Chapter 9

General and summarizing discussion
Integration and discussion of the findings

The main purpose of this thesis was to study (psycho)social aspects of modern pig farming and its consequences for animal welfare. By investigating acute and long-term effects of social defeat, it was aimed to find out whether well-documented reductions in welfare following social mixing may be ascribed to initial fighting for dominance status. Moreover, it was investigated whether interactions with familiar animals following a social stressor improve the ability to adapt to the stressor, and what the consequences are for welfare when no social contact at all is allowed. Finally, attempts were made to identify pigs with different coping strategies, which may explain the nature of animal interactions within social groups and differences in the ability of individual adaptation to environmental changes in general. A definition of welfare and its assessment by a multidimensional approach is given in Chapter 1. One promising and convenient parameter for measurements of the stress response, i.e. salivary cortisol, was more thoroughly investigated (Chapter 2). Its circadian rhythmicity was studied in relation to age, gender and stress. For measurements of salivary cortisol, a radioimmunoassay (RIA) was optimized and validated. One major finding was that the timing of stressor application importantly influenced the acute cortisol response: the increase was higher in morning periods. This finding was accounted for as much as possible in the other experiments (Chapters 3-8) of the project, by restricting (the start of) applications of stressors or testings to certain parts of the day. In the following, an integrated discussion on Chapters 3-8 is given, by raising the main topics and findings of this thesis.

Social defeat versus social support in rats: a model for pigs

Social defeat

One important source of social stress in pigs is the aggression that occurs when unfamiliar conspecifics are mixed, which is generally recognized as a major welfare concern in commercial pig farming. However, for practical reasons, mixing of unfamiliar pigs is an important management procedure in pig farming. In the current thesis an attempt was made to elucidate which social aspect(s) constitute(s) the highest risk for pig welfare during mixing, by separating the effects of initial fighting for dominance, from the continuing social stress that may exist through a permanent coexistence of unfamiliar animals. Fighting for dominance is initially characterized by mutual aggression, and is therefore expected to be a severe acute stressor for both the winner and the loser of the fight. However, it has been repeatedly demonstrated that the stress of being defeated leads to stronger and
more prolonged stress responses (Schuurman, 1980), which was also substantiated by our results in Chapter 7. Haller et al. (1996) suggest that dominance is associated with reductions in corticosteroids, whereas submission elicits a strong increase. The concomitant lack of control of being defeated may thus cause a threat to welfare, especially because a long-lasting effect of social defeat may be observed, characterized by long-term adverse behavioural and physiological changes (Koolhaas et al., 1997b; Miczek et al., 1990). The alterations in behaviour and physiology resemble those in depressed humans and therefore the social defeat model in rats is often used for studies into this type of human psychopathology (Koolhaas et al., 1997b).

Modulating effects of the social environment

In this project, the social defeat model in rats was used to gain more insight in potential harmful long-term effects of acute social defeat in pigs. However, one limitation of this rat model is that isolated animals are used. This is rather unnatural, because, like pigs, wild rats live in social groups. These groups consist of a number of related males (often one dominant and several younger males) and a varying number of females. The validity of the defeat model may importantly be increased when housing conditions are used as an experimental variable. This will mimic different social settings which individuals may experience in everyday life. We investigated the effect of the social environment and found striking differences between socially defeated rats that were individually housed and those that were housed together with familiar conspecifics following the acute social stress. Compared to group-housed rats, individually housed animals showed reduced body growth, high sensitivity to repeated stress, low open field activity, high anxiety and hyperactivity of the HPA-axis. These characteristics of defeated and isolated rats more or less agree with indicators of depression in humans, such as decreased general activity, loss of weight and abnormal high HPA-axis (re)activity. Whether a depression-like state may develop in defeated rats thus strongly depends on contextual social factors. The presence of familiar conspecifics importantly reduces the long-term negative effects of social defeat. Such an amelioration of stress responses by the social environment is called social support (social buffering). Social support cannot be provided by any conspecific, but only by bonding partners (Sachser et al., 1998). The groups of familiar rats used in Chapter 3 consisted of litter-mates and accordingly social bonding between group-members was expected to be strong. The phenomenon of social support is probably widespread among mammals. As McGlone (1990) mentioned: ‘It seems that misery loves company,
even in the animal kingdom’. By maintaining the availability and accessibility of bonding partners, an animal’s way of living is economized and its chances of survival are increased (Sachser et al., 1998).

The importance of a (stable) social environment for pigs

Social defeat and social support

Based on the information on social defeat and social support in rats (Chapter 3), acute and long-term effects of social defeat and modulating effects of the social environment were investigated in pairs of growing gilts (Chapter 4). As for rats, it was demonstrated that social defeat constitutes a severe stressor for pigs, by causing pronounced increases in HPA-axis and sympathetic-adrenal medullary activities, and shifts in leucocyte subsets. When social defeat was followed by the possibility to interact with a familiar conspecific, i.e. a litter-mate, stress responses were generally shorter-lived and habituation to a repeated novel environment test was facilitated. This suggests that litter-mates can act as bonding partners. The increased ability of a defeated pig to adapt to the social threat through social support is considered to be positive for its welfare.

Welfare problems of mixing

Social defeat in pigs always seemed to leave some traces in the longer term, as observed by a higher sensitivity of defeated pigs to (mild) changes in their environment (Chapter 4). However, body growth of defeated pigs was not affected, which contrasts findings in pens of mixed pigs in which subordinate pigs show a depressed growth (Albinsson and Andersson, 1980; Giroux et al., 2000). In line with this, it is shown in Chapter 7 that within pairs of unfamiliar gilts body growth is lower in subordinates compared to dominants. It is therefore likely that the negative effects of the social stress of initial fighting for dominance status, and the social stress that persists through permanent coexistence of unfamiliar animals, together lead to the often observed reductions in welfare following mixing. Being a subordinate in a newly mixed group of strangers may consequently be more stressful than being a subordinate in a group of familiar pen-mates. Chapter 7 also showed that detrimental effects of mixing on body growth develop independent of social stability (stability of relations among animals in social groups). Thus, even when aggressive physical contact is low, social stress may persist through visual exposure to opponents. The higher vulnerability to environmental stimuli after social defeat, together with a reduced body weight gain when being permanently exposed to dominants, may suggest a depressive-like state in subordinate pigs.
General discussion

In Chapter 5 it was studied what impact mixing of unfamiliar pigs has on specific long-term immune responses and protection against infection after vaccination with pseudorabies virus (PRV). As shown for some immune parameters (e.g. lymphocyte proliferation and IFN-gamma responses after vaccination, IgG1/IgG2-ratio after challenge) dominance in itself seemed to guarantee a higher immune response. However, when other parameters (e.g. IFN-gamma/IL-10 ratio after challenge) were considered, the immune response seemed to be more suppressed in mixed dominants than in mixed subordinates. The latter may be unexpected, also on the basis of our findings in Chapter 7, in which we argue for a more serious effect of mixing for subordinates than for dominants. However, our findings with regard to immune capacity may emphasize that the social situation imposed by mixing may not only compromise welfare of subordinates, but is also a ‘uncomfortable’ situation for dominants animals. The latter animals should maintain their high social status and accordingly may experience a continuous threat to control. More or less surprisingly, we also observed a gender-related difference in immune capacity (Chapter 5). It was shown that mixed barrows suffered more from immunosuppression than mixed gilts, although levels of agonistic interactions did not differ. We do not have a sound explanation, but the phenomenon may not be completely new. For example, a large scale research with 18000 pigs showed that barrows more often suffered from chronic inflammations than gilts (De Kruijf and Welling, 1988). It may be speculated that this is due to a higher HPA-activity in barrows, as being argued for in Chapters 2 and 5, leading to a lower immune capacity of males. The stress and the change in hormonal patterns which accompany castration may be the mediators of an increased HPA-(re)activity in barrows.

Individual housing

It was mentioned that the social environment not only has negative effects on individuals but can also act in a positive way. Our findings in Chapter 4 also emphasize that being able to interact with any conspecific, i.e. being socially housed, is a prerequisite to safeguard welfare of pigs. Social isolation by individual housing gradually leads to a state of reduced welfare, as shown by increases in emotional arousal and decreases in abilities to habituate to repeated ‘novel’ stimuli. Moving to another pen may strengthen these effects of isolation, by additionally inducing high acute stress responses to this procedure (Chapter 8). Although individual pigs may not be equally vulnerable to isolation stress (Chapter 8), it is argued that the generally higher emotional arousal of isolated pigs represents a
higher state of fearfulness (Chapter 4). Despite the indications for a disturbance of mood, body growth of isolated pigs was not negatively influenced. Several other studies have even shown a higher growth performance of individually penned animals than those kept in groups (Gomez et al., 2000; Morgan et al., 1999). We argue that body growth is confounded with direct effects of the social environment. Individually housed pigs spent more time in feeding behaviour than animals housed in groups, as a substitute for social behaviour (Morgan et al., 1999). Pigs in groups also tend to synchronize their feeding behaviour, which may lead to a competition for food, especially in case of insufficient trough space. Accordingly, food intake of (certain) members of a group may be less than desired. Despite the opportunity to feed at other times when the trough is vacant, pigs prefer to remain with group mates (Morgan et al., 1999). Thus, (normal) body growth should be carefully interpreted, and we doubt that this parameter may be used as a welfare indicator when different social settings are compared.

**Coping strategies in pigs and their consequences for welfare**

The present project provides further evidence of the large physiological and behavioural variation among pigs living under farm conditions, despite domestication. Importantly, at least for part of the pig population, this variation seems to be determined by fundamental differences in ways of coping, although we were not able to demonstrate the existence of specific categories of pigs (Chapter 6). Nevertheless, extremes within the population differ generally in the same behavioural and physiological parameters and to the same degree, and fulfil the criteria for (more) reactive and (more) proactive coping strategies.

**Validity of the backtest to predict coping characteristics**

Previously, Hessing (1994) suggested that on the basis of behavioural resistance in a backtest, pigs could be divided into reactive and passive copers. His suggested bimodality of coping responses in pigs, however, could not be replicated by others (Forkman et al., 1995), leading to confusion and debate among researchers. From our experiences with the backtest, we conclude that the distribution of reactions to this test is unimodal, with no indication for a limited number of isolated classes. However, we hypothesize that such a distribution may not exclude that animals towards the ends of the scale may have a prevalence for one or another strategy. Indeed, without wanting to create an impression that there are real categories of individuals, extreme responders to the backtest differed in levels of aggression at a later age and had different patterns of stress responses in
various situations. Low resisting pigs are generally low-aggressive and adopt a more reactive way of coping, whereas the high resistant pigs are more aggressive and represent the more proactive copers. Table 1 summarizes the behavioural and physiological characteristics of gilts which represent the (more) reactive and (more) proactive pigs according to behavioural resistance in the backtest (integrated results of Chapter 6, 7 and 8).

**Table 1.** Summary of the behavioural and physiological characteristics of high- and low-resistant pigs in the backtest.

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>High-resistant 'proactive'</th>
<th>Low-resistant 'reactive'</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aggression</td>
<td>High</td>
<td>Low</td>
</tr>
<tr>
<td>Cue dependency</td>
<td>Low</td>
<td>High</td>
</tr>
<tr>
<td>Escape behaviour</td>
<td>High</td>
<td>Low</td>
</tr>
<tr>
<td>Exploration</td>
<td>Low</td>
<td>High</td>
</tr>
<tr>
<td>Vocalizing</td>
<td>High</td>
<td>Low</td>
</tr>
<tr>
<td>Physiology</td>
<td></td>
<td></td>
</tr>
<tr>
<td>HPA-axis reactivity</td>
<td>Low</td>
<td>High</td>
</tr>
<tr>
<td>Parasympathetic activity</td>
<td>Low</td>
<td>High</td>
</tr>
</tbody>
</table>

In Chapter 6 we argue that the quality of a backtest at a very young age is attributed to testing of rather naive animals, unaffected by previous experiences. At this age, pigs already have a clear personality, which is predominantly determined by genetic factors. In the following, we hypothesize from a motivational and functional point of view why the backtest is a valuable tool for predictions of aggression and coping responses. In the pairs of pigs which were studied in Chapter 7, proactive pigs had an equal chance to become dominant or subordinate. When proactive animals became dominant, they always behaved aggressively towards opponents. When they became subordinate, only forced submission through acts of hostility and aggression of opponents evoked aggression. Reactive animals, on the other hand, only used aggression when challenged and their aggressive intentions were much suppressed when their social positions became clear. Being restrained in a supine position during a backtest may represent forced submission, by its resemblance with certain aspects of social fighting. We therefore
argue that reactive animals more readily accept their forced subordinate status and resist less fiercely, whereas proactive animals become frustrated by bodily forced submission and are more eager to resist. A comparable test as the backtest is used in dogs (puppy-selection test), as a tool to predict to what extent these animals accept leadership from humans (Campbell, 1975), although this test is not generally recognized to have a predictive value for this purpose (Beaudet et al., 1994). In contrast to what Hessing et al. (1993) claimed, it is thus more likely that the backtest done with piglets represents a social than a non-social test.

Coping characteristics, aggressive behaviour and social stress after mixing

As shown in Chapter 7, proactive pigs are particularly aggressive when being dominant or frustrated. Reactive animals, in contrast, are only aggressive when challenged, i.e. when fighting for dominance, and their aggressiveness is much suppressed when social relationships are settled. The presence of reactive animals in a group may thus be of advantage for the stability of (relations between individuals in) a social group. We also showed that the most stable social relationships occurred between a reactive and a proactive pig. This may indicate that in social organizations, animals with different or complementary characteristics are needed to establish social stability and to increase the 'survival of the group'. Indeed, Hessing et al. (1994a) previously showed that group performance of pigs was best in groups with a large variation in individual aggressiveness. However, we should emphasize that when a proactive pig takes the dominant position this may not be beneficial for the welfare of a reactive subordinate. Nevertheless, most detrimental for welfare was the situation of cohabitation of two proactive pigs, characterized by relatively high levels of aggressiveness, stress and fear in both animals. The level of aggression following mixing is thus related to the coping strategy of individual pigs, but also depends on the social position of respective individuals within the social group.

Coping strategies, social isolation and effects of domestication

As described in Chapter 8, pigs with reactive and proactive features differed in their strategies to deal with social isolation, as demonstrated by several differences in the temporal dynamics of stress responses. The general impression is that reactive pigs recovered more quickly from the imposed social isolation than proactive animals. Studies with rodents showed that reactive animals more easily adapt to variable conditions and are more flexible than proactive animals. The latter animals deal better with stable environmental conditions (Benus et al., 1991;
Koolhaas et al., 1999). When this is generalized, the better adaptation to social isolation of reactive pigs may represent a generally better ability of these pigs to adapt to a variety of challenges. If this assumption is right, this may support the theory that domestication may favour a certain type of animal (Hopster, 1998; Jensen et al., 1995b), and it is likely that a shift takes place towards the (more) reactive type of pig. Indeed, social structures seem to be more relaxed in domesticated pigs, and their aggression, flight distance and motility are lower than in wild pigs (Hemmer, 1990). The degree of variation in responses of the domesticated pig, though still being large, may be smaller than the original variation in responses of the wild ancestors. Hence, the degree of differentiation into coping strategies may have become weaker through domestication. A relatively large 'middle' group of animals emerges in which no clear strategies to deal with environmental changes can be detected. However, at the extremes, animals still tend towards different coping strategies, and they differ quantitatively and qualitatively in their behavioural and physiological response patterns to stress. These differences between population extremes seem to be large enough to influence susceptibility to stress and diseases.

**Summarizing conclusions and practical implications**

**Mixing**

From a welfare point of view, the best management procedure probably is to keep litter-mates together until slaughter, without disrupting social groups by mixing. This was also suggested in earlier research comparing two site systems, in which pigs are regrouped, with farrowing-to-finish systems, in which pigs are never mixed (Ekkel et al., 1995b; Scheepens et al., 1992). In The Netherlands, specific legislation (Varkensbesluit, 1998) within the frame of the Dutch Health and Welfare Act (Gezondheids- en Welzijnswet voor Dieren, 1992) has come into force, which allows unfamiliar pigs to be mixed only once, within one week after weaning. This measure will probably also be adopted by the European Commission, by amending existing EU legislation (EC Council Directive 91/630/EEC, 1991) on the protection of pigs to improve welfare conditions. The proposal of the Commission for amending Directive 91/630/EEC is based on a recommendation by its Scientific Veterinary Committee (1997). Despite these actions to improve the welfare of pigs, it should be emphasized that groupings imposed by farmers, although only done once, may cause long-term social instability and social stress, and hence reduced welfare. This thesis may provide different solutions to reduce mixing-associated welfare problems:
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Hiding places and resources. In Chapter 4 we showed that when subordinate pigs are separated from dominants following initial fighting for dominance status (social defeat), they do not develop all signs of stress pathology normally seen after mixing. This possibly reflects a reduced state of stress of the subordinate by removal from the stressor, i.e. the dominant. It is therefore likely that in groups of pigs it is advantageous for subordinates to have possibilities to hide and not being confronted with dominants all the time, which means not having to compete for living and feeding space (Chapter 7; McGlone and Curtis, 1985; Rushen, 1987). As can be derived from Chapter 5, a provision of possibilities to decrease the number of interactions may also be beneficial for dominant pigs. The new legislation (Varkensbesluit, 1998) in The Netherlands, which is at present more restrictive than the European legislation (EC Council Directive 91/630/EEC, 1991), may to some extent meet these demands by the requirement that the minimal surface area per pig has to be increased (for pigs of 85-110 kg: from 0.7 m² to 1.0 m²). However, one has to realize that the welfare of pigs cannot simply be translated into square meters per pig. An increase in feeding space (pigs tend to synchronize their feeding behaviour) and possibilities to hide and flee may additionally prove to be valuable measures to improve welfare of fattening pigs.

Subgroups of pigs. From our findings in Chapters 3 and 4, we conclude that the presence of familiar animals may have positive implications for welfare. We hypothesize that negative effects of mixing may be moderated by bringing subgroups of litter-mates together. Not only may familiar group members buffer against the adverse effects of (social) stress by processes of social support, the number and intensity of fightings may also be reduced through the presence of related conspecifics. When further experiments confirm this hypothesis, such a mixing routine can easily be implemented in modern pig farming.

Knowledge on coping strategies and aggression: the value of the backtest. Knowledge on specific coping strategies of individual pigs may be useful to improve welfare of pigs after mixing (Chapter 7). Bringing two proactive gilts together was most detrimental for welfare. In contrast, combining pigs with different coping strategies could lead to low levels of aggression and stress, but this strongly depended on the outcome of social fighting. Provision of variation in weight upon mixing was previously shown to reduce aggression after mixing (Andersen et al., 2000a; Rushen, 1987). Combined with our findings, the advantage for pig welfare by mixing pigs of different size may especially arise when the larger pigs are reactive and the smaller ones have proactive features. Nevertheless, it may not be easy or even impossible to implement this under commercial
conditions. In pig farming, sows are usually synchronized (one production group) to farrow simultaneously as much as possible, so that at the end of the fattening period, large numbers of growing pigs of similar weight can leave the farm at the same time to be slaughtered. Weight differences between pigs of the same production group may thus not be large enough, whereas differences in weight between pigs of different production groups become too large. Although the optimal social situation thus hardly can be established, the opposite, i.e. the worst social situation, may relatively easily be prevented. Mixing of many potentially aggressive pigs in one group can and should be avoided, based on our results of mixing two proactive pigs. For this purpose, the backtest is a valuable tool to be implemented by pig farmers. Routinely, piglets are handled several times at a young age and a (modification of a) backtest should therefore not require too much time and effort. As mentioned in Chapter 7, more research is needed to determine the type of relationships in groups becoming too large to form social hierarchies. When social relationships become weak, the backtest may have no practical value.

**Individual housing**

This thesis emphasizes that the pig is a socially living animal which requires social contact with conspecifics (Chapter 4). Individual housing of growing pigs is not routinely done, but individual housing of sows, in confinement systems such as stalls, is still common. In The Netherlands, national legislation prohibits sows without piglets to be housed individually (Varkensbesluit, 1998), and group-housing systems are therefore increasing. In line with the Dutch legislation, the European Commission will probably come with tougher regulations of individual housing of sows (amended EC Council Directive 91/630/EEC, 1991), by banning the use of individual pens for sows during a period starting from weaning to one week before the expected time of farrowing. By these new requirements, the living environment of sows may be much improved.

For experimental purposes, however, pigs are often individually housed, which facilitates experimental testing and controllability for investigators. However, the negative acute and long-term effects of this procedure may interfere with the outcome of experimental testings. Therefore, experimental work should as much as possible be done with grouped pigs, allowing interactions between members of this social species. Some experiments, however, require individual housing, e.g. for individual monitoring of pigs in metabolism cages. In this case, allowance of some contact with conspecifics may provide a solution to limit the negative effects of individual housing. The degree of exposure to conspecifics
seems to determine the level of stress caused by individual housing. In our experiments, individually housed pigs were not able to have visual and physical contact, which may be a high degree of social deprivation. The individually housed rats in Chapter 3 were able to see conspecifics through transparent walls, but this was not sufficient to recover from the detrimental effects of social defeat. However, it was recently shown that provision of (physical) contact through a wire mesh limits the negative effects of individual housing (Herskin and Jensen, 2000; Hurst et al., 1997). Thus, from a welfare point of view, separation, but not isolation, may provide the best procedure when individual housing of pigs is required.