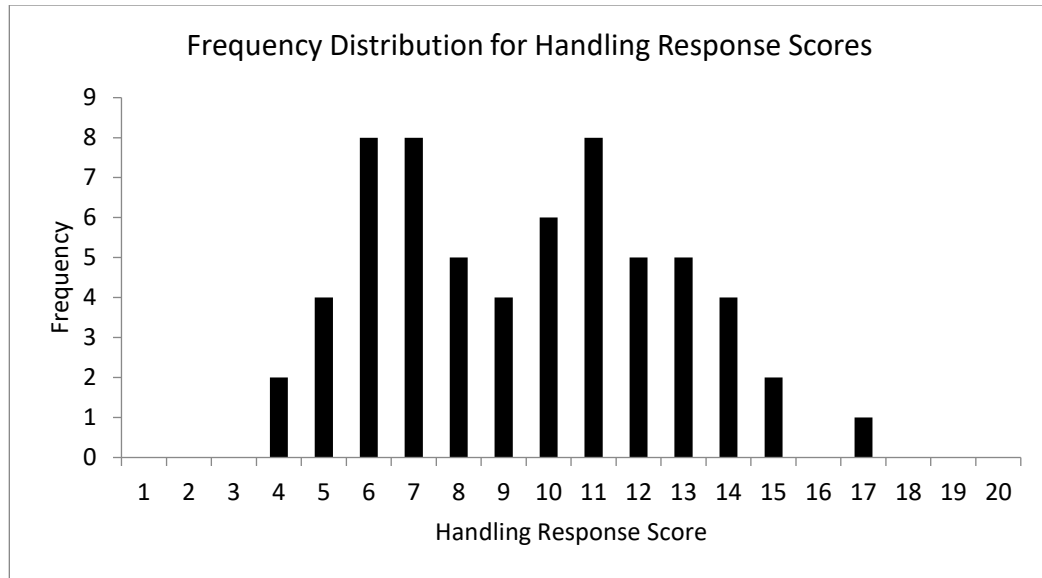


Figure 2. Handling response score distribution.

Although the authors reported no statistically significant evidence of a bimodal distribution of behavioral measures, the data does show some qualitative evidence of a bimodal trend ( $n = 62$ ). This tendency was augmented by the author's decision to include only a small number ( $n=16$ ) of subjects from each end of the spectrum for the final rounds of data collection. Reprinted from Lawrence et al. (1991). See Appendix C for reprint permissions.

Forkman, Furuhaug, & Jensen (1995) adopted the same backtest methods outlined by Hessing et al. (1993) with the specific aim of determining whether the distribution of observations was bimodal or unimodal. Two experiments were carried out with two separate samples. In the first experiment, a group of 65 piglets were tested one time at two weeks of age. In the second experiment a group of 45 piglets were tested once per week, from one week of age to five weeks of age. Instead of dividing the animals into two or three categorical levels, the authors plotted the total number of escape attempts observed during each trial continuously. They reported observing a unimodal distribution, however this appears to have been a qualitative assessment as no statistical tests were reported to verify this claim.

The contrast between studies by Hessing et al. (1993) and Forkman, Furuhaug, & Jensen (1995) provides a good illustration of the way an author's choice of experimental methods can artificially affect the modality of the data. One of Forkman's behavioral measures looked at how quickly each animal aggressed on a conspecific intruder introduced into their pen. As is evident in Figure 3, the attack latency of animals displaying aggression was distinctly unimodal. However, the inclusion of animals who did not display aggressive behavior at all during the finite duration of the experiment give the data a bimodal appearance. If the experiment duration was to decrease, more animals (those exhibiting long attack latencies) would be lumped into this "no contact" category as the experiment would have ended before they had exhibited aggressive behavior. This would cause the apparent bimodality of the data set to increase. Conversely, if the experiment duration were increased we would expect to see a decrease in bimodality as more long-latency animals would have the chance to aggress on the intruder before experimental observations ended.

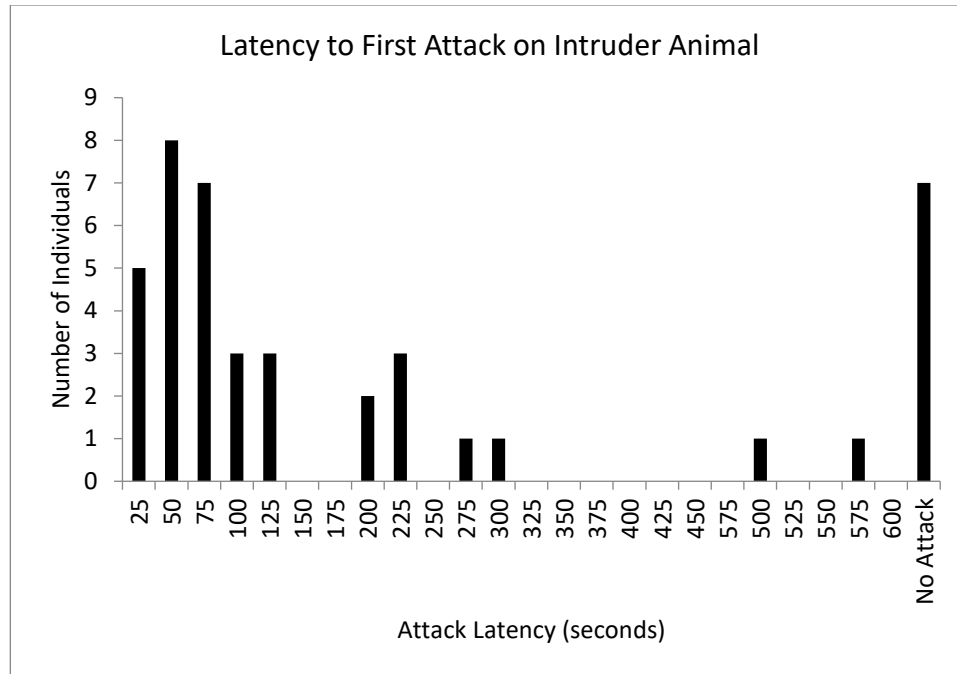


Figure 3. Latency of first attack on an intruder by a resident animal.

Although the data may appear to be bimodal at first glance, this is an artifact of the finite duration over which data was collected. Excluding the categorical “No Attack” data column, the distribution exhibits a unimodal shape suggestive of a lognormal or exponential distribution ( $n = 42$ ). Generated using data from Forkman et al. (1995).

This is the same process that may have been responsible for the apparent bimodality in the backtest results presented by Hessing et al. (1993). Animals who did not struggle over the course of the backtest may have simply been long-latency responders who would have struggled over the course of a longer time scale. This would have created an artificial dichotomy in an otherwise continuous behavioral data set.

#### Practical applications

If distinct behavioral strategies are present in pigs, continuous or otherwise, the question of practical applications should be considered. What components of this field of research can facility operators use to increase production, efficiency, and quality of life for their animals? In the present section we review two areas that this research stands to



have an immediate pragmatic effect on: physiological health of the herd and individual production levels.

Research into the physiological underpinnings of these differences in behavioral strategies has shed light on some possible mechanisms at play. Bolhuis et al. (2000) found that active and passive pigs differed in their behavioral reaction to injections of apomorphine, a dopamine agonist. Active animals exhibited significantly higher levels of stereotypical behavior while passive animals exhibited significantly higher levels of behaviors suggesting a breakdown of integrated motor coordination (e.g., walking with their forelegs while dragging their hindlegs). Due to the fact that dopaminergic pathways are involved in both repetitive behaviors and integration of various subcomponents of locomotion (Teitelbaum, Pellis, & DeVietti, 1990), the authors suggested that the observed behavior might have been the result of innate structural differences in the dopaminergic pathways of these animals. The observation that active animals are more prone to stereotyped behavior are supported by the findings of Bolhuis et al. (2004), who demonstrated that active animals were slower to modify ineffective behavioral strategies that were previously successful, while passive animals adapted significantly faster.

The physiological differences between active and passive animals extend to the endocrine system as well. Passive animals tend to have higher cortisol levels in stable environments as a result of increased sympathetic activity levels (Bolhuis et al., 2003; Hessing et al., 1995). Because cell-mediated immunity is susceptible to suppression by corticosteroids, it is not surprising that passively coping pigs appear to have lower levels of cell-mediated immune function when compared to active animals (Bolhuis et al., 2003; Hessing et al., 1995). However, passive animals do appear to have a stronger humoral

immune response when compared with active animals (Agarwal & Marshall, 1998; Hessing et al., 1995; Schrama et al., 1997). Because cell-mediated and humoral immune responses defend the animal via distinctly different mechanisms, active and passive animals may have different levels of resistance to various pathogens. From this perspective, breeding approaches maintaining a balance of both active and passive animals may serve to increase the herd's overall immunity.

More evidence in favor of maintaining a balance of both active and passive animals comes from the findings of Hessing et al. (1994). The authors investigated productivity (quantity and quality of meat produced) of animals raised under three different conditions; one group was housed with active animals only, one was housed with passive animals only, and the last group was housed with a mix of both active and passive animals. The authors found that animals housed in the mixed group produced more meat at slaughter. Furthermore, groups consisting only of active animals show higher levels of aggression (Hessing et al., 1994; Ruis et al., 2002) as well as slower growth rates (Ruis et al., 2002) than mixed and passive-only groups. However, when active and passive animals are raised in identical environments it appears that active animals tend to grow slower during the early suckling phase of their lives (Cassady, 2007; van Erp-Van der Kooij, Kuijpers, Van Eerdenburg, & Tielen, 2003; Velie et al., 2009), but grow more quickly after weaning (Cassady, 2007; van Erp-van der Kooij et al., 2003). By the time of slaughter, active animals weigh more and produce leaner meat on average (van Erp-van der Kooij et al., 2000; Van erp-van der Kooij et al., 2003).

Although active animals offer increased baseline levels of production and cell-mediated immune function, these benefits appear to be lost when they are raised in an

unstable environment (Geverink et al., 2004; Hessing et al., 1995; Koolhaas et al., 2009). Actively coping animals exposed to changing environmental conditions show higher sympathetic reactivity (Koolhaas et al., 1999), and may be at higher risk of health problems such as hypertension, atherosclerosis and tachyarrhythmia (Ely, 1981; Henry et al., 1993; Hessing et al., 1994; Koolhaas et al., 1999; Manuck, Kaplan, & Clarkson, 1983; Sgoifo et al., 1997). Active animals also showed a significant decrease in cell-mediated immune function when moved to a novel environment, although the immune function of passive animals was unaffected (Hessing et al., 1995). Similarly, although active animals typically grow more quickly than passive animal in the later stages of development, this effect can be temporarily reversed when pigs are moved to a novel environment (Geverink, Heetkamp, Schouten, Wiegant, & Schrama, 2004).

In all, it appears that actively coping pigs are ideally suited for stable environments, passively coping pigs are better suited for unstable environments, and populations composed of a mix of both offer higher levels of overall productivity and herd immunity. However, in order to make use of this information caretakers must first know which coping strategy each animal under their care exhibits. The two methods currently utilized to distinguish coping strategy in the literature have been the backtest (Bolhuis et al., 2000; Hessing et al., 1993; Melotti, Oostindjer, Bolhuis, Held, & Mendl, 2011) and one-on-one pairwise competition (Bolhuis et al., 2005; Cassady, 2007). Unfortunately, neither of these methods is particularly viable in commercial settings. Both require staff and time resources that may be unavailable in the case of large-scale operations. Backtest trials are particularly challenging because they must be performed when the pig is small, usually in the first few weeks of life, and this data may be

unavailable for animals that have been purchased or transported from another facility. Pairwise competition trials could be performed throughout adulthood, but they bring with them the added risk of injury to one or both animals involved.

The current study plans to investigate the use of Smartbow indoor positioning technology as a possible solution to this problem. We propose that location and acceleration data, measured via Smartbow indoor positioning, will reveal two statistical trends. First, we predict that all behavioral variables measured will show evidence of bimodal, as opposed to unimodal, distributions. This prediction will be tested using Hartigan's dip test, which produces a quantity referred to as the Hartigan's dip test statistic. Values of this statistic close to zero are indicative of unimodality while higher values are indicative of multimodality. The Hartigan's dip test null hypothesis assumes the presence of unimodality and predicts the distribution will not deviate from a standard unimodal distribution in a statistically significant way. Therefore, we predict that each distribution will produce a significant dip test statistic ( $p < 0.05$ ), signaling the absence of unimodality in each of our variables.

Our second hypothesis examines whether measures of exploratory behavior, activity levels, social hierarchy, and aggression are correlated with sow productivity in a commercial environment. This prediction will be explored using a multiple regression analysis, the details of which are expanded upon further in our analysis section. The confirmation of our hypothesis would suggest that the aforementioned behavioral variables, measured in the presence of social stressors, are effective predictors of breeding success and viability.

Because our hypotheses are concerned with behaviors and coping strategies that (at least in part) are thought to be heritable, random assignment to control and treatment groups was beyond the scope of our methods. As a result, this study relies largely on correlational analyses and should not be interpreted as confirming any causative relationships between the variables considered.

## CHAPTER II - METHODS

### Facility and subjects

At the Swine Teaching and Research Center of the University of Pennsylvania, School of Veterinary Medicine, approximately 130 gestating sows are housed in one large pen as a dynamic group and fed via electronic sow feeding. The 300.0 m<sup>2</sup> pen (approximately 2.4 m<sup>2</sup>/sow) includes nine 2.9 x 2.2 m concrete lying areas, two 3.6 x 8.2 m deep bedded straw pits, and a total of 184.0 m<sup>2</sup> of slatted flooring. The sows are fed a commercial corn-soy diet via two electronic sow feeding stations (Schauer Agrotronic Compident 7, Prambachkirchen, Austria). Every other week, 20 pre-implantation sows are mixed into the group, while a corresponding number of sows were removed for farrowing. Sows farrowed in either hinged farrow crates (4.1 m<sup>2</sup>) or enriched farrowing pens (7.1 m<sup>2</sup>) at a random schedule throughout their lives. Piglets are weaned following 28 to 35 days of lactation.

### Data collection

#### *Assessment of feed order*

The animals observed at the Swine Teaching and Research Center were fed through the use of an electronic sow feeder (ESF). Each feeder consisted of a small feeding compartment that housed a single animal at a time. Sows were fed, based on their body condition, a standard corn soy diet which for most animals was about 4 lbs of feed. The ESF stations turned on at midnight and by 4 PM the feeding cycle was completed and the feeders closed. The system registered each animal's identity by scanning the RFID chip ear tag located in the animal's right ear upon entry to the feeder. The animal's allotted ration of feed was dispensed into a retractable feed bowl 100 grams every ten

seconds until reaching the sow's allotment for the day. The sow then was given an additional 6 minutes to finish feeding after all the feed for the day had dropped. The time most animals spend in the feeder ranges from 10-15 mins. At the end of this feeding period the feed bowl was removed, signaling to the animal that it was time to leave the station. The entry doors then opened allowing the next animal to enter. Feed delivered to the animal was recorded on a daily basis along with the time each sow entered and exited the feeder. Sows enter the station more or less in the same order every day and this feed order is thought to be a good measure of social hierarchy in group-housed populations (Bressers et al., 1993, Chapinal et al., 2008, Hunter et al., 1988, Strawford et al., 2008).

The fact that the population in the group housing area is dynamic (changing as bred animals enter the pen and late term sows exit), feed order does not necessarily remain constant over time. For this reason, we used feed orders that corresponded to feed times immediately after each data collection. This meant that if Smartbow data for twenty animals was recorded on a given morning, the daily feed order data from the following week was averaged and used to characterize social position for those animals. This ensured that as many variables as possible (e.g., number and identity of conspecifics) were kept constant between both data collection periods.

#### *Preliminary testing of Smartbow tags*

The Smartbow indoor positioning system works in a manner very similar to GPS systems. Each animal is fitted with an ear tag that includes an accelerometer, a transmitter, and an on-board battery. Each animal's tag transmits acceleration and location data to an array of receivers that are mounted at various points along the wall of

the holding area. Receivers are placed so that, regardless of an animal's location in the pen, it will have a line-of-sight connection with at least three receivers at any given time. This allows for triangulation of each animal's location over the duration of data collection. Location and acceleration information were logged by Smartbow software for monitoring and later processing.

As is the case with GPS systems, Smartbow's indoor positioning system has a degree of error variance in its position and acceleration measurements. Before full data collection on live animals began, we collected baseline data on nine stationary tags in order to determine whether this error variance is similar for each tag. Each tag was positioned around the data collection for ninety-six hours. Because the tags were stationary, any variance in location observed during this period would be due to measurement error.

#### *Collection of data from Smartbow tags*

Data collection occurred during the first several hours following each sow's return to group housing from the breeding stalls. Due to the fact that these animals were absent from the larger group for six or more weeks while farrowing and being rebred, their reentry was frequently characterized by agonistic interactions with conspecifics as they reinserted themselves into the existing social structure. Tags were fastened to each animal using straps placed around the animal's chest, immediately behind their front legs. The Smartbow tags themselves were positioned at the top of the animal's back, directly in line with the spine. This placement was ideal as it was near the animal's center of gravity, out of reach of conspecifics that might tamper with the device, and easily accessible to facility staff.



Approximately twenty sows are reintroduced to group housing every two weeks. In order to better characterize instances of antagonistic interactions, we released each of these animals in staggered groups of five individuals. After a full data set was collected on one group of five, the next group would be released, and so on until all twenty had been reintroduced. Our study aimed to include a minimum of eighty animals, which is a sample size on par with several other studies in the literature (Bolhuis et al., 2000; Bolhuis et al., 2005; Geverink et al., 2004; Hessing et al., 1995) and provided us with a sufficient amount of statistical power, which we discuss in more detail in the following section.

Tags were activated immediately prior to each animal's transfer, and the exact time of reentry was recorded by hand. Because the bulk of agonistic interactions between sows tend to occur in the first thirty minutes after introduction (Otten, Puppe, Kanitz, Schön, & Stabenow, 2002), this is the period that our analysis focused on. Tags were allowed to run beyond this thirty-minute point, but the data was not included in our final results.

Acceleration and location data were used to produce four distinct variables (discussed in greater detail below) characterizing different aspects of each subject's behavior. These variables were entered into a principal component analysis (PCA) and the resulting component variables were compared to measures of sow productivity via multivariate regression. The total number of piglets produced per birth for a given animal and the average weight of each piglet at birth were used to assess sow productivity quantitatively. To account for the effect of experience on birthing success, parity was entered as a control variable.

## CHAPTER III - ANALYSIS

### Calculation of dependent variables

#### *Location variables*

Smartbow's indoor positioning tags provide measurements of two parameters that were used to quantify four distinct variables. The first parameter is location, which was used to measure total ground covered (in meters squared), new ground covered (also in meters squared) and time spent engaged in locomotive behavior (in proportion of total observation time). Total ground covered was a measure of the cumulative area traversed by the animal over the course of data collection. The area of the enclosure was broken into grids, with the exact sizing of the grid being determined based on the spatial resolution measurements taken from the preliminary testing of Smartbow tag noise discussed earlier. Grid size was equivalent to the smallest amount of area that can be meaningfully distinguished by the tags based on our measurements of static tag variance. The total area covered was measured as the total number of grid boxes the animal traversed over the course of data collection.

New ground covered was a measure of exploratory behavior (as opposed to total ground covered, which includes redundant behavior such as localized milling). In this case, areas that the animal has already visited were not counted twice. The final measure of new ground covered was a summation of locations in the pen (marked by grid boxes) that the animal visited one or more times during the course of data collection.

Time spent engaged in locomotive behavior was a measure of activity during the course of data collection. In theory, time spent moving and total distance traveled could be calculated using either acceleration or location data sets. Using acceleration data to

measure locomotion would entail making behavioral observations of the animal and noting the corresponding increase in acceleration as they begin to walk. Unfortunately, the shifts in acceleration associated with standing, sitting, scratching, and other stationary behaviors would be difficult to distinguish from true locomotion using this method. One possible solution to this problem that was considered involved making a note of the direction of the acceleration. Walking would produce acceleration along axes parallel to the ground while behaviors like standing and sitting would produce more acceleration along the vertical axis. Unfortunately, the straps used to fix each tag to the animal's body frequently shifted and rotated throughout the data collection period. Without a consistent tag orientation, assumptions about the directionality of acceleration could not be made.

As a result of these difficulties, we decided to use Smartbow's location data to assess the presence or absence of locomotion. When an animal was stationary, its movement dropped to the level of noise in the Smartbow system measured in our preliminary trials. This meant that motion could be identified by finding periods during which each animal's apparent movement exceeded this noise threshold. The analysis used to calculate this threshold is discussed in more detail in our Results section. Periods of time during which the animal is inactive were summed and the total amount of time spent engaged in sedentary versus locomotive behavior was calculated for each subject.

#### *Acceleration variables*

The second parameter that was investigated was acceleration, measured by an on-board accelerometer built into each Smartbow tag. While the majority of a pig's life is spent in either stationary or engaged in relatively slow ambulatory movement, brief periods of antagonistic interaction are signified by a marked increase in acceleration. This

increase exceeds average baseline values and is comparatively brief. These fast acceleration events can be used as a measure of the frequency with which an animal engaged in social competition or was displaced by another animal. The exact threshold (in  $m/s^2$ ) that was used to define a fast acceleration event was determined from experimenter observations of the animals.

In order to determine the value of this threshold, focal follow observations were conducted on a sample of 20% of the animals observed. For each group of five animals that are released into the pen, one animal was randomly chosen for a focal follow lasting the duration of our thirty-minute data collection period. The duration and time of all antagonistic interactions was recorded. Aggressive instances were defined using the framework laid out by Jensen (1980) who defined aggression as attacks, encroachments, or any other signal suggesting eminent attack between two or more animals. For our purposes any occurrence of biting, headbutting or charging involving physical contact between conspecifics will denote an aggressive occurrence. The duration of the aggressive instance will be measured as the time between the first and last point of physical contact between conspecifics. Acceleration data from these periods was isolated and used to determine a threshold by which to separate aggressive and non-aggressive events. This threshold was used as the threshold defining fast acceleration events during our primary analysis.

### Statistical analysis and predictions

#### *The existence or absence of bimodality*

As mentioned earlier, although the existence or absence of bimodal distributions has been a topic of prolonged debate, there have been very few statistical investigations

into the modality of these distributions. The presence or absence of bimodality in our data was assessed using Hartigan's dip test (Hartigan & Hartigan, 1985). The dip test compares a data set's empirical distribution function with a standard unimodal distribution, and provides a measure of the similarity between the two. Scores closer to zero suggest that a given data set is unimodal while higher scores suggest the presence of multimodality. These calculated values can be compared to known statistical models to calculate a p-value, with values less than  $p = 0.05$  suggesting the existence of multimodality (Freeman & Dale, 2013). Hartigan's dip test was used to calculate likelihood of unimodality for total ground covered, new ground covered, time engaged in sedentary behavior, and number of fast acceleration events.

#### *Correlation matrix*

In order to justify our use of PCA, a correlation matrix was calculated between each of the five behavioral variables. Two-tailed Pearson correlation coefficients were examined for each comparison and p-values less than 0.05 were considered significant. Significant correlations between several behavioral variables would suggest the presence of redundancy in the data set. If this was the case, PCA would allow for the simplification of this data set by describing the same behavioral constructs using fewer independent variables.

#### *Principal component analysis*

Our analysis followed the precedent set by Horback & Parsons (2016), in which PCA was successfully used to describe stability of personality traits in group-housed sows. Each of our measured variables was clustered into composite traits using principal component analysis (PCA). Bartlett's test for sphericity and a Kaiser-Meier-Oklin test

was used to assess homoscedasticity and adequacy of data sampling beforehand ( $p = 0.05$ ). Our PCA utilized a varimax rotation to simplify the expression of our component subspace. Principle components with eigenvalues higher than one were extracted for further analysis. Factor scores for each sow were calculated using the least squares regression approach. This process results in a standardized score for each sow (ranging between -3.0 and 3.0) that is functionally similar to a z-score. Hartigan's dip test was used once again to check for the presence of unimodality in these composite scores.

### *Multiple regression*

Composite traits identified by PCA were compared with measures of sow productivity via multivariate linear regression ( $p = 0.05$ ). Each principal component was entered simultaneously as a predictor variable, while controlling for parity to account for the effect of ontogenetic physiological changes on productivity over the sow's lifespan. Our first regression assessed the ability of each principal component to explain variance in the total number of live born piglets produced per pregnancy by each sow. Our second regression determined whether each principal component is able to explain variance in average weight at birth of each piglet. Records of litter size and average birth weight have been recorded over the years by facility staff and were made available to us for this study.

Three binary measures of animal status were considered as well. The first, herd status, is a measure of whether the animal was removed from the herd before the following insemination and farrowing cycle. Animals received a score of one if they remain in the herd and a zero if they were removed. Removals from the herd are typically the result of veterinary complications or a lack of production by the sow; removed animals are euthanized or sold. The second variable measured pregnancy status. Animals

who were successfully inseminated in the next reproductive cycle received a score of one, animals whose insemination failed received a zero. The final variable was a measure of farrowing success. Animals that successfully gave birth received a score of one, and those who did not received a zero.

Minimum sample size for PCA analysis has been a point of contention over the last several decades. Although some authors have proposed universal concrete minimum sample sizes (Comrey & Lee, 2013; Gorusch, 1983; Kline, 2014), others have argued that a ratio of the number of variables to the number of subjects is a better minimum threshold to work with (Everitt, 1975, Hair, Anderson, Tatham, & Black, 1995). However, many of these recommendations are contradictory and lack foundations in empirical evidence (Arrindell & van der Ende, 1985; Mundfrom, Shaw, & Ke, 2005). In a particularly in-depth analysis of the effects of sample size on PCA, Mundfrom et al. (2005) found that the minimum sample size requirements were dependent on several aspects of the data set including communality, number of independent variables, and number of principal components. Although the authors found that PCA was too complex to establish and universal minimum sample size, they argued that samples between 70 and 100 were sufficient in the majority of cases.

## CHAPTER IV – RESULTS

### Sample size

Technical difficulties, along with time constraints, resulted in a smaller sample size than was initially proposed. Data collection was scheduled to take place between June and September of 2016. However, an equipment failure at the beginning of this period delayed collection until the middle of August. Data for a total of seventy animals was collected before the end of September. One animal was removed from the sample during observation and was therefore eliminated from the study, resulting in a sample size of sixty-nine animals for the final analysis.

### The presence of unimodality

#### *Hartigan's dip test*

Total number of boxes traversed, unique boxes traversed, and proportion of the observation period spent moving, PCA1, and PCA2 all produced p-values larger than 0.05. This indicates the absence of bimodal behavior, supporting the presence of unimodality in each distribution. Figure 4 gives further qualitative confirmation of the unimodality of these variables. One variable, acceleration events, appeared to exhibit significant bimodal behavior ( $p < 0.05$ ).



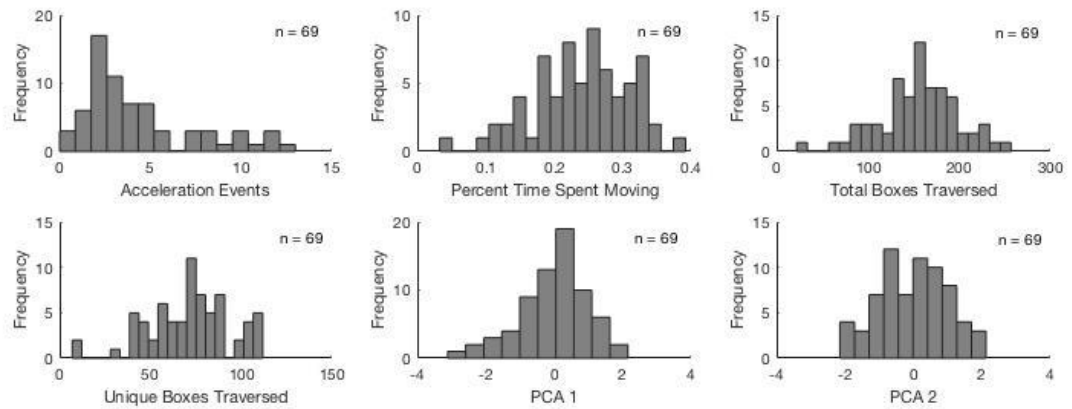


Figure 4. Histogram plots of behavioral and PCA variables.

With the exception of acceleration events, all variables were confirmed to exhibit unimodality via Hartigan's dip test.

#### Analysis of focal follow footage

Seventeen instances of aggression on video were flagged and their timestamps were used to isolate the corresponding Smartbow acceleration data. Fourteen non-aggressive instances of increased acceleration (e.g., scratching, slipping, and traversing a concrete staircase) were also identified and plotted for comparison. Plots were visually inspected and peak values were recorded (a representative example of an aggressive event is shown in Figure 5). Instances of aggression were defined as interactions in which at least one animal made physical contact with a conspecific (either biting or headbutting). This excluded displacements that occurred without physical contact (e.g., a charge that led another animal to flee before contact was made). We also excluded non-aggressive instances if they consisted exclusively of an animal running by itself. These two behaviors were excluded due to the fact that, from an acceleration standpoint, they are almost identical. They both entail the animal running without making contact with another object or animal in its environment. As a result, including these ambiguous behaviors in our acceleration threshold calculation would serve to decrease the effect size

between the two groups, reducing the power of our overall analysis. Eliminating them from our calculation allows us to establish a clear and distinct threshold separating aggressive behaviors involving physical contact from all other behaviors. The resulting aggressive instances ( $n = 17$ ) produced peak acceleration values that were significantly higher ( $p < 0.01$ ) than those produced by non-aggressive instances ( $n = 14$ ).

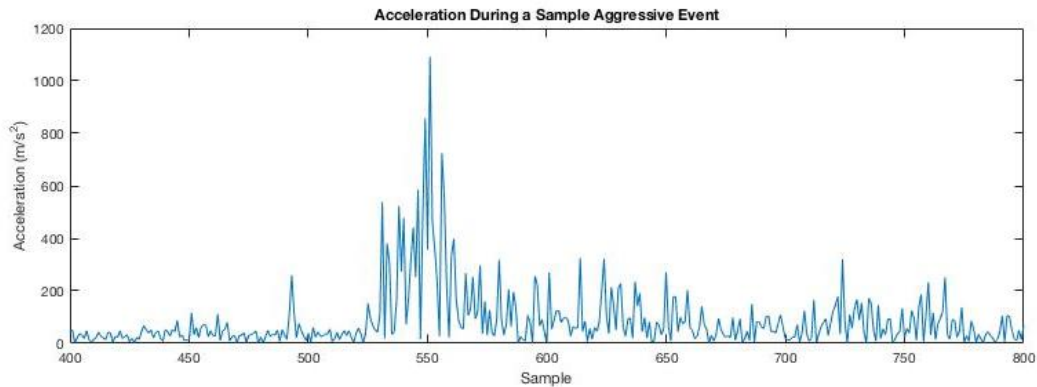


Figure 5. Smartbow acceleration data during a representative aggressive event.

The event itself unfolds between samples 530 and 560.

Non-aggressive interactions had a mean peak acceleration of  $906 \text{ m/s}^2$  and a median peak acceleration of  $713 \text{ m/s}^2$ . Aggressive interactions had a mean peak acceleration of  $1849 \text{ m/s}^2$  and a median peak acceleration of  $2088 \text{ m/s}^2$ . Due to the fact that the data set included several notable outliers, median values were used as a guide to establish our final threshold value of  $800 \text{ m/s}^2$ . Although some aggressive events had peaks slightly below this value (e.g.,  $600$  to  $700 \text{ m/s}^2$ ), lowering it further would have resulted in several non-aggressive events (e.g., running and scratching) being incorrectly identified as aggression.

In order to verify that our findings were robust, we performed the same analysis without excluding the previously mentioned ambiguous running events. We once again

found that aggressive events ( $n = 22$ ) produced peak acceleration values that were significantly higher ( $p < 0.01$ ) than those produced by non-aggressive events ( $n = 20$ ). This supported our previous findings that the acceleration values belonging to each group were significantly different, with aggressive behavior being marked by comparatively higher levels of acceleration. However, the mean and median values of each group were higher than those found in our previous analysis. Aggressive interactions produced a mean peak acceleration of  $1783 \text{ m/s}^2$  and a median peak acceleration of  $2053 \text{ m/s}^2$ . Non-aggressive interactions produced a mean peak acceleration of  $1288 \text{ m/s}^2$  and a median peak acceleration of  $1311 \text{ m/s}^2$ . For this reason it is important to reiterate that all subsequent findings rest on an operational definition of aggression that assumes actual physical contact between conspecifics.

Focal follow observations also revealed that aggressive interactions were often prolonged events punctuated by brief periods of rest. To ensure that each aggressive bout was counted as a single event as opposed to a series of smaller events, we required a total of 30 seconds of acceleration values below the  $800 \text{ m/s}^2$  threshold to pass before a new event was registered.

#### Analysis of behavioral variables

##### *Preliminary analysis*

Initial processing of raw Smartbow data was completed using a custom Matlab program. The program was designed to track each target animal's position and acceleration over the entire thirty-minute observation period. To calculate distance traveled, the barn area was broken into a grid of two meter by two meter boxes. As each animal traveled across the grid, the number of boxes traversed was tallied. The program

calculated two distinct box-counting variables. “Total boxes” included every box the animal traveled through, even if it had already passed through that same box before. “Unique boxes” counted every box a single time, meaning repeat visits to the same region of the grid were not included. Although both variables were measures of locomotion, total boxes included repetitive behaviors such as pacing while unique boxes were more representative of initial exploration.

Table 1 *Position standard deviation for stationary tags*

<b>Axis</b>	<b>Minimum Standard Deviation (m)</b>	<b>Maximum Standard Deviation (m)</b>	<b>Average Standard Deviation (m)</b>
X-Direction	0.464	1.648	0.927
Y-Direction	.383	1.396	0.744

Data was collected from nine tags over the course of ninety-six hours. Our movement threshold of two meters was greater than twice the average standard deviation and encompassed all individual standard deviation values observed.

As mentioned previously, the Smartbow system has a degree of error variance in its position measurements. This means that an animal may appear to exhibit a small amount of movement in a localized area when it is actually completely stationary. In order to correct for this, we required the animal to exceed a given distance threshold before movement was recognized. We determined the value of this movement threshold using the position data from nine stationary test tags collected over a period of ninety-six hours. The tags had an average standard deviation of 0.927m in the x-direction and 0.744 in the y-direction (see Table 1), with no individual tag exceeding 1.646 meters standard deviation in either direction. As a result, our movement threshold was set to a radius of two meters. This meant that, as long as an animal’s position remained inside a radius of

two meters, it would be considered at rest. Once the animal's signal left the two-meter radius, movement would be registered and the animal's location would be updated. The animal's recorded position for a given period of rest was determined by averaging each raw position data point for that period.

Table 2 *Behavioral variable correlation matrix*

	<b>Feed Order</b>	<b>Acc Events</b>	<b>Unique Boxes</b>	<b>Total Boxes</b>	<b>Move Percent</b>
<b>Feed Order</b>	1	.201	.097	.215	.207
<b>Acc Events</b>	.201	1	.241*	.335*	.283*
<b>Unique Boxes</b>	.097	.241*	1	.713*	.647*
<b>Total Boxes</b>	.215	.335*	.713*	1	.928*
<b>Move Percent</b>	.207	.283*	.647*	.928*	1

Correlations that are significant ( $p < 0.05$ ) are marked with an asterisk. TotalCount, UniqueCount, and MovePercent are all measures of the total amount of ground covered by each animal and therefore exhibit significant correlations. AccEvents is a measure of acceleration, and therefore an indirect measure of ground covered. This may account for the observed correlations with TotalCounts, UniqueCounts, and AccEvents.

*Correlation matrix*

As is evident from the correlation matrix presented in Table 2, multiple significant correlations were observed between our behavioral variables. This redundancy raises the possibility that these five variables may not be measuring five distinct behavioral constructs. Rather, they may be measuring one or two distinct constructs from different empirical vantage points. In situations like these, PCA allows for the simplification of the data set by describing constructs using a reduced number of

variables. This observation allows us to move forward with our primary PCA analysis knowing it is particularly well suited for the current data.

Table 3 *Loadings for PCA*

<b>Behavioral Variable</b>	<b>PCA 1</b>	<b>PCA 2</b>
Feed Order	.004	.871*
Acceleration Events	.265	.633*
Unique Boxes	.856*	.045
Total Boxes	.936*	.222
Percent Time Spent Moving	.913*	.197

High loading values (>0.4) are marked with an asterisk.

#### *Principal component analysis*

Bartlett's ( $p < 0.01$ ) and Kaiser-Meier-Oklin ( $KMO > 0.6$ ) test results confirmed homoscedasticity and sampling adequacy, validating the use of PCA with this data set. After entering all behavioral variables into the analysis (see Table 2 for correlation matrix) two principal components were identified (see Table 3). PCA 1 had strong loadings ( $\geq 0.4$ ) on new ground covered (unique boxes), total ground covered (total boxes), and proportion of the observation period spent moving. PCA 2 had strong loadings on feed order and acceleration events.

#### *Multiple regression*

Parity was entered first in all regressions to control for the effect that age and maturity might have on each production variable. Both PCA variables were entered simultaneously following this step. PCA 1 was a statistically significant predictor of herd

status ( $\beta = 0.399$ ,  $t(68) = 3.579$ ,  $p < 0.01$ ), pregnancy status ( $\beta = 0.443$ ,  $t(68) = 3.878$ ,  $p \ll 0.01$ ), and farrow status ( $\beta = 0.449$ ,  $t(68) = 3.964$ ,  $p \ll 0.01$ ). It was also a marginally significant predictor of total number of young born ( $\beta = 0.228$ ,  $t(68) = 1.856$ ,  $p = 0.068$ ) and total number of young stillborn ( $\beta = 0.232$ ,  $t(68) = 1.898$ ,  $p = 0.062$ ). PCA 2 was a statistically significant predictor of average piglet birthweight ( $\beta = -0.393$ ,  $t(68) = -3.285$ ,  $p < 0.01$ ). Average piglet wean weight and number of pigs weaned were not significantly predicted by either PCA variable.

For the sake of being thorough, we investigated whether our PCA factors were significant predictors of parity as well. PCA 1 was a marginally significant predictor ( $\beta = -0.196$ ,  $t(68) = -1.704$ ,  $p = 0.093$ ) while PCA 2 was a significant predictor of parity ( $\beta = -0.305$ ,  $t(68) = -2.656$ ,  $p = 0.01$ ). This meant that as exploration and measures of aggression increased, the sows were more likely to have produced a lower number of litters. Because parity is often used as a proxy for age, this can also be interpreted as suggesting that older animals are less mobile and less likely to engage in aggressive interactions.

## CHAPTER V – DISCUSSION

Hartigan's dip test results suggest the presence of unimodality in three of the four behavioral variables. Proportion of observation period spent moving, unique boxes traveled, and total boxes traveled all produced nonsignificant dip scores ( $p > 0.05$ ), indicating the absence of bimodality. The only variable that was not confirmed to exhibit unimodality by Hartigan's dip test ( $p < 0.05$ ) was the total number of acceleration events. It should be noted that visual inspection (top left corner of Figure 4) does not depict a dramatically bimodal distribution, and could be interpreted as approximating a roughly unimodal lognormal shape. It is worth considering whether a future study with a larger sample size would reveal the emergence of stronger bimodal or unimodal characteristics.

PCA extracted two principal components, which appear to correspond to distinct behavioral categories (see Table 1). PCA 1 had strong loadings ( $\geq 0.4$ ) on new ground covered (unique boxes), total ground covered (total boxes), and percent of the observation period spent moving. These were the variables pertaining to exploration and locomotion, suggesting PCA 1 is a measure of sow movement. PCA 2 had strong loadings on feed order and acceleration events, which are measures of social hierarchy and aggressive interaction respectively. It should be noted that the tally of aggressive events each sow engaged in does not take into consideration whether the animal instigated the event. Acceleration data would be similar regardless of whether that particular animal was the aggressor or a passive recipient.

Multiple regression results showed these principal components were able to predict a range of production variables. PCA 1 was a significant predictor of herd, pregnancy, and farrow status as well as a marginal predictor of total young born (both



healthy and stillborn). This suggests that animals who engaged in higher levels of locomotion are more likely to have reproductive success than animals who are less active. PCA 2 was a significant predictor of average piglet birthweight, suggesting that animals who are in lower social standing and engage in more aggressive events are likely to give birth to smaller piglets. These findings appear to be in disagreement with some of the existing literature concerning size and aggression. A direct positive correlation between size and frequency of aggression has been observed in some non-mammalian species (Hazlett, 1968; Okada & Miytake, 2009), and Melotti et al. (2011) found that pigs were more likely to initiate aggression with conspecifics when they were larger than their adversary. However, it is not clear whether larger size at birth translates to a larger size in adulthood, as growth rates can vary significantly throughout development (Cassady, 2007; Ruis et al., 2000; van Erp-Van der Kooij, 2003). It is also worth considering the fact that our analysis did not specify which animal instigated aggressive interaction. Our results could alternatively be interpreted as suggesting that animals who were the recipients of aggression tended to give birth to smaller piglets. Further research may be needed to clarify the relationship between birth and adult weight, as well as effect that these measures have on aggressive tendencies.

We were able to predict the characteristics of a given litter based on the mother's behavioral characteristics while that litter was gestating. This suggests it may be possible to identify animals with higher productivity levels, animals that are more likely to have successful pregnancies, and animals that are more likely to be removed from the population using data collected via indoor positioning systems like Smartbow. The fact that these traits can be predicted using exclusively behavioral data suggests it may be

possible to predict an animal's production before the first litter is born, as behavioral data is available preceding and throughout each animal's gestation period. Although this study did not include any animals that had not given birth previously, there is no reason that the same analysis performed here would not be applicable to a sample of gilts in subsequent studies. This would allow for more informed selection and breeding decisions from a much earlier point than would be possible using retroactive production data alone.

The fact that animal movement was predictive of herd removal status suggests these methods have potential veterinary applications as well. Herd removal is frequently the result of locomotion-related health complications such as lameness and injury. If animal movement is predictive of locomotion-related health problems in particular, systems like Smartbow could allow for early identification of potential health complications in real time. These questions will require future research as the present study did not take into account the specific reasons for individual herd removals.

Smartbow technology allows a unique approach to data collection with applications extending far beyond the scope of this study. The relatively high sampling rate and long-term twenty-four hour collection afforded by the system lend themselves to a range of unique analytical methods that remain unexplored. Fractal analysis is one such data analysis category concerned with quantifying the complexity of behavioral data sets in a range of situations. It has been used as a non-invasive means of characterizing the extent of parasitic infection in Japanese macaques (MacIntosh, Alados, & Huffman, 2011), stress due to food limitation in domestic chickens (Maria, Escós, & Alados, 2004), the extent of heat-stress in cattle (Hahn, Chen, Nienaber, Eigenberg, & Parkhurst, 1992), and levels of acute and chronic stress in hens and pigs (Rutherford, Haskell, Glasbey,

Jones, & Lawrence, 2004). Batchinsky, Cooke, Kuusela, & Cancio (2007) used fractal analysis of heartbeat intervals in swine undergoing hemorrhagic shock and were able to establish the severity of each animal's reaction to significant blood loss from these measures. The study's authors suggest similar methods could be used to assist in assessment of life-threatening injuries and inform decision-making in the triage process for both humans and animals. Future studies combining the power of fractal analysis with the unique data collection abilities of the Smartbow system may lead to advancements in an array of veterinary, breeding and herd management applications.

Assessment of animals using this process would be largely non-invasive and could be fully automated, with analysis scoring and flagging animals in real time as data is received and processed. Smartbow technology is relatively new and has not yet established itself as a widely-used tool in the swine industry. However, when combined with methods similar to those outlined in this study, it offers a powerful tool that can be used to better understand and predict animal production and health.

APPENDIX A – IRB Approval Letter



THE UNIVERSITY OF  
SOUTHERN MISSISSIPPI

INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE


118 College Drive #5116 | Hattiesburg, MS 39406-0001  
Phone: 601.266.6791 | Fax: 601.266.4377 | [iacuc@usm.edu](mailto:iacuc@usm.edu) | [www.usm.edu/iacuc](http://www.usm.edu/iacuc)

NOTICE OF COMMITTEE ACTION

The proposal noted below was reviewed and approved by The University of Southern Mississippi Institutional Animal Care and Use Committee (IACUC) in accordance with regulations by the United States Department of Agriculture and the Public Health Service Office of Laboratory Animal Welfare. The project expiration date is noted below. If for some reason the project is not completed by the end of the approval period, your protocol must be reactivated (a new protocol must be submitted and approved) before further work involving the use of animals can be done.

Any significant changes should be brought to the attention of the committee at the earliest possible time. If you should have any questions, please contact me.

PROTOCOL NUMBER: 16072501  
PROJECT TITLE: Characterization of pig coping strategies using measurements collected via indoor positioning system  
PROPOSED PROJECT DATES: 07/2016 - 09/2018  
PROJECT TYPE: New  
PRINCIPAL INVESTIGATOR(S): Alen Hajnal  
DEPARTMENT: Psychology  
FUNDING AGENCY/SPONSOR: N/A  
IACUC COMMITTEE ACTION: Full Committee Approval  
PROTOCOL EXPIRATION DATE: September 30, 2018

  
\_\_\_\_\_  
Jake Schaefer, PhD  
IACUC Chair

\_\_\_\_\_  
Date 9/6/2016

## APPENDIX B - Letter of Permission for Figure 1

2/26/2018

Gmail - Permission to include figure in dissertation



Shaun Perisho <sperisho@gmail.com>

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### Permission to include figure in dissertation

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Ruis, Marko <marko.ruis@wur.nl>  
To: Shaun Perisho <sperisho@gmail.com>  
Cc: "sperisho@calpoly.edu" <sperisho@calpoly.edu>

Mon, Feb 28, 2018 at 1:06 AM

Dear Shaun,

Sorry for my late answer. You are welcome to use figure 2 from my 2000 paper titled, "Personalities in female domesticated pigs .."

Please acknowledge the source of the figure in the caption of the figure.

All the best,

Marko Ruis

Dr. Marko A.W. Ruis

Wageningen UR Livestock Research  
PO box 338  
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The Netherlands

Mobile phone: +31 317 480 646

E-mail: marko.ruis@wur.nl

Visiting address: De Elst 1, 6708 WD Wageningen, The Netherlands

**From:** Shaun Perisho [mailto:sperisho@gmail.com]  
**Sent:** zaterdag 24 februari 2018 4:05  
**To:** Ruis, Marko <marko.ruis@wur.nl>  
**Subject:** Permission to include figure in dissertation

[Quoted text hidden]

## APPENDIX C - Letter of Permission for Figure 2

3/3/2018

Gmail - Permission to include a figure in my dissertation



Shaun Perisho <spersh@gmail.com>

---

### Permission to include a figure in my dissertation

---

Alistair Lawrence <Alistair.Lawrence@sruc.ac.uk>  
To: Shaun Perisho <spersh@calpoly.edu>  
Cc: Tamsin Coombs <Tamsin.Coombs@sruc.ac.uk>

Mon, Feb 26, 2018 at 11:30 PM

Dear Shaun – this is to confirm that I am happy for you to include the figure in your work and appreciate you asking

My best wishes

Alistair

Professor Alistair Lawrence

Chair of Animal Behaviour & Welfare (SRUC and University of Edinburgh)

SRUC, Roslin Institute Building, Easter Bush, Midlothian, EH25 9RG

0131 651 9343

**SRUC: Leading the way in Agricultural and Rural Research, Education and Consultancy.**

**From:** Shaun Perisho [mailto:spersh@calpoly.edu]  
**Sent:** 26 February 2018 17:33  
**To:** Tamsin Coombs; Alistair Lawrence

[Quoted text hidden]

[Quoted text hidden]

## REFERENCES

- Agarwal, S. K., & Marshall, G. D. (1998). Glucocorticoid-induced type 1/type 2 cytokine alterations in humans: A model for stress-related immune dysfunction. *Journal of Interferon & Cytokine Research, 18*(12), 1059-1068.
- Alados, C. L., Escos, J. M., & Emlen, J. M. (1996). Fractal structure of sequential behaviour patterns: An indicator of stress, *Animal Behaviour, 51*(2), 437-443.
- Arrindell, W. A., & Van der Ende, J. (1985). An empirical test of the utility of the observations-to-variables ratio in factor and components analysis. *Applied Psychological Measurement, 9*(2), 165-178.
- Bandler, R., Keay, K. A., Floyd, N., & Price, J. (2000). Central circuits mediating patterned autonomic activity during active vs. passive emotional coping. *Brain Research Bulletin, 53*(1), 95-104.
- Bandura, A. (1991). Social cognitive theory of self-regulation. *Organizational Behavior and Human Decision Processes, 50*(2), 248-287.
- Batchinsky, A. I., Cooke, W. H., Kuusela, T., & Cancio, L. C. (2007). Loss of complexity characterizes the heart rate response to experimental hemorrhagic shock in swine. *Critical Care Medicine, 35*(2), 519-525.
- Benus, R. F., Koolhaas, J. M., & Van Oortmerssen, G. A. (1987). Individual differences in behavioural reaction to a changing environment in mice and rats. *Behaviour, 100*(1), 105-121.
- Benus, R. F., Bohus, B., Koolhaas, J. M., & Van Oortmerssen, G. A. (1991). Heritable variation for aggression as a reflection of individual coping strategies. *Experientia, 47*(10), 1008-1019.

- Blanchard, R. J., Yudko, E., Dulloog, L., & Blanchard, D. C. (2001). Defense changes in stress nonresponsive subordinate males in a visible burrow system. *Physiology & Behavior*, 72(5), 635-642.
- Blokhuis, H. J., & Metz, J. H. M. (1992). Integration of animal welfare into housing systems for laying hens. *Netherlands Journal of Agricultural Science*, 40, 327-337.
- Boissy, A. (1995). Fear and fearfulness in animals. *Quarterly Review of Biology*, 70(2), 165-191.
- Bolhuis, J. E., Parmentier, H. K., Schouten, W. G., Schrama, J. W., & Wiegant, V. M. (2003). Effects of housing and individual coping characteristics on immune responses of pigs. *Physiology & Behavior*, 79(2), 289-296.
- Bolhuis, J. E., Schouten, W. G. P., De Jong, I. C., Schrama, J. W., Cools, A. R., & Wiegant, V. M. (2000). Responses to apomorphine of pigs with different coping characteristics. *Psychopharmacology*, 152(1), 24-30.
- Bolhuis, J. E., Schouten, W. G., de Leeuw, J. A., Schrama, J. W., & Wiegant, V. M. (2004). Individual coping characteristics, rearing conditions and behavioural flexibility in pigs. *Behavioural Brain Research*, 152(2), 351-360.
- Bressers, H. P. M., Te Brake, J. H. A., Engel, B., & Noordhuizen, J. P. T. M. (1993). Feeding order of sows at an individual electronic feed station in a dynamic group-housing system. *Applied Animal Behaviour Science*, 36(2-3), 123-134.
- Briffa, M., Rundle, S. D., & Fryer, A. (2008). Comparing the strength of behavioural plasticity and consistency across situations: Animal personalities in the hermit



- crab *Pagurus bernhardus*. *Proceedings of the Royal Society of London B: Biological Sciences*, 275(1640), 1305-1311.
- Broom, D. M. (1991). Assessing welfare and suffering. *Behavioural Processes*, 25(2), 117-123.
- Brown, G. K., & Nicassio, P. M. (1987). Development of a questionnaire for the assessment of active and passive coping strategies in chronic pain patients. *Pain*, 31(1), 53-64.
- Buss, D. M. (1991). Evolutionary personality psychology. *Annual Review of Psychology*, 42(1), 459-491.
- Carere, C., Drent, P. J., Privitera, L., Koolhaas, J. M., & Groothuis, T. G. (2005). Personalities in great tits, *Parus major*: Stability and consistency. *Animal Behaviour*, 70(4), 795-805.
- Carver C. (2013). Coping. In Gellman M.D., Turner J.R. (Eds.) *Encyclopedia of Behavioral Medicine* (pp. 496-500). New York, NY: Springer.
- Cassady, J. P. (2007). Evidence of phenotypic relationships among behavioral characteristics of individual pigs and performance. *Journal of Animal Science*, 85(1), 218-224.
- Chapin III, F. S., Autumn, K., & Pugnaire, F. (1993). Evolution of suites of traits in response to environmental stress. *The American Naturalist*, 142, S78-S92.
- Chapinal, N., Ruiz-de-la-Torre, J. L., Cerisuelo, A., Baucells, M. D., Gasa, J., & Manteca, X. (2008). Feeder use patterns in group-housed pregnant sows fed with an unprotected electronic sow feeder (Fitmix). *Journal of Applied Animal Welfare Science*, 11(4), 319-336.

- Clarke, A. S., & Boinski, S. (1995). Temperament in nonhuman primates. *American Journal of Primatology*, 37(2), 103-125.
- Cohen, J. (1988). *Statistical power analysis for the behavioral sciences* (2<sup>nd</sup> ed). Hillsdale, NJ: Lawrence Earlbaum Associates.
- Compas, B. E., Connor-Smith, J. K., Saltzman, H., Thomsen, A. H., & Wadsworth, M. E. (2001). Coping with stress during childhood and adolescence: Problems, progress, and potential in theory and research. *Psychological Bulletin*, 127(1), 87.
- Comrey, A. L., & Lee, H. B. (2013). *A first course in factor analysis*. Psychology Press.
- Connor-Smith, J. K., Compas, B. E., Wadsworth, M. E., Thomsen, A. H., & Saltzman, H. (2000). Responses to stress in adolescence: Measurement of coping and involuntary stress responses. *Journal of Consulting and Clinical Psychology*, 68(6), 976-992.
- Coppens, C. M., de Boer, S. F., & Koolhaas, J. M. (2010). Coping styles and behavioural flexibility: Towards underlying mechanisms. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 365(1560), 4021-4028.
- Cote, J., & Clobert, J. (2007). Social personalities influence natal dispersal in a lizard. *Proceedings of the Royal Society of London B: Biological Sciences*, 274(1608), 383-390.
- De Boer, S. F., & Koolhaas, J. M. (2003). Defensive burying in rodents: Ethology, neurobiology and psychopharmacology. *European Journal of Pharmacology*, 463(1), 145-161.

- Dingemanse, N. J., Both, C., Drent, P. J., & Tinbergen, J. M. (2004). Fitness consequences of avian personalities in a fluctuating environment. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 271(1541), 847-852.
- Dingemanse, N. J., Both, C., Drent, P. J., Van Oers, K., & Van Noordwijk, A. J. (2002). Repeatability and heritability of exploratory behaviour in great tits from the wild. *Animal Behaviour*, 64(6), 929-938.
- Dingemanse, N. J., Kazem, A. J., Réale, D., & Wright, J. (2010). Behavioural reaction norms: Animal personality meets individual plasticity. *Trends in Ecology & Evolution*, 25(2), 81-89.
- Dingemanse, N.J., & Réale, D. (2005). Natural selection and animal personality. *Behaviour*, 142(9-10), 1159-1184.
- Ebner, K., Wotjak, C. T., Landgraf, R., & Engelmann, M. (2005). Neuroendocrine and behavioral response to social confrontation: Residents versus intruders, active versus passive coping styles. *Hormones and Behavior*, 47(1), 14-21.
- Eisenberg, N., Fabes, R. A., & Guthrie, I. K. (1997). Coping with stress. In S. Wolchik & I. N. Sandler (Eds.), *Handbook of children's coping* (pp. 41-70). New York, NY: Springer US.
- Ely, D. L. (1981). Hypertension, social rank, and aortic arteriosclerosis in CBA/J mice. *Physiology & Behavior*, 26(4), 655-661.
- Erhard, H. W., & Mendl, M. (1999). Tonic immobility and emergence time in pigs: More evidence for behavioural strategies. *Applied Animal Behaviour Science*, 61(3), 227-237.

- Everitt, B. S. (1975). Multivariate analysis: The need for data, and other problems. *The British Journal of Psychiatry*, 126(3), 237-240.
- Flügge, G., Kramer, M., & Fuchs, E. (2001). Chronic subordination stress in male tree shrews: Replacement of testosterone affects behavior and central alpha2-adrenoceptors. *Physiology & Behavior*, 73(3), 293-300.
- Folkman, S., & Moskowitz, J. T. (2000). Stress, positive emotion, and coping. *Current Directions in Psychological Science*, 9(4), 115-118.
- Forkman, B., Furuhaug, I. L., & Jensen, P. (1995). Personality, coping patterns, and aggression in piglets. *Applied Animal Behaviour Science*, 45(1), 31-42.
- Freeman, J. B., & Dale, R. (2013). Assessing bimodality to detect the presence of a dual cognitive process. *Behavior Research Methods*, 45(1), 83-97.
- Geverink, N. A., Heetkamp, M. J. W., Schouten, W. G. P., Wiegant, V. M., & Schrama, J. W. (2004). Backtest type and housing condition of pigs influence energy metabolism. *Journal of Animal Science*, 82(4), 1227-1233.
- Geverink, N. A., Schouten, W. G. P., Gort, G., & Wiegant, V. M. (2002). Individual differences in aggression and physiology in peri-pubertal breeding gilts. *Applied Animal Behaviour Science*, 77(1), 43-52.
- Geverink, N. A., Schouten, W. G. P., Gort, G., & Wiegant, V. M. (2003). Individual differences in behaviour, physiology and pathology in breeding gilts housed in groups or stalls. *Applied Animal Behaviour Science*, 81(1), 29-41.
- Ginsburg, G. S., & Willard, H. F. (2009). Genomic and personalized medicine: Foundations and applications. *Translational Research*, 154(6), 277-287.
- Gorsuch, R. L. (1983). *Factor analysis* (2<sup>nd</sup> ed.). Hillsdale, NJ: Lawrence Erlbaum

Associates, Inc.

- Gosling, S. D. (2001). From mice to men: What can we learn about personality from animal research? *Psychological Bulletin*, *127*(1), 45.
- Groothuis, T. G., & Carere, C. (2005). Avian personalities: Characterization and epigenesis. *Neuroscience & Biobehavioral Reviews*, *29*(1), 137-150.
- Hahn, G., Chen, Y. R., Nienaber, J. A., Eigenberg, R. A., & Parkhurst, A. M. (1992). Characterizing animal stress through fractal analysis of thermoregulatory responses. *Journal of Thermal Biology*, *17*(2), 115-120.
- Hair, J. F., Jr., Anderson, R. E., Tatham, R. L., & Black, W. C. (1995). *Multivariate data analysis* (4<sup>th</sup> ed.). Saddle River, NJ: Prentice Hall.
- Hartigan, J. A., & Hartigan, P. M. (1985). The dip test of unimodality. *The Annals of Statistics*, *13*(1), 70-84.
- Hazlett, B. A. (1968). Size relationships and aggressive behavior in the hermit crab *Clibanarius vittatus*. *Ethology*, *25*(5), 608-614.
- Henry, J. P., Liu, Y. Y., Nadra, W. E., Qian, C. G., Mormede, P., Lemaire, V., ... & Hendley, E. D. (1993). Psychosocial stress can induce chronic hypertension in normotensive strains of rats. *Hypertension*, *21*(5), 714-723.
- Hessing, M. J. C., Coenen, G. J., Vaiman, M., & Renard, C. (1995). Individual differences in cell-mediated and humoral immunity in pigs. *Veterinary Immunology and Immunopathology*, *45*(1), 97-113.
- Hessing, M. J. C., Hagelsø, A. M., Van Beek, J. A. M., Wiepkema, R. P., Schouten, W. G. P., & Krukow, R. (1993). Individual behavioural characteristics in pigs. *Applied Animal Behaviour Science*, *37*(4), 285-295.

- Hessing, M. J. C., Schouten, W. G. P., Wiepkema, P. R., & Tielen, M. J. M. (1994). Implications of individual behavioural characteristics on performance in pigs. *Livestock Production Science*, *40*(2), 187-196.
- Hobfoll, S. E. (1989). Conservation of resources: A new attempt at conceptualizing stress. *American Psychologist*, *44*(3), 513.
- Horback, K. M., & Parsons, T. D. (2016). Temporal stability of personality traits in group-housed gestating sows. *Animal*, *10*(8), 1351-1369.
- Hunter, E. J., Broom, D. M., Edwards, S. A., & Sibly, R. M. (1988). Social hierarchy and feeder access in a group of 20 sows using a computer-controlled feeder. *Animal Science*, *47*(1), 139-148.
- Jensen, P. (1980). An ethogram of social interaction patterns in group-housed dry sows. *Applied Animal Ethology*, *6*(4), 341-350.
- Jensen, P., Rushen, J., & Forkman, B. (1995). Behavioural strategies or just individual variation in behaviour? A lack of evidence for active and passive piglets. *Applied Animal Behaviour Science*, *43*(2), 135-139.
- Jones, R. B., & Satterlee, D. G. (1996). Threat-induced behavioural inhibition in Japanese quail selected for contrasting adrenocortical response to mechanical restraint. *British Poultry Science*, *37*(2), 465-470.
- Kettlewell, H. D. (1958). A survey of the frequencies of *Biston betularia* and its melanic forms in Great Britain. *Heredity*, *12*(1), 51-72.
- Kirkwood, T. B., Kapahi, P., & Shanley, D. P. (2000). Evolution, stress, and longevity. *Journal of Anatomy*, *197*(4), 587-590.
- Kline, P. (2014). *An easy guide to factor analysis*. New York, NY: Routledge.

- Koolhaas, J. M., Korte, S. M., De Boer, S. F., Van Der Vegt, B. J., Van Reenen, C. G., Hopster, H., ... & Blokhuis, H. J. (1999). Coping styles in animals: Current status in behavior and stress-physiology. *Neuroscience & Biobehavioral Reviews*, *23*(7), 925-935.
- Korte, S. M., Bouws, G. A. H., Koolhaas, J. M., & Bohus, B. (1992). Neuroendocrine and behavioral responses during conditioned active and passive behavior in the defensive burying/probe avoidance paradigm: Effects of ipsapirone. *Physiology & Behavior*, *52*(2), 355-361.
- Lawrence, A. B., Terlouw, E. M. C., & Illius, A. W. (1991). Individual differences in behavioural responses of pigs exposed to non-social and social challenges. *Applied Animal Behaviour Science*, *30*(1), 73-86.
- Lazarus, R. S. (1966). *Psychological stress and the coping process*. New York, NY: McGraw Hill.
- Lazarus, R. S. & Folkman, S. (1984). *Stress, Appraisal, and Coping*. New York, NY: Springer.
- Lazarus, R. S. (1986). Stress: Appraisal and coping capacities. In A. Eichler, M. M. Silverman, & D. M. Pratt (Eds.), *How to define and research stress* (5-12). Washington, DC: American Psychiatric Press.
- Lazarus, R. S., & Cohen, J. B. (1977). Environmental stress. In I. Altman & J.F. Wohlwill (Eds.), *Human behavior and environment* (pp. 89-127). New York, NY: Springer US.

- Levine, S., Weinberg, J., & Ursin, H. (1978). Definition of the coping process and statement of the problem. In H. Ursin (Ed.) *Psychobiology of stress: A study of coping men* (pp. 3-21). Academic Press New York.
- MacIntosh, A. J., Alados, C. L., & Huffman, M. A. (2011). Fractal analysis of behaviour in a wild primate: Behavioural complexity in health and disease. *Journal of the Royal Society Interface*, 8(63), 1497-1509.
- Majerus, M. E. (2009). Industrial melanism in the peppered moth, *Biston betularia*: An excellent teaching example of Darwinian evolution in action. *Evolution: Education and Outreach*, 2(1), 63-74.
- Manuck, S. B., Kaplan, J. R., & Clarkson, T. B. (1983). Behaviorally induced heart rate reactivity and atherosclerosis in cynomolgus monkeys. *Psychosomatic Medicine*, 45(2), 95-108.
- Maria, G. A., Escós, J., & Alados, C. L. (2004). Complexity of behavioural sequences and their relation to stress conditions in chickens (*Gallus gallus domesticus*): A non-invasive technique to evaluate animal welfare. *Applied Animal Behaviour Science*, 86(1), 93-104.
- McEwen, B. S., & Wingfield, J. C. (2003). The concept of allostasis in biology and biomedicine. *Hormones and Behavior*, 43(1), 2-15.
- Melotti, L., Oostindjer, M., Bolhuis, J. E., Held, S., & Mendl, M. (2011). Coping personality type and environmental enrichment affect aggression at weaning in pigs. *Applied Animal Behaviour Science*, 133(3), 144-153.
- Mroczek, D. K., & Almeida, D. M. (2004). The effect of daily stress, personality, and age on daily negative affect. *Journal of Personality*, 72(2), 355-378.



- Mundfrom, D. J., Shaw, D. G., & Ke, T. L. (2005). Minimum sample size recommendations for conducting factor analyses. *International Journal of Testing*, 5(2), 159-168.
- Otten, W., Puppe, B., Kanitz, E., Schön, P. C., & Stabenow, B. (2002). Physiological and behavioral effects of different success during social confrontation in pigs with prior dominance experience. *Physiology & Behavior*, 75(1), 127-133.
- Perdeck, A. C., Visser, M. E., & Van Balen, J. H. (2000). Great tit *Parus major* survival and the beech-crop. *Ardea*, 88, 99-106.
- Piersma, T., & Drent, J. (2003). Phenotypic flexibility and the evolution of organismal design. *Trends in Ecology & Evolution*, 18(5), 228-233.
- Pinel, J. P., & Treit, D. (1978). Burying as a defensive response in rats. *Journal of Comparative and Physiological Psychology*, 92(4), 708.
- Réale, D., & Dingemanse, N. J. (2010). Personality and individual social specialisation. In T. Székely, A. J. Moore, & J. Komdeur (Eds.), *Social behaviour: genes, ecology and evolution* (p. 562). Cambridge, UK: Cambridge University Press.
- Réale, D., & Festa-Bianchet, M. (2003). Predator-induced natural selection on temperament in bighorn ewes. *Animal Behaviour*, 65(3), 463-470.
- Réale, D., Gallant, B. Y., Leblanc, M., & Festa-Bianchet, M. (2000). Consistency of temperament in bighorn ewes and correlates with behaviour and life history. *Animal Behaviour*, 60(5), 589-597.
- Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, 82(2), 291-318.

- Relyea, R. A. (2001). Morphological and behavioral plasticity of larval anurans in response to different predators. *Ecology*, 82(2), 523-540.
- Ruis, M. A., de Groot, J., te Brake, J. H., Ekkel, E. D., van de Burgwal, J. A., Erkens, J. H., ... & Koolhaas, J. M. (2001). Behavioural and physiological consequences of acute social defeat in growing gilts: Effects of the social environment. *Applied Animal Behaviour Science*, 70(3), 201-225.
- Ruis, M. A., te Brake, J. H., Engel, B., Buist, W. G., Blokhuis, H. J., & Koolhaas, J. M. (2001). Adaptation to social isolation: Acute and long-term stress responses of growing gilts with different coping characteristics. *Physiology & Behavior*, 73(4), 541-551.
- Ruis, M. A., te Brake, J. H., Engel, B., Buist, W. G., Blokhuis, H. J., & Koolhaas, J. M. (2002). Implications of coping characteristics and social status for welfare and production of paired growing gilts. *Applied Animal Behaviour Science*, 75(3), 207-231.
- Ruis, M. A., te Brake, J. H., van de Burgwal, J. A., de Jong, I. C., Blokhuis, H. J., & Koolhaas, J. M. (2000). Personalities in female domesticated pigs: Behavioural and physiological indications. *Applied Animal Behaviour Science*, 66(1), 31-47.
- Rutherford, K. M. D., Haskell, M. J., Glasbey, C., Jones, R. B., & Lawrence, A. B. (2004). Fractal analysis of animal behaviour as an indicator of animal welfare. *Animal Welfare*, 13(1), 99-103.
- Sapolsky, R. M. (2004). *Why zebras don't get ulcers: The acclaimed guide to stress, stress-related diseases, and coping*. New York, NY: Holt paperbacks.

- Schrama, J. W., Schouten, J. M., Swinkels, J. W., Gentry, J. L., de Vries Reilingh, G., & Parmentier, H. K. (1997). Effect of hemoglobin status on humoral immune response of weanling pigs differing in coping styles. *Journal of Animal Science*, 75(10), 2588-2596.
- Schuler, R. S. (1982). An integrative transactional process model of stress in organizations. *Journal of Organizational Behavior*, 3(1), 5-19.
- Selve, H. (1936). A syndrome produced by diverse nocuous agents. *Nature*, 138(3479), 32.
- Sgoifo, A., De Boer, S. F., Haller, J., & Koolhaas, J. M. (1996). Individual differences in plasma catecholamine and corticosterone stress responses of wild-type rats: Relationship with aggression. *Physiology & Behavior*, 60(6), 1403-1407.
- Sgoifo, A., De Boer, S. F., Westenbroek, C., Maes, F. W., Beldhuis, H., Suzuki, T., & Koolhaas, J. M. (1997). Incidence of arrhythmias and heart rate variability in wild-type rats exposed to social stress. *American Journal of Physiology-Heart and Circulatory Physiology*, 273(4), H1754-H1760.
- Sih, A., & Bell, A. M. (2008). Insights for behavioral ecology from behavioral syndromes. *Advances in the Study of Behavior*, 38, 227-281.
- Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: An ecological and evolutionary overview. *Trends in Ecology & Evolution*, 19(7), 372-378.
- Sih, A., Kats, L. B., & Maurer, E. F. (2003). Behavioural correlations across situations and the evolution of antipredator behaviour in a sunfish–salamander system. *Animal Behaviour*, 65(1), 29-44.

- Skinner, E. A., & Zimmer-Gembeck, M. J. (2007). The development of coping. *Annual Review of Psychology, 58*, 119-144.
- Sluyter, F., Bult, A., Lynch, C. B., van Oortmerssen, G. A., & Koolhaas, J. M. (1995). A comparison between house mouse lines selected for attack latency or nest-building: Evidence for a genetic basis of alternative behavioral strategies. *Behavior Genetics, 25*(3), 247-252.
- Snow-Turek, A. L., Norris, M. P., & Tan, G. (1996). Active and passive coping strategies in chronic pain patients. *Pain, 64*(3), 455-462.
- Strawford, M. L., Li, Y. Z., & Gonyou, H. W. (2008). The effect of management strategies and parity on the behaviour and physiology of gestating sows housed in an electronic sow feeding system. *Canadian Journal of Animal Science, 88*(4), 559-567.
- Teitelbaum, P., Pellis, S. M., & DeVietti, T. L. (1990). Disintegration into stereotypy induced by drugs or brain damage: A microdescriptive behavioural analysis. In I. Stolerman (Ed.), *Encyclopedia of Psychopharmacology* (pp. 169-199). New York, NY: Oxford University Press.
- Thoits, P. A. (1995). Stress, coping, and social support processes: Where are we? What next? *Journal of Health and Social Behavior, 53*-79.
- Van Erp-van der Kooij, E., Kuijpers, A. H., Schrama, J. W., Ekkel, E. D., & Tielen, M. J. M. (2000). Individual behavioural characteristics in pigs and their impact on production. *Applied Animal Behaviour Science, 66*(3), 171-185.

- Van Erp-Van der Kooij, E., Kuijpers, A. H., Van Eerdenburg, F. J. C. M., & Tielen, M. J. M. (2003). Coping characteristics and performance in fattening pigs. *Livestock Production Science*, *84*(1), 31-38.
- Verbeek, M. E., Boon, A., & Drent, P. J. (1996). Exploration, aggressive behaviour and dominance in pair-wise confrontations of juvenile male great tits. *Behaviour*, *133*(11), 945-963.
- Verbeek, M. E., Drent, P. J., & Wiepkema, P. R. (1994). Consistent individual differences in early exploratory behaviour of male great tits. *Animal Behaviour*, *48*(5), 1113-1121.
- Von Holst, D. (1985). Coping behaviour and stress physiology in male tree shrews (*Tupaia belangeri*). *Experimental Behavioral Ecology and Sociobiology*, *31*, 461-470.
- Wechsler, B. (1995). Coping and coping strategies: A behavioural view. *Applied Animal Behaviour Science*, *43*(2), 123-134.
- Wilson, D. S., Coleman, K., Clark, A. B., & Biederman, L. (1993). Shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): An ecological study of a psychological trait. *Journal of Comparative Psychology*, *107*(3), 250.
- Wingfield, J. C., & Kitaysky, A. S. (2002). Endocrine responses to unpredictable environmental events: Stress or anti-stress hormones? *Integrative and Comparative Biology*, *42*(3), 600-609.
- Wolf, M., Van Doorn, G. S., & Weissing, F. J. (2008). Evolutionary emergence of responsive and unresponsive personalities. *Proceedings of the National Academy of Sciences*, *105*(41), 15825-15830.