

Alarm signalling between rats: a potential model for
conservation of endangered species?

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Abstract

In this study male and female rats were exposed to mildly aversive stimuli, namely, an open-field and 5, 90-dB noise bursts. The rats were exposed alone and in pairs. When pairs were used, some of the partners were pre-treated to exhibit calm or alarmed behaviour during noise-burst trials. This test was conducted to assess whether freezing behaviour by the target rat was reduced or enhanced by the presence and/or behaviour of a companion. Results indicated a marked sex difference, males freeze more than females.

No companion influence was found for male rats. In contrast, female rats increased freezing duration when accompanied by an alarmed partner as opposed to a naïve one. The results suggest that female rats habituate rapidly to the environment, more so than males, and thus enhance the likelihood of attending to the behaviour of the companion.

Introduction

1.1 Conservation

Conservation of endangered fauna is critical to the biological diversity of our planet. Worldwide approximately 3000 taxa, many of which are avian species, are nearing extinction because of man-made interventions to their ecosystems (Ebenhart 1995). These changes include the removal of natural vegetation, such as the burning of native bush and the logging of indigenous timber, to the disturbance of the natural balance by the introduction of predators and other species occupying the same ecological niche (Magin, Johnson, Groombridge, Jenkins & Smith 1994).

Careful breeding of threatened avian species by conservationists has helped to establish viable colonies that are ready to be reintroduced to their original habitats. However, earnest attempts at reintroduction have on average an 11% survival rate. This low rate is partially contributed to inadequately prepared release areas where the original cause of extinction has not been addressed (Kleiman 1989). In areas where these issues have been addressed such as predator free and/or sequestered environments the success rate has increased. For example, the habitats of the last 86 surviving Kakapo birds (*Strigops habroptilus*) on New Zealand coastal islands of Maud, Little Barrier (Hauturu) & Codfish (Whenau Hou) are predator free; currently the annual survival rate is now 99%. (D.O.C, 2003).

It is not always feasible or justifiable, or perhaps even necessary to eradicate all predators. First, the cost is sometimes prohibitive. In addition, in certain circumstances predators have in the past cohabited with the now endangered species, but through a change in the ecological niche the balance of survival may have tipped in favour of the

predator. In these cases, perhaps the balance may be tipped back in the opposite direction, without eliminating the predator species, perhaps by preparing the target species in ways that improve its ability to defend against the predator. To illustrate, many of these endangered species have been bred successfully in captivity but on release there are some vital behavioural deficits that compromise survival. Some species exhibit a lack of parenting skills and appropriate sexual orientation, and more importantly many have lost or never developed fear of predators – particularly introduced predators. For reintroduction to be more successful, it is important that the animals are competent in recognising and reacting appropriately to these predators. These skills need to be established before release.

Evidence suggests that some animals are innately equipped with highly developed predator recognition skills, while others are not. For example, Göth (2001) found in ground-dwelling 2 day-old megapode hatchlings some evidence for innate predator recognition. Megapodes are singly hatched and parentless birds that have neither siblings nor parents to present cues that may indicate the presence of predators. These two-day old hatchlings show appropriate anti-predator behaviour when presented with various predator stimuli (raptors, snakes, cats and dogs). Hatchlings also take note of alarm calls emitted by locally present birds and use this information to exhibit distinctive anti-predator behaviour. In contrast, a study conducted by Maloney and McLean (1995) using the New Zealand native Robin, indicated that predator recognition may not always be innate. These Robins inhabit some predator-free islands but are also found on mainland pockets that do contain predators. The predator naïve birds did not react to predators

when presented with predator like stimuli (stuffed stoat). Conversely, on the mainland, predator-experienced birds showed appropriate anti-predator behaviour when they were exposed to model predators. When naïve, island-bred robins were exposed to a taxidermically prepared conspecific that was emitting alarm calls, displaying mobbing posture, and paired with a stuffed stoat, the naïve birds quickly learned to emit fear behaviour to the stimulus of the stuffed stoat (Maloney & McLean 1995). This suggests that, although not all species have innate predator recognition they may be capable of learning it, quite readily, in adulthood.

Animals with innate predator recognition may be easier to reintroduce than animals that appear to learn recognition skills in later life. For conservation purposes it is important to concentrate on the second category, animals that do not appear to have innate, fully developed predator recognition.

The opportunities to learn predator recognition may depend on the experiences available in the natural environment. This may include aversive learning experiences through immediate but non-fatal contact with the predator. While such experiences could in principle be arranged in captivity, this is in some countries illegal and is not always in the best interests of conservation. Alternatively, learning can occur through interaction with parent and siblings. In natural habitats animal populations consist of animals with varying levels of survival skill, such as juveniles who are learning from adults and siblings, young parents who develop the finesse of raising and defending offspring and nest sites, (Kullberg & Lind 2002) but also fine-tuning predator recognition and

avoidance skills (Seyfarth, Cheney & Marler 1980; Durrant 2000). Further, these skills have been found to be transferable, not only between conspecifics but also between species that inhabit the same ecological niche (Danchin, Boulinier & Massot 1998). In communities of captive-bred animals, however, this knowledge is sometimes incomplete (Jones & Waddington 1992). For example, offspring raised by naïve parents are less likely to exhibit anti-predator skills at an early age than offspring raised by experienced parents (Sheppardson, 1994).

1.2 Fear Conditioning

Various methods have been attempted in order to teach captivity-bred animals about predators, one of these is Pavlovian conditioning. Pavlov suggested that much learned behaviour can be traced back to innate reflexes. Although the behavioural reaction to a particular predator may be learned, the fear reaction *per se* is an innate reflex. Through “pairing” of a neutral stimulus (called a “conditional stimulus”, CS) to a fear-producing one (“Unconditional Stimulus”, US), a fear response to the neutral stimulus can be generated. The linking of a conditioned stimulus (CS) such as a stuffed animal (e.g. fox, stoat etc.), to an aversive unconditioned stimulus (US) or event (being ‘chased’) results in the CS becoming linked with an innate response, in this case fear. That in turn becomes the conditioned response (CR) when seeing the predator. For example, when training wallabies Griffin, Evans & Blumstein (2001) paired a taxidermically-prepared model fox (CS) with an aversive stimulus (a disguised human with catch net (US)). The wallabies exposed to this training regime exhibited fear (CR) towards a predator (CS). Further, the wallabies then generalised this newly-acquired skill

to respond fearfully to other, similar stimuli (a taxidermically prepared cat), but not to non-similar stimuli (goat).

In Pavlovian conditioning the aversiveness of the US partially determines the ability to learn the association between the CS and the CR, and up to a point the more aversive the US the more likely learning is going to eventuate (Annua & Kamin, 1961) and be retained for a considerable time. Thus if the US is not aversive enough, then the CR is unlikely to reach the maximum response rate. That is, if the US is mediocre the subject may only respond correctly for part of the time. If the US is very weak, not only will there be limited learning, but more importantly, habituation to the stimulus may eventuate. However, if the CS is presented without the US then a phenomenon called extinction may take place. Extinction refers to the reduction of responding to the stimulus. These factors extinction, habituation, and lack of stimulus strength can be very detrimental to the overall effect of pairing a conditioned stimulus, such as a stuffed animal, to a loud noise or other aversive stimuli to induce fear to a predator. McLean Lundie-Jenkins & Jarman (1996) found very little evidence for long-term retention of predator recognition when using a loud noise or a water squirt as the aversive stimulus. However, as the US intensity increased, for example, through the use of a dog that chased the naïve animals around in a cage the long-term retention increased (McLean, Schmitt, Jarman, Duncan & Wynne, 2000). Long-term retention was also found in bustards that were exposed to a muzzled live fox in their cage and in which some animals sustained physical damage such as a broken wing or leg. These bustards however, were more cautious when released into the wild and this resulted in a significant post release survival

rate (Heezink, Seddon & Maloney, 1999). Similar results were found when brook trout were exposed to damage-released alarm signals. These are signals that an injured fish releases, and this signal was paired with a predator's odour. In these fish the retention duration was about 10 days. This was deemed adequate for in the wild fish encounter predators on a daily basis (Mizra & Chivers, 2000).

Seligman, Ives, Ames & Mineka (1970) suggested that animals may have a tendency to learn certain problems faster than others. Seligman et. al. termed this "biological preparedness". In other words the animal has a propensity to learn certain things faster than others. Fear of predators would most likely be one of those. As Seligman et al. stated such preparedness in learning is selective, highly resistant to extinction and if the animal is highly prepared to learn about predators this can be acquired in one trial.

The above-mentioned methods involve exposing the animal to harsh regimes that may border on unethical animal treatment. Since it is questionable and potentially harmful to subject animals, and especially endangered species, other methods need to be investigated. As pointed out, predator-prey interaction can be costly and therefore it would be advantageous if part of the overall predator recognition repertoire may be acquired through observational or vicarious learning. Observational learning is the transfer of information between conspecifics whereby the observer does not interact with the stimulus but watches a demonstrator and learns from that experience. However, the observer not only has to attend to the stimulus (local enhancement) but also needs to interpret the meaning of the observed behaviour. Furthermore, it then needs to apply this newly acquired knowledge appropriately and more importantly, successfully!

1.3 Observational learning of fear

Evidence for observational learning has been found in naïve monkeys who rapidly acquired and maintained a strong fear of snakes when they observed a conspecific demonstrating strong fear responses towards a snake. This is observational learning. Many of the relations observed with Pavlovian fear conditioning are also found with observational learning. For example, the observationally conditioned fear of snakes was found to be robust enough for transfer to a previously-neutral stimulus, a phenomenon known as second-order conditioning. Second-order conditioning entails the transfer of the conditioned response, fear, from one stimulus, i.e. the snake (CS), to another previously-neutral stimulus, in this case a black-striped box (CS). Thus, when the monkey was presented with the box it displayed fear towards this. This box was in no respect paired with the snake or the demonstrator monkey (Cook & Mineka, 1987). Not only can fear be conditioned from natural to non-natural stimuli, more importantly, it can be generalized to other similar stimuli as found by Griffin, Evans & Bloomstein (2003) who demonstrated that observationally learned predator recognition could sometimes be generalized to other predators.

Not only can animals learn from conspecifics, but also from non-conspecifics as demonstrated in fish by Mathis, Chivers & Smith (1996). They found that naïve stickleback fish could learn fear from minnows and then pass this information, albeit attenuated, on to other naïve sticklebacks. Since fish live in shoals, it was conceivable that allelomimetic behaviour and family relationships may have been an influencing factor. However, in higher-order social animals such as monkeys it was found that the

relationship between the animals was unimportant for fear to be vicariously learned and transmitted to other unrelated monkeys (Cook, Mineka, Wolkenstein & Laitsch, 1985). The aforementioned concepts of second-order conditioning and generalisation have in common that experienced animals demonstrate to naïve animals something about the environment. The ‘pseudo-naive’ animal can then manipulate this information to display fear to other objects and predators. In the interests of conservation it is important to concentrate on the concept that the experienced animal ‘signals’ fear to the naïve animal and that the naïve animal interprets this information and reacts accordingly.

Some concepts need to be taken into consideration for successful signalling. Firstly, if the naïve animal is exposed to the pending harmful stimulus in a harmless manner such as seeing a conspecific play with the stimulus than it becomes difficult to establish fear to this at a later stage (Mineka & Cook 1986). In Pavlovian conditioning, this is called the “CS-pre-exposure effect”, or sometimes, “latent inhibition”. Secondly, order of presentation is significant but as well as magnitude, relevance and the completeness of the information about the stimulus is influential. As is found with the intensity of the US in Pavlovian conditioning, the magnitude and intensity of fear displayed by the demonstrator is important for the naïve subject to focus attention to the stimulus. Not only does the demonstrator show fear of the stimulus but also possibly appropriate flight and fight behaviours. McLean, Holzer & Studholme (1999) showed in the line of sight of juvenile birds, parent birds being attacked by a stuffed predator whereby the adult birds displayed appropriate fear and flight behaviours. The juvenile birds were tested at a later date and emulated an increase in fear and flight behaviour. Not only is intensity and clarity of the demonstrator’s behaviour significant but also the

relevance of the stimulus enhances learning. Cook & Mineka (1989) showed naïve monkeys a video of a conspecific displaying fear towards a snake. The naïve monkeys emulated this behaviour themselves when exposed to a snake. However, this was not repeated when the videotape was edited and a flower replaced the snake. Suggesting a biological ‘preparedness’ to certain objects while not to others (Seligman, Ives, Ames & Mineka, 1970). Van de Veen (2002) found with birds that incompleteness of information about the potential threat increased vigilance, which in turn affected the foraging duration. The birds that had complete information assessed the risk and foraged sooner than the birds who only heard the alarm calls of fully informed conspecifics but did not observe the predators themselves.

More evidence for observational learning of behaviours has been found in chickens which have been observed to rapidly learn feather pecking (Zeltner Klein & Huber-Eicher, 2000), vocalization in ravens (Enggist-Dueblin & Pfister, 2002) and anti-predator behaviour in fish (Kelley, Evans, Ramnarine & Magurran, 2003). However, not all animals learn from each others success but sometimes also from their failures (Templeton, 1998) or learn nothing at all (Boal, Wittenberg & Hanton, 2000).

Thus, there is good reason for optimism about observational learning as a means of training individuals of an endangered species in appropriate predator responses. Whatever the origin of specific fear responses (i.e., whether innate or learned) it is quite clear that they are substantially modified by social factors.

Simple fear training was shown by Cook & Mineka (1990) who presented a snake and a fear displaying monkey together to a naïve monkey. This newly trained monkey displayed fear when confronted with a snake. This scenario can be broken down into true imitation, local enhancement and social facilitation. True imitation entails the naïve animal learning behaviours that are not normally found in its repertoire or behaviours that could have been learned through trial and error. Therefore true imitation is not necessary, for fear responses are usually part of the behavioural repertoire.

Local enhancement draws the naïve animals' attention to the stimulus and allows it to link, for instance snake to fearful monkey, and so possibly learn that the snake is something to be avoided. Since the snake was a neutral stimulus previous to this it is conceivable that most of the information is contained in the behaviour of the monkey. By excluding the snake we are left with the behaviour of the monkey. Now how can this behaviour influence another animal? More specifically why would one animal change its behaviour when paired with another?

1.4 Social Facilitation

This is one of the oldest questions in psychology, and was first termed Social Facilitation by Triplett in 1898. Here, a subject changes behaviour that is already in its repertoire through the mere presence of a conspecific. Behaviour can be either attenuated or augmented depending upon the behaviour studied. To illustrate, Triplett posed the question: why do cyclists cycle faster together than when alone?

1.5 Social Influences on Fear Expression

Many studies have been conducted exploring facets of social facilitation using human participants and animal studies. The animal studies have shown varied results and these were mainly influenced by the experimental conditions, such as novelty, potential fear factor of the environment and the behaviour of the companion animal, such as fear expression.

According to Izard & Youngstrom (1996) the main function of fear expression is to signal conspecifics of imminent danger. It is therefore conceivable that fear expression is more likely to occur in social species than non-social species. Because social species are more likely to have a finely tuned interaction repertoire in which subtle hints are adequate to convey meaning and intent.

Historically rats were deemed to be an antisocial species until Latané (1969) showed that male rat's prefer each others company (Werner & Latané 1974) over no company, caged company, anaesthetised company or toys (Latané & Glass 1968). Although rats are social creatures when allowed to freely interact, they are classified to be non-allocomimetic. In other words, they tend not to display synchronised behaviour as found in shoals of fish or flocks of birds.

Belonging to a group of social animals has potential benefits such as the sharing of parenting, acquiring food and water resources, and predator detection and protection. Living socially also has possible benefits of reducing the need to continuously monitor the behaviour of other group members; living together creates a certain level of familiarity. Accordingly, there appears to be some evidence that familiarity between animals may reduce the amount of fear displayed (File & Pope 1974) when confronted

with novel and potentially threatening stimuli. Conceivably, familiar animals are more predictable than unfamiliar animals so the cognitive resources used to evaluate the novel stimulus do not need to be allocated between potential threats, unfamiliar conspecifics and novel stimuli.

Group animals seldom spend time alone except possibly while giving birth when the intrusion of conspecifics may harm mother and offspring. Particular care must be taken when housing social animals in isolation as this is a stressful event and may influence the natural expression of social facilitation (Lore & Flannelly 1977). Especially if social facilitation is a learned behaviour, as suggested by James (1960). Thus, it is important to take housing into consideration when searching for social facilitation effects.

Furthermore, novelties of testing environment and social structure amongst rats are other aspects to take into consideration. Dominant animals may increase fear in non-dominant animals and so influence the results. The level of averseness of the testing environment needs to be adjusted to elicit the studied behaviour but not suppress or override it. For example rats habituated to novel environments are more gregarious than non-habituated rats. (Eckman, Meltzer & Latané 1969, Moore, Byers & Baron 1981) They also found when one of a pair of rats was pre-exposed there was more interaction than when neither had been pre-exposed.

There is evidence that rats reduce their natural freezing behaviour (a fear response) when in the presence of a companion. In general this has been established by Latane (1969), Eckman et al., (1969) Epley (1974) Thor, Wainwright & Holloway (1981), Taylor (1981) and Moore et al., (1981) however, there were some experimental

differences. Some did not induce fear; others housed animals individually or tested rats in groups of more than two animals. Latane (1969) indicated that rats are more gregarious and prefer to spend time together when paired in circular open-field. The rats were housed individually prior to experimentation. This may partially explain the desire to be close to a conspecific and hence reduce the distance between the animals. Furthermore, the rats were repeatedly exposed to the same environment and exhibited overtime a decrease in distance between them. However, at the initial exposure to the procedure there appears to be little difference in the mean distance between the caged rat, empty cage, and the paired rats. That is, conceivably because the attraction to the cage-mate under novel circumstances is not as immediate as suggested. It is plausible that habituation to the environment reduced fear and hence allowed the conspecific to be the next focal point and so become more attractive. Finally, only male rats were used conceivably different effects may have been found using both sexes.

Epley (1974) stated in his review that one of two conditions were necessary to reduce fear. Firstly there must be a calm animal, secondly, that the companion could interfere with the subject animal, with other words could physically interact. This interaction may then distract the target animal.

Thor, Wainwright & Holloway (1981) used both sexes and found that males spent more time investigating active sterile males and females than haloperidol induced inactive rats. Females on the other hand showed less investigatory behaviour, and were marginally more attracted to active rats than to inactive ones. The animals were not exposed to a novel environment as testing took place in the subjects' home cage. This may explain why male rats spend more time investigating the active conspecific, as males

are more likely to be territorial and hence need to know more information about the intruding conspecific.

In this thesis, rats were exposed to a novel environment that was a dimly lit, black painted openfield, and exposed to 5, 90 dB noise bursts to induce fear. The environment had to be aversive enough to induce some fear but not to inhibit all social interaction since fear may compete with social interaction (Will, Wesley, Moore & Sisemoore, 1983). Rats were exposed to this singularly and paired; in the paired condition the companion was either familiar or unfamiliar. Furthermore, in the familiar condition the companion was either naïve, or pre-trained to be calm or alarmed. Additionally, a sex difference may also be involved because, biologically speaking, females have different drives and roles than males. Although fear reactivity is a universal phenomenon, the expressed levels of fear between animals may also vary. The influence of a companion can be framed in various social facilitation theories.

1.6 Social facilitation theories.

Since 1898, three major theoretical areas have been developed to clarify the effects of social facilitation. As psychology advanced so did the explanations beginning with an elegant but simple drive theory, followed by cognitive and social conformity theories.

1.7 Social conformity theory

Social conformity theory assumes that humans monitor their behavioural output and try to conform to individual and societal expectation. The core of this theory is that humans attach a social value to their behaviour. This judgement of social value influences

people by creating an internal feeling that urges them to work faster because they want to attain the standard we have for ourselves and assume that other people expect. For example, the typist types faster when the boss walks into the office. The typist assumes that speed and efficiency is a criterion to stay employed. The boss however does not notice the industrious typist but is preoccupied with other problems. The typist has nevertheless increased production without the boss being aware of this. The boss may have created evaluation apprehension in the typist and this may provide a social explanation why humans increase drive and display social facilitation effects. These values are learned and not innate, and are acquired during socialisation processes. Although animals have 'social rules' it is unlikely that they are influenced by social values as found in human populations. In animal populations social order may influence decision making but these are not based on social values, for example dominant animals may react differently to subordinates than to other dominant animals and vice versa. Thus, social conformity explains social facilitation through use of social values found conceivably only in human societies.

1.8 Cognitive Process Theory.

The second major theoretical area is also influenced by values but these are less clear. Cognitive process theories are based on dissecting behaviour into temporal stages, whereby the past is compared to the present and assessed, and this assessment leads to a decision that may or may not lead to an observable change in behaviour. Thus, the process consists of different stages including attention to stimulus, processing of information by comparing it to previous information or experiences then drawing a

conclusion and acting upon this. In the attentional process the subject may notice the most salient behaviours of the conspecific, such as the display of emotions, intentions, mobility, etc. So what do these behaviours indicate and what actions are required to safely negotiate these interactions at the least possible cost with the most profitable outcome?

The cognitive theories can be subdivided into physical, cognitive, distraction-conflict, attentional process model, arousal and information processing models. (Guerin, 1993). They all have in common an explanation of social facilitation in cognitive terms, but these cognitive processes cannot be directly measured. However, the cognitive theories overlap with the earlier developed drive theory.

9 Drive theory.

Zajonc (1965), stated that the mere presence of a conspecific was sufficient to alter the behaviour of the studied subject. The mere presence of others increased general drive or arousal and this affected the performance of tasks. Thus, the presence of a conspecific increased general internal-arousal that in turn was suggested to increase 'drive'. The mere presence 'drove' the subject to increase correct responses on easily executable tasks but to increase errors in more difficult tasks. Task difficulty was explained as either simple well-learned and highly practised or as complex and involving higher cognitive functioning. Thus raising the question what are simple and well-learned responses in animal behaviour? Many responses are well-learned such as eating, sleeping, freezing and fleeing. However, how they are influenced may dependent upon the behaviour of the approaching second individual. For example if a conspecific is approaching in a

threatening manner then a correct or appropriate freezing response may turn into a correct flight or fight response. Conversely if the conspecific is exhibiting non-threatening behaviour than this plausibly leads to investigatory behaviour on behalf of the subject. All responses are well-learned and correct but display is partially dependent upon the conspecific.

The amount of arousal elicited by the conspecific may well influence the dominance of the response. That is, low arousal may allow for more types of responses while high arousal may well lead to one specific strong response, such as a fear response. The above points all have in common that the introduced conspecific is exhibiting behaviour. However, if the introduced conspecific is not involved in observable behaviour than social facilitation becomes non-existent. To illustrate, in animal studies it has been found that anaesthetised rats elicit no social facilitation (Latané & Glass 1968); even though the rat is breathing, the subject ignores the animal. Similarly, this was found in humans when the subject was paired with a blindfolded companion and the subject ignored the companion.

Zajonc's theory could not adequately explain why blindfolded conspecifics could not induce social facilitation, because his theory only required that a conspecific be present. The subject appears to draw a conclusion about what behaviour the conspecific is exhibiting. Plausibly the subject used a cognitive process to evaluate the situation and responded accordingly. Zajonc (1969, 1980) later added to his theory that the behaviour exhibited by the introduced conspecific was important in social facilitation. In fact it was the need to be in a state of response preparedness by the subject that formed the base of arousal increase. This is where the cognitive and drive theories overlap, the subject is

using a cognitive process whereby the past is compared to the present and this influences arousal. However, none of the above-mentioned theories are capable of totally explaining social facilitation or able to consistently predict when it is going to occur, especially in research using animals.

1.10 'Mere' Presence, Learned Drive and Distraction/Conflict.

Possibly the most likely areas in which a potential theory may be found to predict social facilitation in animals are in the drive and cognitive theories. According to Sanders (1981) the drive theory can be split into three partial theories-(1) mere presence (Zajonc, 1965) (2) learned Drive (Cottrell, 1972) and (3) the distraction/conflict (Sanders, 1981). As discussed above, the “mere presence” theory entails that the subject’s dominant responses are augmented and the non-dominant responses impaired in the presence of a conspecific. More importantly it is the unpredictability of the conspecifics’ behaviour that should always increase drive, and so influence the subjects’ behaviour.

The learned-drive theory suggests that a conditioned response is elicited by the presence of a conspecific. In the past the subject has learned that the presence of a conspecific predicts a positive or negative outcome (Cottrell, Wack, Sekerak & Rittle 1969). Thus, it is a learned response and is influenced by the expected outcome of the social interaction. For example, a person has learned at an early age that a good performance creates praise by parents and this stimulates a desire to perform well. However, the same performance may create envy in siblings and peers, and therefore may create apprehension and so possibly reduce performance. In 1981, Geen modified the

theory to exclude the positive outcome and only use the negative outcome to explain the increase in drive. Human and animal studies (e.g. James 1960, James & Gilbert, 1955) support these findings of learned responses. James and Gilbert (1955), for example, found that puppies raised in isolation would not increase their rate of food consumption when paired with a conspecific. However, once socialised, the puppies showed strong facilitation effects lending support to social facilitation as a learned concept.

The 'distraction/conflict theory states that distraction caused by conspecifics conflicts with concentration of the task at hand. This conflict is compensated by an increase in drive that allows for an improvement of simple tasks but not of complex tasks. (Sanders 1981). This theory has a cognitive component, it assumes that the conflict of attention, which is an internal process and difficult to empirically measure, increases 'drive' that is measurable. As can be envisaged it is difficult to establish in animals if the increase in drive is actually caused by an internal conflict.

In summary: the drive theory is based on the presence of, and behaviour exhibited by, conspecifics. Learned-drive postulates that social facilitation is learned and distraction-conflict states that the presence of interference/distraction creates conflict and therefore increases drive.

1.11 Predictions.

The three theories described above lend themselves to prediction of possible outcomes when they are applied to the following experiment. In the current experiment rats are tested alone or with a companion, in a procedure where they are exposed to 5, 90-dB noise bursts. The subject rat's behaviour is studied as a function of whether it is alone

or accompanied, and if accompanied, whether its companion is familiar (a cage-mate) or unfamiliar. These were compared because there is some reason to expect that the effects of the companion's behaviour might be affected by familiarity (File & Pope 1974). Further, the effects of a familiar companion are compared across three conditions that vary the nature of the companion's behaviour as follows: 1) shows calm behaviour, 2) is naive or 3) shows obvious fear behaviour. (These various responses are achieved by pre-training described below.)

In pre-training both calm and alarmed rats were exposed to the experimental procedure in which a small house light preceded the noise bursts in the calm condition but the light predicted shock in the alarmed condition. The calm companions were habituated to the experimental procedure and 20 light-noise pairings over 15 minutes. 10 light-shock pairings were presented over a 15-minute session to the 'alarmed' rat. These pairings were to ensure that during actual testing the rat anticipated shock on light presentation, but instead the light was paired with noise. This is a common procedure to elicit startle and freezing responses in rats (Bolles & Collier 1976, Davies 1992).

The 'expected' results depend upon which theory is used to predict the results. Zajonc's mere presence theory would predict that rats with companions will show more freezing behaviour than when alone. Freezing is a well-learned task thus it should increase in duration when paired. This is not so. Social animals, like rats, are said to experience increased arousal when separated (possibly fear), thus the companion actually reduces freezing by reducing the 'separation' arousal (i.e. fear reduction) (Guerin & Innes, 1982) Therefore a reduction in freezing is expected when paired. However this

does not take account of the behaviour displayed by the companion. Thus if the subject rat displays a freezing response to the noise burst when alone, then one would expect to see an decrease in this behaviour when a companion is present. However, if the rat does not freeze when alone, the presence of a companion will not induce it to do so because the behaviour exhibited by the subject rat such as eating may well be increased for it is also a well-learned task.

While no specific prediction regarding familiarity, or calmness or fearfulness of a companion arises directly from Zajonc's theory, the *predictability* of the companion's behaviour is important in the theory, and this may be affected by familiarity. If the companion is unfamiliar, then the predictability of its behaviour is low; it could be friend or foe. This unpredictability creates an increase in drive, enhancing any freezing behaviour. A familiar companion, on the other hand, should reduce freezing. So when two familiar naïve rats are together when the noise bursts are presented, it is more likely that they reduce freezing behaviour, and increasing other behaviours, in one another.

This may be even more obvious if the companion is both familiar and calm, (perhaps indicating high predictability). Thus, in the alarmed versus calm comparison, an extended duration of freezing is predicted when the target rat is paired with a familiar and alarmed animal, because the behaviour displayed by the alarmed rat is very clear. That is, the alarmed companion will startle and freeze, so its behaviour may be very obvious, and hence the subject should increase freezing behaviour. In contrast, the response to the calm companion is to reduce freezing because firstly it is a familiar animal thus low arousal. Secondly it is showing no fear behaviour and is likely to interact with the target rat.

The learned drive theory postulates that the response to the companion is learned, that is, a specific drive as opposed to Zajonc's general drive. The predicted outcomes for the experiment in this thesis utilising the learned drive are similar to the 'mere presence' theory. In the alone condition, the rat may show freezing behaviour because there is no companion to indicate anything else. All experimental rats used for this experiment have always been socially housed so the subject rat has never experienced being alone. In relation to this in the familiar condition the naïve rat is paired with a familiar but naïve companion and hence freezing is predicted to be reduced. Since both animals are tested in neutral territory the rats would quickly re-establish ranking without the need for major battles. The naïve subject would previously have learned that once ranking is established a companion is a non-threatening object. Furthermore, the subject has only encountered unfamiliar rats once and that was 21 days post-parturition when the experimental cages were formed. Experimentation for this thesis commenced 4 months later and it is unclear what other experiences the rats previously had when randomly combined with three others.

Pairing the naïve animal with an unfamiliar and never previously encountered rat, the learned drive theory would possibly predict, an increase in freezing compared to the familiar condition. In the calm condition it was predicted that the subject would show no change to being with a familiar because the subject has never been exposed to a familiar rat displaying calm behaviour in a novel and potentially threatening situation. The same is applicable to the alarmed condition, but as freezing behaviour is a fear response it is likely that the subject will show some increase in freezing.

In predicting the possible results using the distraction/conflict model, the alone condition should show fear, because there is no distraction from conspecifics. A decrease in freezing behaviour is expected in the familiar condition compared to the alone condition because of the potential for distraction from the companion rat. Hence, in the unfamiliar condition the subject is confronted with a conflict conceivably caused by the novelty of the companion. Thus more likely to increase freezing as compared to the familiar companion. A likely reduction in freezing is expected in the calm condition for the calm rat will be more familiar with the procedure and hence display no fear behaviour. Rats are drawn to novelty and conspecifics; thus the calm rat is most likely to investigate the naïve subject. This investigatory behaviour might be distracting for the naïve subject and therefore interfere with the display of fear behaviour. However, a strong response is also expected in the alarmed condition for there is conceivably little interference from the companion who is showing a great amount of freezing. Additionally, the information emitted by the companion may result in conflict for the environment is partially endangering but not so much as to emit an extreme amount of fear. Hence it may be prudent of the subject to err on the side of caution and increase freezing till the risk is assessed. The three theories predict similar results with as difference the response strength.

Accordingly, if rats are to be used as a model for signalling alarm to conspecifics then, we need to know if we can reduce freezing by pairing with a calm rat but more importantly so if we can increase freezing by being paired with an alarmed conspecific. Epley (1974) stated that calm rats could reduce the magnitude and frequency of freezing.

The main interest for conservation is do naïve rats increase freezing behaviour when paired with alarmed rats.

Normal fear behaviour may be viewed as behaviour on a continuum. That is it ranges from no fear (for example engaged in other behaviours), to fear, (for example showing vigilance or action; fleeing, fighting or freezing depending upon cue). If fleeing and fighting are inappropriate, (as when there is nowhere to run to or no adversary to fight) then the next possible choice is to freeze until either the internal or the external signals indicate that other behaviour is more appropriate. Freezing is also the behaviour of choice when confronted with alternatives such as escape. (Fanselow & Lester 1988). Therefore, the only variable able to change is the duration of freezing.

Taylor (1981) conducted an experiment in which male rats were exposed to a stressful noise to induce some fear, while immobility duration and faecal boluses were counted as indication of fear. Isolation and familiarity were manipulated in the first experiment. The results showed that companions could reduce freezing and defecation. However, housing conditions and familiarity made no major impact on reactivity. It was noted though that individually housed rats tested alone, showed more fear than socially housed rats that were tested alone.

Taylor's second experiment investigated the use of a non-social stimulus to reduce freezing in the form of a hand vibrator to vibrate the floor of the apparatus. However, this manipulation did not affect fear reduction. Taylor's final experiment involved exposing rats to a T-maze with partitioned arms in which the target rat had to choose one arm that contained a conspecific. The target rat could not see the conspecific

until it had made a choice. The sounding of a noise during the choice phase increased the preference for the conspecific.

1.12 The Current Experiment

The current experiment is based on the methodology and findings of Taylor with a few modifications to examine some further hypothesis. Rats were tested in an openfield and exposed to a stressful noise singularly, paired with a familiar companion and paired with an unfamiliar companion. All animals were socially housed. Taylor's experiment used four rats in the group condition this may have increased the opportunity for fear reduction, as more opportunity exists to interact between the rats. That is one of the conditions for fear reduction as stated by Epley (1974). So if social facilitation is a plausible explanation, then it should be possible to replicate findings of fear reduction using only 1 companion that is 2 rats in the companion condition and 1 rat in the alone. Unfortunately, the alone condition is problematic for if socially housed animals are separated before and during experimentation than this could amplify fear by the separation process itself and hence there is more fear than 'ideal' aloneness. As Taylor described, individually housed animals tested alone showed more fear than socially housed rats tested alone.

In an attempt to clarify Taylor's results the first question of this thesis is: can companionship reduce freezing duration when two rats are exposed to mild aversive stimuli? That is, is there a difference between alone and paired? The second question asked: is the familiarity of the companion important, that is, is there a difference in freezing reduction when paired with a naïve familiar companion or an unfamiliar

companion? Some evidence found by File & Pope (1974) indicated that unfamiliar animals are more likely to exhibit active contact with the target rat than familiar animals. Contrary Latané (1969) has found little evidence for an increase in social interaction.

To investigate further if the behaviour of the companion was an important factor 10 rats were pre-trained to either show fearful or calm behaviour. For that reason the third question asked: is the type of behaviour displayed by the companion a factor in fear alteration? That is, will a familiar calm rat reduce freezing and can a familiar but alarmed rat increase freezing duration. Finally, since little data is available on fear behaviour of female rats, the three questions were investigated using both male and female rats.

Method for Experiment 1

Experiment 1 examined whether the introduction of a companion rat to the experimental setting will modify the duration of freezing behaviour in a target rat, when both rats are exposed to five 90 dB noise bursts? If the companion rat is an influence, is then the familiarity (i.e. shared home-cage or not) between the rats important? In other words, will a familiar animal reduce freezing behaviour more than an unfamiliar one? Finally, is the behaviour displayed by the companion important? That is, will a familiar calm animal likely to reduce freezing as compared to an alarmed one. These questions were examined using both male and female Lister hooded rats.

Each target rats was exposed to five noise bursts in each of the five different conditions as illustrated in Table 1 below.

Table 1. illustrates the five social conditions.

Control	1. Alone	
Familiarity	2. With a familiar but naïve companion	3. With a unfamiliar but naïve companion
Displayed behaviour	4. With a familiar but calm companion	5. With a familiar but alarmed companion

All the familiar rats resided in the same cage, and so were presumably habituated to each other, and held little or no novelty when reintroduced to each other in the

experimental setting. The unfamiliar rat came from a different cage and was presumed to be more novel than the familiar rats.

The calm and alarmed rats were pre-treated to induce habituation or fear. Pre-treatment consisted of either being exposed to the experimental environment and the noise bursts (habituation thus calm), or of being exposed to the experimental environment and 10 light/foot-shock pairings (fear conditioning thus alarmed). Habituation ensured that the companion rat showed little or no freezing behaviour to the 5 light-noise bursts. The light/foot-shock pairing ensured that the alarmed companion rat readily showed freezing behaviour when exposed to the light followed by the noise; i.e. fear potentiated startle followed by freezing behaviour.

Subjects

The subjects were 48 male and 48 female Lister hooded rats aged approximately 150 days. They were housed in groups of four same-sexed animals per cage with access to ad lib food and water. Relative humidity was approximately 50%, ambient temperature close to 20°C, and a 12 hour light-dark cycle operated. The dark cycle commenced at 4:30 p.m. to coincide with testing.

Apparatus

Rats were tested in an enclosed 'openfield' box with internal measurements of 60cm. x 60cm. The floor insert was a brass bar floor that could, when required, conduct electricity. A manually-controlled house light (2 lux), suspended 70 cm above the

openfield, could be linked to a non-scrambled shock generator (Lafayette Instruments Co. - Model 82400) which delivered a 0.2 mA footshock conducted through the brass bar floor.

To reduce visibility for the rat, a black curtain was erected around the openfield. An infrared camera, suspended 70 cm above the open-field, was connected to a video recorder and CRT monitor. This allowed the observer to monitor and record the freezing duration. Discharging a manually-operated upholstery stapler, on an empty table, produced a 90 dB noise burst at approximately the rats' ear level in the centre of the openfield.

Procedure

Two rats were pre-treated from each cage. One was habituated, and the other shocked.

Habituation pre-training

To habituate the rat to the surroundings and the procedure it was placed in the openfield for 15 minutes prior to the test session. During these 15 minutes there were 20 light-noise pairings. The delay between light and noise was 1 second, and intertrial intervals varied between 60 and 180 seconds. This procedure was designed to reduce fear in the companion animal and establish a calm demeanour during the experimental phase.

Shock pre-training

To incite both fear and fear potentiated startle in the rat when exposed to the light-noise pairing, the animal was placed in the open-field for 15 minutes and presented with 10 light–shock pairings with a 1-second delay between light and shock. Intertrial intervals varied between 60 and 180 seconds. These presentations were designed to ensure that the rat learned that onset of light in the experimental phase was most likely to be followed by shock, and hence display fear behaviour (Davies 1992).

Testing procedure

Two naïve animals from each cage were tested in the five conditions in a pseudo random order.

The five conditions were:

- 1) Alone.
- 2) In the presence of a familiar and naïve companion.
- 3) In the presence of an unfamiliar and naïve companion (i.e. a rat from another home-cage).
- 4) In the presence of a familiar and calm companion.
- 5) In the presence of a familiar and alarmed companion.

In the Alone condition the target rat was placed in the openfield and was able to explore the environment for one minute, after which the first light-noise pairing was presented. The duration of the resulting freezing behaviour was recorded from the

moment the rat startled and froze until the rat showed movement. A stopwatch was used to measure the freezing duration and the rats' location was marked on a spreadsheet. Frequently, the first movement was a small sniffing motion or a head movement. Subsequently, the rat was allowed to explore for one minute before the second light-noise pairing was presented. This procedure was repeated for a total of five light-noise pairings. In previous research conducted by Taylor (1981), if the rat showed a freezing duration longer than four minutes, then the next noise burst was presented without the one-minute delay. In this experiment, this time limit was extended to six minutes. Thus, if the rat displayed 6 minutes of continuous freezing behaviour the next noise burst was presented without the 1 minute delay.

In the paired conditions, the target and companion rat were placed in the apparatus, allowed to explore for one minute, and then exposed to the first light-noise burst. This was repeated for a total of five light-noise burst presentations. Freezing duration of the target rat was measured as described above and the location of both rats in the openfield at the time of the noise burst was also noted.

In the pre-treated condition the calm or fearful companion was pre-treated immediately prior to the testing session. The target animal was then introduced and the one-minute familiarisation was followed by the first light-noise pairing and repeated for a total of five times. Again the position of both rats were noted when the noise bursts happened.

The openfield box and the brass floor were both cleaned between sessions but not between a pre-treatment and a test.

The data were analyzed using a repeated measures design. A possible limitation of a repeated measures design is that rats may display habituation to the noise burst over time. In an attempt to reduce habituation, there were at least 8 days between exposures to the different experimental conditions

In summary, the target rat was pseudo-randomly exposed to five social conditions (alone, paired with a familiar naïve companion, an unfamiliar naïve companion and with a familiar companion displaying calm or alarmed behaviour). In each of these conditions the animals were presented with five light-noise pairings. The freezing response and openfield locations of the rats were recorded.

Results of Experiment 1

Experiment 1 examined if the inclusion of a companion rat to the experimental setting modified freezing duration in a naïve target rat when both were exposed to five light–noise pairings. It was also asked whether any observed effect of having a companion was modified by 1) the type of behaviour exhibited by the companion rat (i.e., calm or alarmed), or 2) the level of familiarity between target and companion rats. These questions were examined using both male and female rats.

The raw data were analysed using a repeated measures ANOVA using the statistical program *Statistica* (Statsoft. Inc.) The repeated measures were 5 social conditions (alone, familiar, unfamiliar, calm, and alarmed) and 5 noise bursts as within-group measures, and 2 sex as between-group measures. The results of the ANOVA are summarised in Table 2 below.

Table 2. Analyses of variance.

<u>Analyses of variance for exposure to noise bursts.</u>		
Source	<u>df</u>	<u>F</u>
	Between subjects	
Sex	1	15.25 **
Within-group error	46	
	Within subjects	
Social	4	0.9271
Social x Sex	4	0.3933
error	184	
Noise	4	2.9479 *
Noise x Sex	4	2.1660
error	184	
Social x Noise	16	0.5741
Social x Noise x Sex	16	1.1302
error	736	
<u>Note.</u> * $p < .05$. ** $p < .01$		

Overall, no statistically significant reduction in freezing behaviour resulted from the inclusion of a companion rat to the experimental setting. Neither was the type of behaviour displayed by the companion, nor the familiarity between target and companion rats important in altering freezing duration. Indeed, Table 1 shows only one important statistically significant effect, namely a sex difference. Male rats spent more time freezing than females when exposed to the 5 noise bursts in a novel environment ($F(1,46) = 15.25, p=.0003$). This difference is depicted in Figure 1, which shows mean freezing duration for male and female rats, collapsed across social conditions and noise bursts.

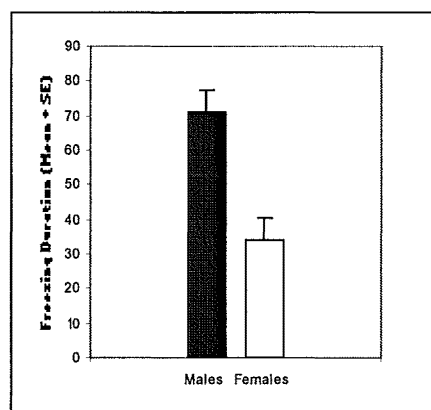


Figure 1. Mean freezing duration (sec) for male ($n=24$) and female ($n=24$) rats. The error bars show the standard errors of the means.

The failure to find statistically significant effects of social condition was inconsistent with previous research. Such research has indicated that a companion should have considerable effect on the behaviour of the naïve target rat (Taylor, 1981), and a calm companion animal ought to considerably reduce freezing in the naïve animal (Epley, 1974). The remainder of the data analysis for Experiment 1 explores two possible reasons for the failure to find such effects, namely, 1) the possibility that effects were obscured by habituation to noise bursts, and 2) the possibility that the pre-training given

to companion rats (calm vs. alarmed) was ineffective in producing behavioural differences that might in turn affect the behaviour of the target rats.

Manipulation check

A manipulation check was conducted in order to evaluate the effectiveness of the pre-treatment of the calm and alarmed rats. Each social condition that used a calm or alarmed companion was reviewed on video-tape. The duration of freezing behaviour of the pre-treated rats, and the distance between the target and companion animals were measured. The distance between animals was measured because it was suggested that rats may huddle to reduce fear (File & Pope 1974). In addition, other obvious behaviours such as startle, grooming and escape behaviours were noted from the videotape.

A statistically significant differences in freezing behaviour between the pre-treated alarmed and calm rats for both male and female target rats was found ($t=3.736$, $p>.0005$ and $t=3.79$, $P<.00004$, males and females respectively). Figure 2 presents the mean freezing durations in these two conditions for males and females separately, and shows that calm rats showed significantly less freezing behaviour than the alarmed ones in each case. It was observed that all alarmed rats exhibited potentiated startle and extended freezing behaviour but no escape behaviours. The calm rats still startled to the noise burst but continued with exploration and various other behaviours such as grooming.

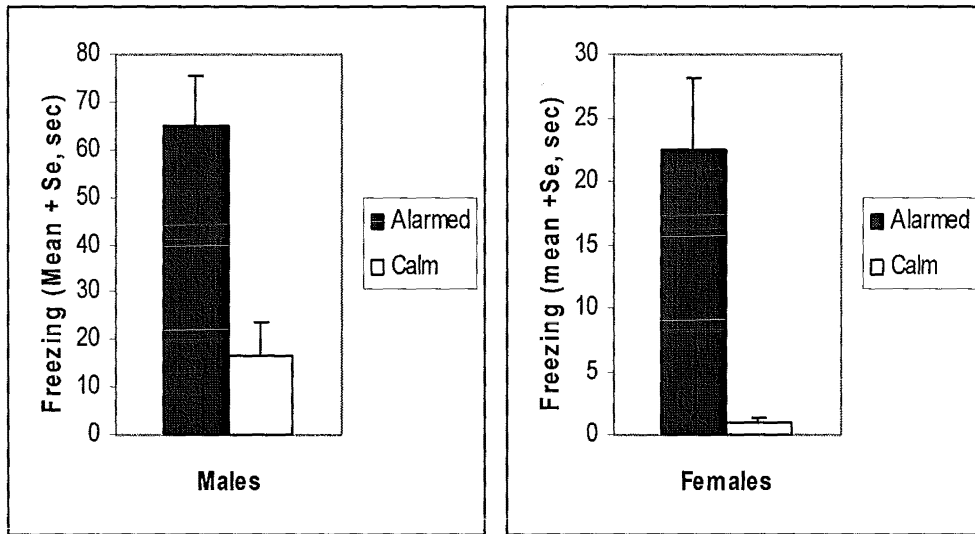


Figure 2. Mean freezing duration of pre-treated alarmed and calm male ($n=24$) and female ($n=24$) rats. Error bars show the standard error of the means.

The distance between the pre-treated and the naïve companion was also noted. The mean inter-individual distances are shown in Figure 3 for two pre-treatments, separately for males and females. Both sexes showed greater distances between target and companion rats when the companion was alarmed than when it was calm. Although statistical significance was not reached, both sexes appeared to show similar responses in terms of increased inter-individual distance when the companion was alarmed.

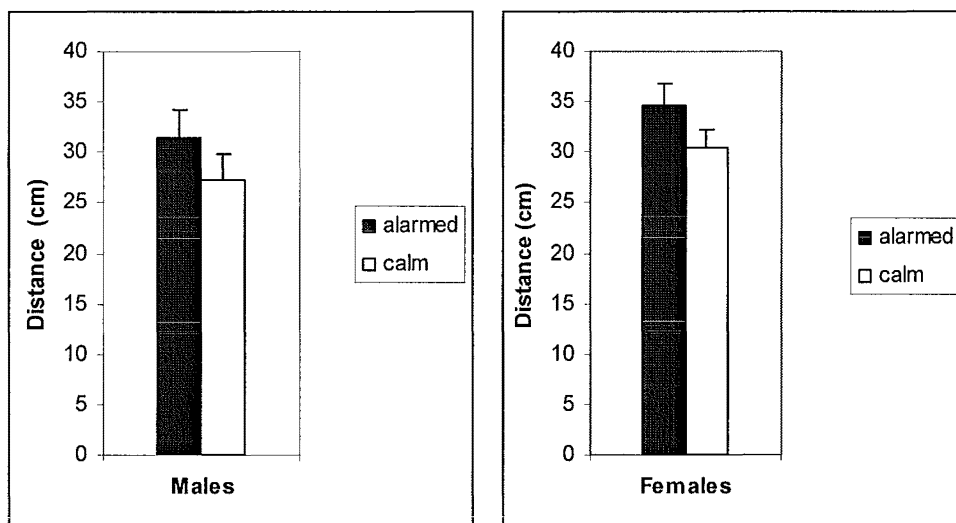
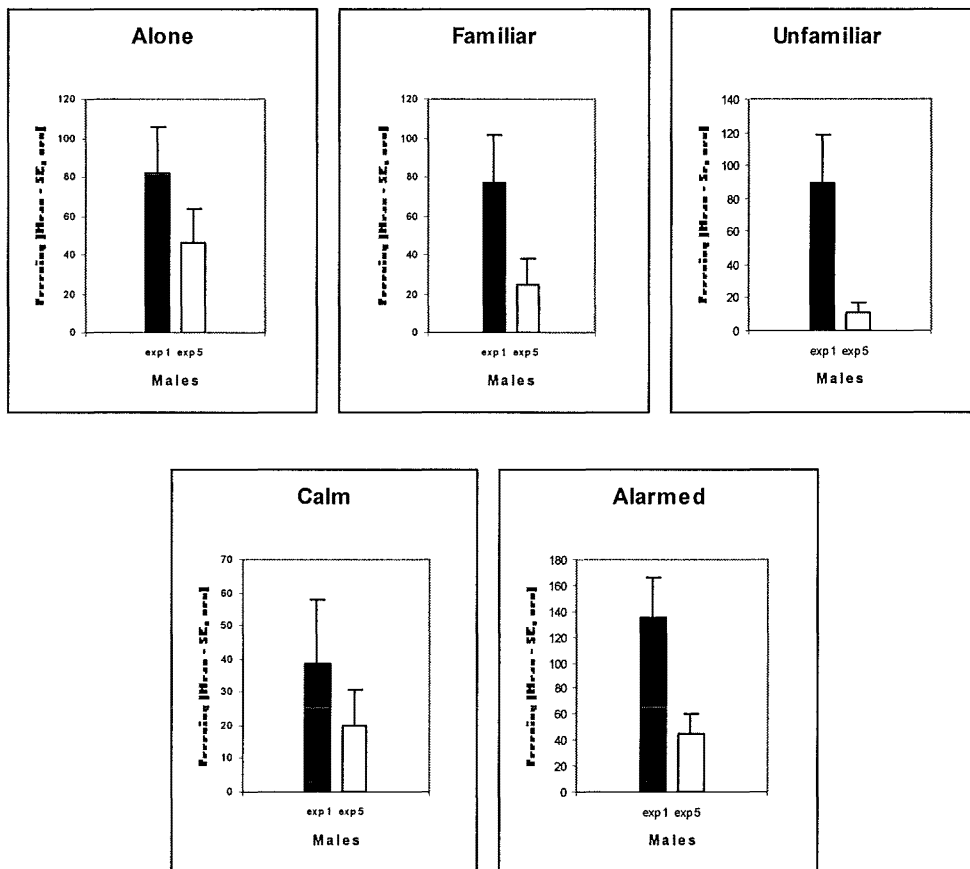


Figure 3. Mean distance between the pre-treated and the naïve companion in the alarmed ($n=24$) and calm ($n=24$) social condition. Error bars show the standard error of the means.

Both the freezing duration of the pre-treated rats and the distance between the naïve and the pre-treated animals suggested that the pre-treatment made a difference to the behaviour of the pre-treated rats. Therefore, the manipulation of companion-rat behaviour was successful, and perhaps other factors may have played a role in obscuring the differences in the role of the companion.

In a repeated measures design, habituation or carry-over effects can potentially be a source of error. In the present case, habituation might obscure differences between social conditions. Since rats were exposed to the social conditions in an irregular order, habituation was investigated by comparing the data of the rats whose first exposure to the experiment (collapsed across the five noise bursts) was in a given social condition with those whose fifth and last exposure was in that condition. It was expected that rats that had already experienced the 5 noise-burst sequences on four previous occasions would

show less freezing than naïve rats in each case. As shown in Figures 4 and 5 below, this is precisely what occurred for males and females alike. Figures 4 a-e compares mean freezing durations for male rats whose first exposure was for example alone to male rats whose fifth exposure was alone. Therefore the fifth exposure included habituation of four previous exposures. Overall, male rats showed less freezing in the fifth exposure in each social condition, but only significantly so in the alarmed condition ($F(1,44)=8.31$, $p=.006$).



Figures 4 a-e. Habituation to noise bursts of male rats between exposure 1 and exposure 5. Error bars show the standard error of the means

Results for females are shown in Figures 5 a-e. In contrast to males, females showed significant habituation in all social conditions except the familiar condition. (alone $F(1,44)= 10.53, p=.002$, unfamiliar $F(1,44)=4.09, p=.049$, calm $F(1,34)=4.82, p=.034$, alarmed $F(1,44)=19.06, p=.00008$).

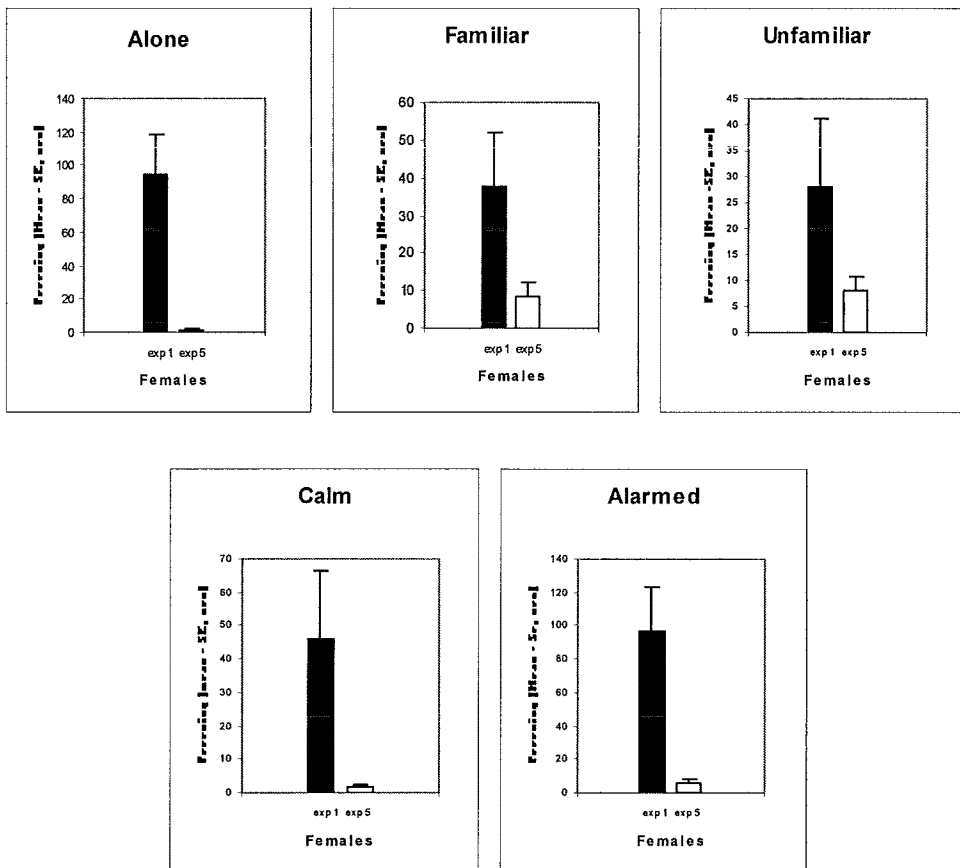


Figure 5 a-e. Habituation to noise bursts of female rats between exposure 1 and exposure 5. Error bars show the standard error of the means

Overall in all conditions habituation was evident thus conceivably masking the companion effect.

Habituation may also occur across the five noise bursts presented in a single session. To examine this possibility, results from each of the five successive noise bursts were collapsed across social conditions but separated for sex. In figure 6 it can be observed that male rats responded at a similar level for the 2nd till the 5th noise burst. Females however, showed some increase in freezing behaviour up until the 4th noise burst, but the freezing behaviour then reduced marginally of by the 5th noise burst. Although some levelling of responses occurred for both sexes at the end of the experimental session this, was not significant. Thus no significant habituation was found within session.

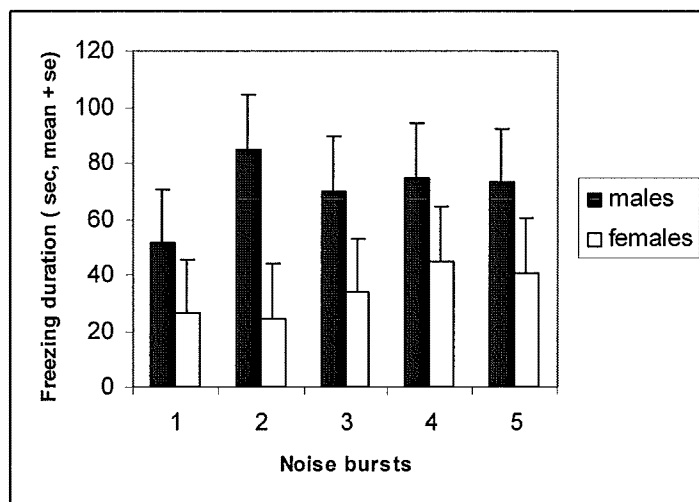


Figure 6. Habituation to noise burst, collapsed over social conditions. The error bars show the standard errors of the means.

Further analysis of the response patterns to the noise bursts suggested that in general all rats showed little reaction to the first and second noise bursts. Most animals started to respond at the third and fourth noise burst – as evidenced by an augmentation in freezing behaviour, but by the fifth noise burst exposure, no significant increase was

found. Since the data was collapsed over social conditions this masked possible any differences between the groups. To unmask this, data of the third and fourth noise burst was separated for sex and social condition. Both figures 7a and 7b illustrate the 3rd and 4th noise burst reaction of all the rats and show that for both sexes the fourth noise burst is firstly similar between the sexes but also suggestive that the companions may have an influence.

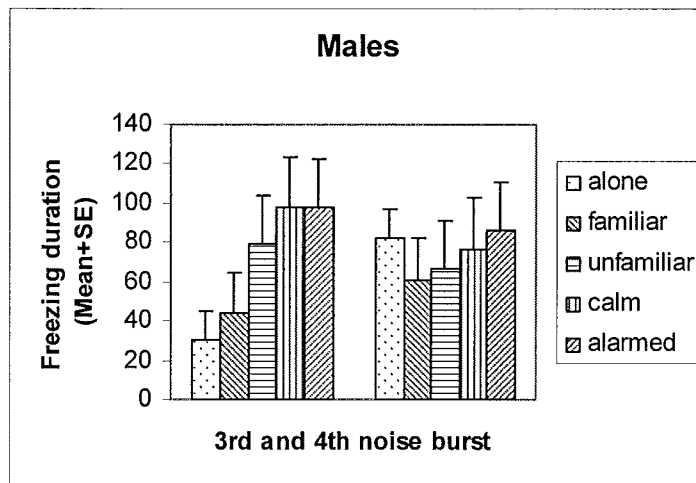


Figure 7a. Mean freezing behaviour of male rats for the 3rd and 4th noise burst separated by social condition. The error bars show the standard errors of the means.

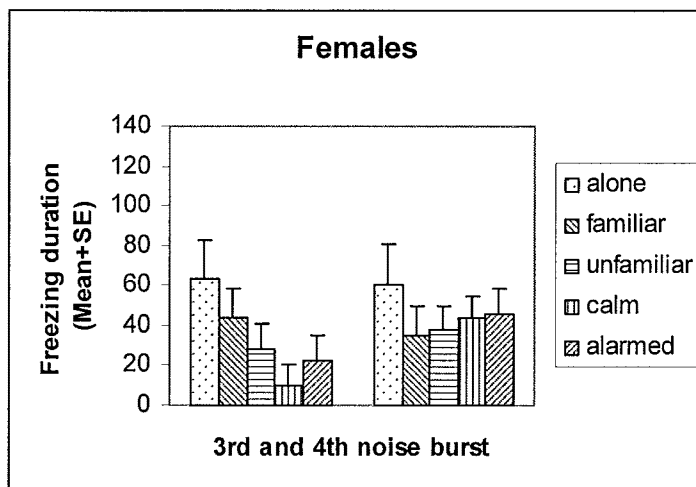


Figure 7b. Mean freezing behaviour of female rats for the 3rd and 4th noise burst separated by social condition. The error bars show the standard errors of the means.

Since both males and females reacted in a similar manner to the fourth noise burst, the fourth noise burst was analysed using only the data of the first exposure to the experimental setting. As it was shown previously that the other exposures were affected by habituation. Thus, by excluding those it was postulated more conclusive results would be unmasked.

Statistical analyses indicated no significant effects $F(4,19) = .3521, p = .8393$ for the males, and $F(4,19) = .5813, p = .6798$ for females. However the numbers were reduced to either 4 or 6 animals per group. The trends shown in Figure 8 illustrate that inclusion of a conspecific may alter freezing duration if effects for habituation can be controlled.

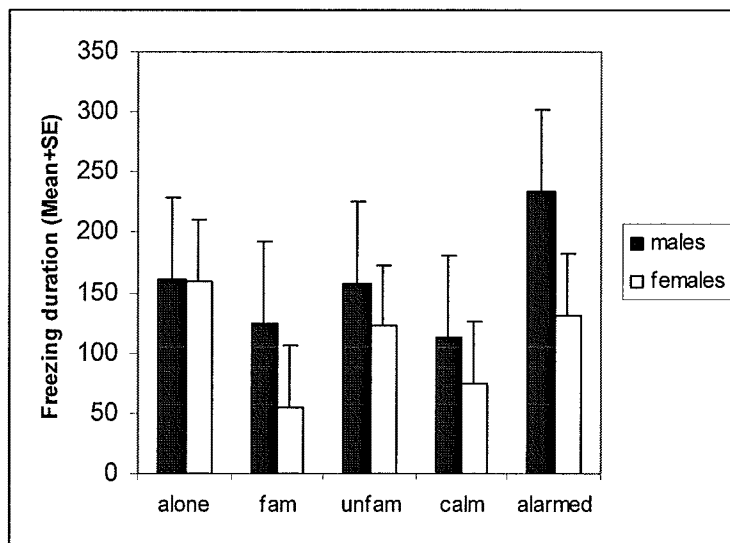


Figure 8. Mean freezing behaviour for male and female rats during their first exposure using only the fourth noise burst. The error bars show the standard errors of the means.

As a result of habituation in this experiment, a second, more modest experiment was conducted in which larger groups of subjects were exposed to the procedure once

only in each of three social conditions, alone, naive and alarmed. Thus, a between-groups design was used instead of the within-groups design experiment.

Discussion of the results for Experiment 1

The main question of Experiment 1 asked if the inclusion of a conspecific to the experimental setting could influence the behaviour of the target rat. Specifically, it was predicted that the freezing behaviour of the target rat would be reduced when paired with a familiar or calm companion, and increased when paired with an unfamiliar or an alarmed conspecific. The results failed to support the main hypothesis. The inclusion of a conspecific did not significantly alter the behaviour of the target rat. The second and third questions asked if both the type of companion (familiar or unfamiliar) and the behaviour displayed by the companion (calm or alarmed) would significantly influence the behaviour of the target rat. In view of the failure of the first question, the second and third questions were necessarily not supported. The fourth question stated that there was a sex difference. The data supported a large sex effect. Male rats did respond differently to the noise burst than females. Under all five social conditions, the males tended to freeze for longer than females.

4.1 Sex differences

Increased reactivity, expressed as freezing, to noise bursts by males has been linked to a higher “emotionality” or “fearfulness” by Gray (1971). This was also reflected in the factor analysis completed by Fernandes, González, Wilson & File (1999), who suggested that anxiety and sex are primary factors for males in various behavioural tests, such as the elevated plus maze, the hole board test, and the sexual orientation test. On the other hand, it appears that females show much more activity and exploration behaviour in these earlier tests.

The higher levels of fearfulness and anxiety present in males suggested by Gray and Fernandes et al. may have been a reason for the large difference in reactivity to the noise bursts in the current study. Conversely, this increased reactivity may not only be emotionally based, but it could conceivably be a behavioural adaptation. Male rats may be more sensitive to mildly-aversive stimuli and this in turn could make them more cautious. This cautiousness may not necessarily be more emotionally based, but just different adaptations to certain stimuli and conditions. Furthermore, males were overall less active, and this may be interpreted as males are more emotional because they show no obvious other behaviour. For example, Gentsch, Lichtsteiner & Feer (1981) found that locomotion was not a reliable response to emotional stress, but conversely defecation and corticosterone excretions were. Archer (1974), who found little evidence for a sex difference when exposing rats to novel stimuli also raised this point. He stated that there was little evidence to suggest that an emotional difference between sexes existed. However, Archer did find that females were overall more active. This higher activity may have been a factor in why the females stopped freezing sooner and continue exploring the experimental chamber. Archer refuted that activity relates to emotionality. When paired together the activity in females may have been part of the driving force in reducing the freezing behaviour of the target rat.

An alternative suggestion to the sex differences is that females are more visually based. As suggested by Hughes (1999, 2001), females are more inclined to explore novel but inaccessible areas using visual cues, whereas males may possibly use more olfactory cues. This appears plausible because the main biological role of males is to procreate, which requires the use of odours to identify the sexual state of the females (Carr, Loeb, &

Dissinger 1965; Ågmo 2003). In the factor analysis conducted by Fernandes et al. (1999), male rats were more inclined to spend time with a pro-oestrous female than with a male, indicating that a sexually active female was more appealing than a sexually active male. In addition males also use odour cues to identify potential intruders. Food preference is also transmitted via odour. Rats were able to recognise and show a preference for the food the conspecific had consumed (Galef 1988). However, if males rely more on their olfactory process to analyse their surroundings then this did not noticeably influence their behaviour towards any companion in the current study. Especially to the companion who had just received 10 shocks prior to the introduction of the target rat, and so would still be emitting odours relating to fear but this did not influence the behaviour of the target rat nor did it influence the distance between them. If olfactory cues were important, why then did the target rat not significantly increase its freezing duration or the distance from the alarmed companion? Fanselow (1985) suggested that fear odours may elicit analgesia in unstressed rats. Alternatively coordinating vigilance is a time consuming task and relies upon trust but also status and dominance (Ruxton & Roberts 1999) and vigilance is influenced by outside stimuli more so than internal stimuli (Ferriere, Cazelles, Cezilly & Desportes 1999).

In the current experiment, the chamber was cleaned between trials but not between pre-treatment and testing. This was because in nature the alarmed animals are likely to be emitting fear odours and possibly emitting alarm calls. Apparently these cues in the current study were not enough to alter the males' response to an alarmed companion. As suggested before, males may be more sensitive to external aversive stimuli. Meng & Drugan (1998) researched internalisation as the potential source of anxiety. They did this

by injecting an anxiolytic directly into the animal and found that males were more affected by the drug. Females were able to override the effects of the anxiolytic and showed little influence under low dosage. Under higher dosage, they also reduced activity as measured by open-field activity, rearing and exploration. This may indicate that males are more sensitive to anxiolytics and therefore they reduce their behavioural activity earlier compared to females. It is also conceivable that females are more resistant to anxiolytics as a function of hormones. Zimmerberg & Farley (1993), for example found that the activity in females can be attenuated by gonadal hormone reduction. Reducing these hormones through drugs and surgery resulted in females reducing their activity level similar to males.

The biological role of female task includes the task of raising young. Most of their adulthood is spent either pregnant or lactating or both. These conditions require more nutrition thus a greater need to forage for longer and conceivably more often. Hence, female rats may need to take more risks than males to access food. That is, males may be able to be more selective about when they forage thus have more time to be cautious.

Although no significant change in freezing behaviour was found when paired, both sexes showed some changes in freezing behaviour when combined with various types of companions. However, these were not statistically significant. Both sexes reduced freezing and distance when paired with a familiar or calm rat compared to when alone. Further to this they slightly increased freezing duration when paired with an unfamiliar and alarmed rat. These trends were in the expected direction, i.e. calm and familiar should reduce and unfamiliar and alarmed should increase.

The failure of the companion effect was not due to the failure to respond to the noise bursts. Observations made during experimental trials, and a review of the videotapes showed that some target rats showed little or no freezing behaviour at all. Others however, showed extreme reactions and displayed freezing behaviour for the total duration of the test session. This may indicate that the noise level was at an appropriate level to elicit responses ranging from no freezing to continuous freezing.

Another potential source of error was that the companion rat was not displaying calm or alarmed behaviour in accordance with their prior training, but this was also discounted when the videotapes were reviewed. A manipulation check showed that the companion rats used to elicit a behaviour change in the target rats did display the expected behaviours. The calm companion showed little or no freezing behaviour when the noise bursts were sounded. Instead, they showed startle behaviour (normally a precursor to freezing) and then continued to explore the experimental chamber. Conversely, the alarmed companion showed high levels of fear as indicated by severe reactions to the noise bursts, starting with fear-potentiated startle. Fear potentiated startle was marked by an increase in startle response to the light-noise pairing. These pre-treated rats showed potentiation, in extreme cases by jumping high enough to execute back-flips, and in one case hitting the plexi-glass ceiling of the open field box. After the fear-potentiated display, most rats returned to a freezing posture that included an arched back and total immobility. Therefore, there was no reason to believe that the companion rats failed to show the predicted behaviours. The naive familiar and naive unfamiliar companions were not pre-treated and these rats were not expected to show any particular

behaviour. Completing a further check in which the distance between the target and the calm or alarmed rat was measured showed that both males and females exhibit a significantly greater distance between target and alarmed rats than between target and calm rats. This is consistent with the findings of Eckman, Meltzer & Latané (1969).

The problem of statistically insignificant results seems to be in the wide variability in freezing behaviour itself. As mentioned above some rats displayed little freezing, namely the females, while the males showed more freezing, however not all rats respond in this pattern.

Furthermore, there appeared to be a strong habituation across test sessions (see figures 4 and 5). Russell (1977) and Hughes (1990) have found some support for a rapid increase in habituation in females, particularly when the experimental duration was relatively short, i.e. less than thirty minutes. In this experiment, the total time spent in the open-field equipment was usually no more than thirty minutes. This may have been a reason that females habituated faster than male rats.

Since the rats were exposed to all five social conditions in a pseudo-random order, it was important to investigate how soon habituation started to take place. By comparing the rats' behaviour from the first exposure to the last, it was noted that a large decline in freezing behaviour was found. This was particularly true in social conditions where rats showed more, although not statistically significant freezing i.e. in the alone, alarmed, and unfamiliar conditions. Rats that were exposed to these conditions as their final exposure

showed little overall reactivity, and most were habituated to the point of displaying startle behaviour but no noticeable freezing behaviour.

As mentioned above, there was habituation to the noise bursts across social condition exposures. The reactions to the first two noise bursts across most rats and social conditions were very similar. However, by the third noise bursts differentiation started to occur, and by the fourth noise burst the maximum differentiation between the social groups was visible. See figures 7a and 7b. These figures suggest that both males and females appear to be influenced by the behaviour of the companion rat although again not statistically significant. Furthermore, the inclusion of familiar or calm companions appeared to reduce freezing responses while both the unfamiliar and the alarmed companions appeared to increase freezing responses. However, by only analysing the first exposures and the fourth noise burst, the numbers per group dropped below an acceptable level for statistical analysis.

Since most rats showed some change in freezing behaviour when paired with a conspecific, it was postulated that these potential effects might have been masked by habituation to the experimental setting, the stimuli and also the procedure. To ask again whether rats actually do respond to a conspecific in this task, a second experiment was conducted to avoid habituation effects. Furthermore, in order to increase statistical power a smaller number of groups and larger number of subjects per group were used than in the first experiment.

Method Experiment 2

The second experiment was a between design using 3 social groups, alone, naïve and alarmed. 40 male and 40 female rats were housed in similar conditions as in experiment one. That is, ad lib food and water a reverse light cycle and 4 rats of the same sex per cage. These rats were split into four groups of 10 animals per sex. One group was tested naïve alone; the second group was the naïve familiar group consisting out of two groups of 10 familiar but naïve animals each. The third and final group consisted out of 10 naïve rats that were paired with shock pre-treated animals that originated from the alone group. In other words, after the data was collected for the alone group these animals were then pre-treated with light paired to foot-shock to condition them to show fear to the light. After conditioning, these rats were paired with the third naïve group to form the alarmed condition.

The experimental procedure was the same as for experiment one. However, some minor changes to the pre-treatment design were implemented. The .2mA foot-shock was administered at 2-minute intervals instead of the previously varying inter-trial intervals ranging between 60 and 180 seconds. Additionally a short delay-conditioning paradigm was put in place, i.e. the shock commenced in the last portion of the light-phase. This has been shown to create a strong fear association with the light. Ten minutes after the last shock the lid of the open-field was open and closed. 2 minutes later the target rat was placed in the open-field and the experiment commenced.

Results for experiment 2

The aim of the second experiment was to answer the following questions. Was the reaction to a set of unfamiliar noise bursts the same for male and female rats? Experiment one suggested that a sex difference exists. Secondly, do both sexes react in a similar manner when alone and when paired with a companion? Previous research suggests that male rats significantly reduce freezing duration when paired with a companion (Taylor 1981); little evidence is available for the behaviour of paired female rats. Additionally, it has been unclear if behaviour shown by a companion influences the behaviour of the naïve animal. Hence the final question, is the behaviour displayed by the companion, in this experiment, alarmed, an important factor in modifying the freezing duration of the target rat?

In the second experiment all the animals were naïve to the experimental conditions, unlike the first experiment where animals were used in a repeated measures design and hence had the opportunity to habituate to the experiment.

The data was analysed in an ANOVA design using the statistical software program 'Statistica (Statsoft,Inc)'. The first question asked if there was a sex difference in reactivity to noise bursts. The results showed that overall males freeze longer than females when exposed to unfamiliar noise bursts ($F(1,56)=18.305$ $p=.00007$).

This can be seen in figure 9 that illustrates the difference in freezing behaviour to 5 noise bursts by males and females; the data was collapsed over 3 social conditions.

Thereby illustrating that male rats show longer freezing duration than females when they are exposed to five noise bursts in a novel environment.

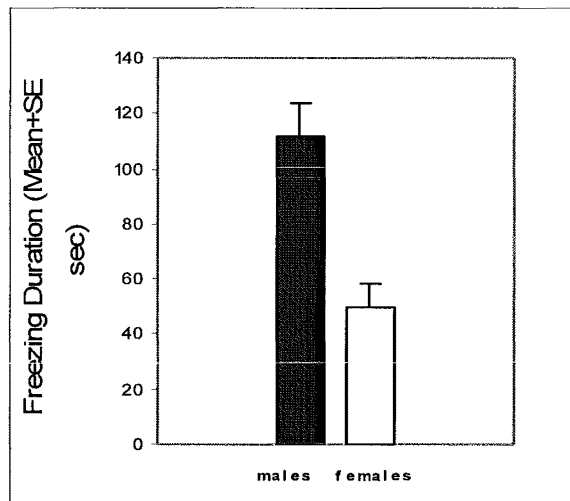


Figure 9 Overall sex difference in mean freezing duration between males ($n=30$) and females ($n=30$) after 5 noise burst exposures. The error bars show the standard error of the mean.

Since large behavioural differences between the sexes were found in both experiments the data were separated for the sexes and analysed individually.

The second question asked were rats influenced by a companion in a novel setting as compared to alone. Figure 10 suggest that males show little difference in freezing behaviour between social conditions ($F(2,27)=0.839, p=0.44$). They appeared not to significantly adjust their freezing behaviour when paired with a naive nor with an alarmed companion compared to being alone. Thus for males the inclusion of a companion to the experimental setting appeared to have little or no influence on the freezing behaviour of the target rat.

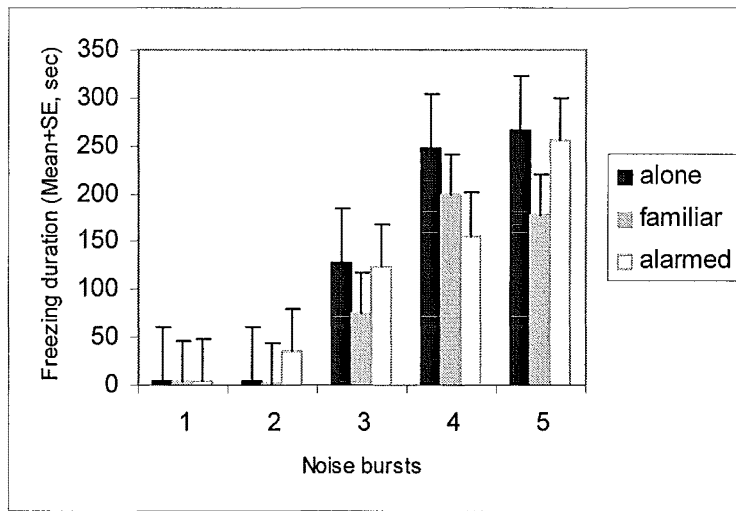


Figure 10. Mean freezing duration of male rats ($n=30$) when exposed to 5 noise bursts in 3 social conditions. The error bars show the standard error of the mean.

Female rats were more likely to adjust their freezing behaviour to the social conditions. Figure 11 illustrated the mean freezing duration of female rats when exposed to 3 different social conditions. A trend was visible in which they reduced freezing when paired with a naive rat but increased freezing when paired with an alarmed rat, this compared to being alone. Suggesting that there was some influence however, there was no statistical significance found between the alone and both social groups ($F(2,27) = 2.163$ $p= 0.134$).

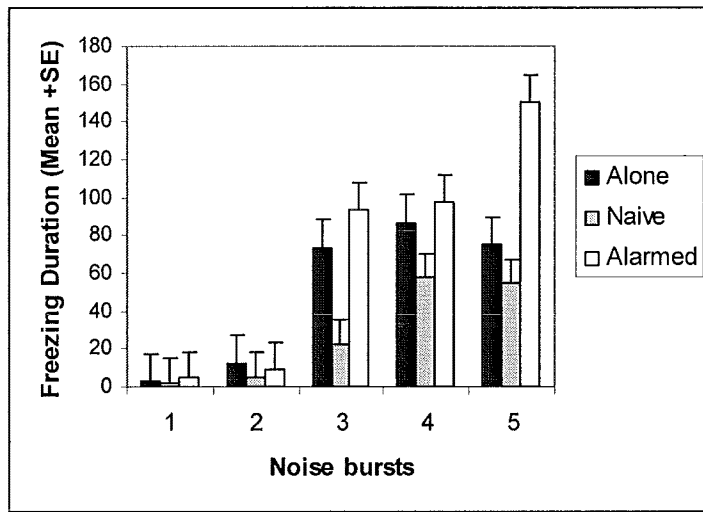


Figure 11. Mean freezing duration of female rats ($n=30$) when exposed to 5 noise bursts in 3 social conditions. The error bars show the standard error of the mean.

To investigate if the pre-treated alarmed rats showed significantly different behaviour from the naive companion the same manipulation checks were conducted as in experiment 1. The freezing behaviour and the distance between the animals were measured. It appeared that the males did not show sufficient behavioural differences, for both the freezing duration and the distance between the animals were statistically insignificant. This suggested that the pre-treatment of ten light shock pairings was not substantial enough to significantly influence the behaviour of the alarmed rat. Conversely, the pre-treated females both showed significantly more freezing duration and a larger distance between themselves and the naïve animal compared to the non pre-treated naïve animal. This suggested that the ten light-shock pairings influenced the behaviour of the alarmed rat. Thus, the behaviour of the alarmed rat was significantly different than the familiar animal. It appeared that the pre-treatment for the males failed

but worked for the females. This is later reflected in the results to the reaction to the pre-treated rats.

The final question asked if the behaviour displayed by the companion influenced the behaviour of the target rat. Thus is there a difference in response to naive rat as opposed to an alarmed one. In males it appeared that the behaviour displayed by the companion had little influence on freezing duration. As illustrated in figure 12 very little difference in freezing behaviour was found between the familiar and the alarmed condition ($F(1,27) = 0.579$ $p = 0.45$). Similarly no difference in distance between the animals was found. That is, both with the alarmed and familiar companion the target rat showed no increase or decrease in distance from them. This could have resulted from a failed manipulation in which the alarmed rat showed no significant difference in behaviour to the naive rat.

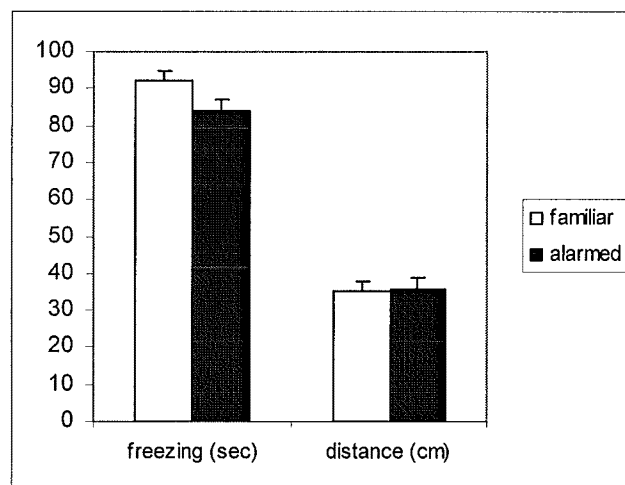


Figure 12. Mean freezing duration and mean distance between male target rats and a naïve ($n=10$) or an alarmed ($n=10$) companion. The error bars show the standard error of the mean.

Conversely, the females showed a significant difference between familiar and alarmed. ($F(1,27)=4.3263$, $p<0.05$). This is illustrated in figures 13 that illustrates the

mean freezing duration and mean distance between target rats and a naive or an alarmed companion. The reaction to the alarmed animal resulted in a longer freezing duration after each noise burst, it also resulted in a greater distance between the alarmed and the target rat then when paired with a familiar rat ($p < 0.05$ one tail).

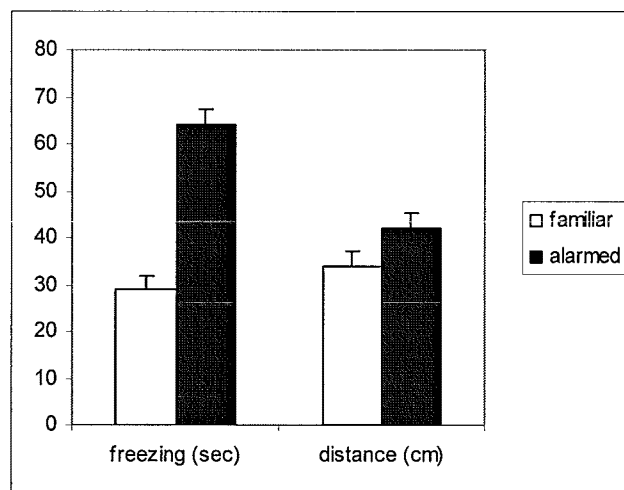


Figure 13. Mean freezing duration and mean distance between female target rats and a naive ($n=10$) or alarmed ($n=10$) companion. The error bars show the standard error of the mean.

In summary, males displayed longer freezing duration to unfamiliar noise bursts. They froze for longer duration but did not significantly change freezing duration nor distance when paired with an alarmed rat or naive rat. Overall the addition of a companion rat resulted in no observable change in behaviour of the target rat.

Females reacted less prolonged, although the duration of freezing was not significantly influenced by the addition of a conspecific compared to alone. However the type of companion was important. A significant difference was found between naive and alarmed. Furthermore the distance between rats was greater when paired with an alarmed one then with a naive one.

Discussion of the results of Experiment 2

The second experiment asked whether the presence of a companion was able to influence freezing behaviour of target rats. As in Experiment 1, a sex difference was found. Specifically, the presence of a companion affected the behaviour of females but not males. For males, freezing durations were the same regardless of whether the target rat was alone or accompanied by either a naïve or alarmed companion. Similarly, distances between target and companion animals were the same regardless of whether companions were naïve or alarmed. On the other hand females did marginally change their behaviour; they reduced freezing when paired with a naïve animal, and more importantly, they increased freezing behaviour when paired with an alarmed companion. These changes were also reflected in the distance between the target rat and companion animals. Distances were greater when the companion was pre-trained to be alarmed.

7.1 Habituation

Male rats appear not to attend to a companion in the experimental setting although some observations were made that they huddle in between noise bursts, this was not reflected in the distance between them just after the noise burst. So during the freezing period the rats were inclined not to congregate, if anything as the test progressed the distance increased. This contrasts with the findings of Meaney & Stewart (1987) who found that under low-stress circumstances male rats were more likely to engage in affiliative behaviour than females. However, their rats were not exposed to stressful noise bursts but were allowed to freely interact.

In the current experiment it was observed when males were exposed to the noise burst they startled and either froze on the spot or if they were within the vicinity of a corner they scuttled into this. Similarly, Grossen & Kelly (1972) indicated that male rats do not freeze arbitrarily; they make a choice where to freeze, usually near corners and walls. Thus, it is possible that more huddling would have been found if a circular (rather than rectangular) test apparatus had been used. However if this was true then it would mean that a corner was a stronger cue for safety than a companion, since the distance between the rats increased as the experiment progressed.

The failure of males to attend to conspecifics as predictive or distractive cues, in the present experiment, is contrary to the results that Blanchard & Blanchard (1989) reported. They introduced a cat to a visible burrow system. The dominant rat, who spend most of his time on the surface, was found to emit 22hz cries that caused conspecifics who were within the burrows to display hiding and freezing behaviour for extended periods, even though they had not seen the cat. Thus, calm conspecifics were responsive to alarm cues emitted by the alarmed dominant rat, whereas in the present work, fearful male rats did not become more fearful in response to such cues from a pre-trained alarmed one. It seems possible that the environment was too aversive for our males to show companion influence, especially since they exhibited little habituation to the 5 noise bursts in the second experiment. If so, then perhaps extending the duration of the experiment (that is, exposure to for example 10 noise bursts) they may eventually show habituation. Indeed, Hughes (1990) reported that males appear to habituate slower than females to novel environments.

Females in the present experiment showed overall less reactivity than males to a novel and stressful environment, and they appeared to be influenced by the presence and the behaviour of a companion. They marginally reduced freezing when accompanied by a naive companion, and they increased freezing duration when accompanied by an alarmed one. Furthermore, the inter-animal distance increased when the companion was alarmed as opposed to a naive. Thus, it may be that the appearance of a “companion effect” may be mediated by the ambient level of stress or fear. This is congruent with the findings of Eckman, Meltzer and Latané (1969) who showed that rats pre-exposed to the open-field exhibited more social interactions than rats that had not been exposed. Rats habituated to the surroundings were more sociable.

Thus, habituation to the environment may well play a role in fear responses to conspecifics. This was also demonstrated in the firsts experiment in which habituation to the environment reduced responding overall because it was a repeated measures design. It also masked the potential differences between reactions to calm or alarmed conspecifics. However, in the second experiment whereby the rats had less opportunity to habituate to the environment the female rats were still calm enough to exhibit reactions to the companions.

The calmness exhibited by the female rats may be mediated by risk assessment and behavioural competition. Behavioural competition is a form of time management in which rats engage in one form of behaviour or another, thus how time is spend depends upon the behavioural requirements such as foraging, parenting and mating (Staddon

1983). There appears to be an optimal time allocation to each behavioural task. The behavioural tasks are also influenced by a risk-cost trade-off, that is if the animal is hungry but food can be found in high predation risk environments than the animal may well engage in higher than normal risk-taking behaviour. To attenuate the risk, the ability to use predictive cues from others may lead to an overall adaptive advantage.

For females, efficient risk assessment of the environment is potentially necessary. Firstly, they are smaller and so have relative less mass to body surface and therefore require more kilojoules to stay at a biological stable level. In addition, they are usually either lactating or pregnant or both so therefore have higher nutritional requirements. To obtain these requirements females may need to forage further and longer than males and this increases the opportunity of being preyed upon. To reduce predation risks females may be more inclined to use available cues afforded by conspecifics.

In the current study there were no obvious extra environmental cues available to the target rat other than the ones displayed by the companion. Thus when confronted the target rat could use the alarmed expression to possibly predict something about the environment. This was suggested by the results in that the target rats increased their freezing behaviour and the distance from the alarmed companion. If it was the actual presence of the companion that increased the freezing duration than this should have been reflected in the results of the pairing with the naïve companion, this was not so. The only difference between the naïve and alarmed companion was that the alarmed companion exhibited more fear as reflected in the freezing duration. Therefore, the target rat may have used this information to increase freezing behaviour.

7.2 Signalling

The results of this study suggested that female rats were influenced by the behaviour of the companion. This does not necessarily indicate that the alarmed rat was intentionally signalling to the target rat. Interestingly male chickens do signal with intent, they produce more alarm signals in response to aerial predator models when an audience is present (Karakashian, Gyger, & Marler 1988). Another plausible explanation is that the exaggerated startle response of the alarmed animal that is, the very high jump possibly combined with ultrasonic sound emissions actually frightened the target rat. Thus, not the signalling *per se* but just the actual physical fright response of the alarmed rat invoked freezing in the target rat.

For a signal to reach the target rat it must be transmitted in an understandable manner, followed by the target rat receiving, decoding, act or not. It is plausible that the alarmed rat was showing fear but not with the intention of signalling this to others. To communicate with intent the signaller must be aware that other animals are present. Thus, there needs to be awareness in both animals that the other animal is present. Furthermore, the alarmed one then has to transmit the information. However, this specificity is unlikely for alarmed rats display fear behaviour when alone when exposed to fear evoking stimuli. In other words, it is unlikely that the alarmed rat signalled with intent. However, it is plausible that the target rat used the available information displayed by the alarmed rat as an additional cue to evaluate the risk presented by the five noise bursts.

7.3 Incompleteness of information

In the current study there was no obvious predator to the target rat in the alarmed condition, only a novel environment, 5 noise bursts paired with a light and an alarmed

companion. Possibly the cues were only partial since the alarmed rat had information that the light predicted an aversive event (shock), but to the target rat the light was inconsequential. The target rat only had incomplete information. For example wallabies (Blumstein, Daniel, Griffin & Evans 2000) and birds (van der Veen 2002) need to see and hear the predator to be able to make accurate and correct decisions. If the birds had incomplete information then they were vigilant for longer and so reduced feeding. Thus incomplete information could also increase unpredictability and increase freezing. Better to sit a little longer and get a little hungry than to be devoured.

7.4 Future research

The first and second experiment suggested that females froze less as opposed to males. Under mildly stressful conditions females appeared to react differently to a familiar or an alarmed companion. Thus it may be interesting to note how mother and young react to the above experiment. For example some evidence exists for mothers to be somewhat more effective in teaching fear to juveniles (Mineka, Davidson, Cook & Keir 1984). Do pre-weaning young react to a fearful mother, what would they do considering that startle and freezing behaviour (Richardson & Vishney 2000) but also defence behaviour (Hubbard, Blanchard, Yang, Markham, Gervacio, Chun-I, L. & Blanchard 2004) are a developmental process. Would there be a sex difference in the juvenile? Can both sexes once habituated to the environment show more distinction between a calm or alarmed companion?

Furthermore, using adult rats would the naïve female be able to conclude that the light is the source of fear for the alarmed rat? Hence would she be able to use this

information in the future??? That is, show fear to the light when tested at later date or in a different environment? Could she transmit this information to other conspecifics? Curio (1988) for example found that blackbirds could transfer information at least 6 times between experienced birds to naïve who then trained other naïve etc.

The reactivity difference to different behaviours displayed by companion rats may even have been greater if the naïve female was paired with a calm animal compared to an alarmed one thus possibly enhancing the freezing behaviour difference. In addition the distances between calm and alarmed need further investigation. For this may indicate some sort of interpretation is happening by the target rat. However, it was unclear in this experiment if the target rat moved away from the alarmed or vice versa.

From a survival point of view it is important to stay away from an animal that is showing fear behaviour. In particular if the alarmed animal predicted the presence of a predator thus by increasing the distance the target rat may increase survival rate.

Another avenue to investigate signalling behaviour is the matching mixed-sex pairs. Sloane & Latané (1974) found no significant increase in gregariousness in cross sex pairs so this may offer an opportunity to investigate signalling behaviour without the sex effect. That is do male rats increase freezing when paired with an alarmed female rat and vice versa. Plausibly alarmed female rats display more obvious fear behaviour that lends itself for quicker interpretation by conspecifics.

General discussion.

Experiment 1 asked four questions: firstly do rats' change their freezing duration when paired with a companion? This was disconfirmed; rats appeared not to alter their freezing behaviour when paired with a companion. This automatically disconfirmed the second and third questions that asked if the type of companion and the behaviour of the companion were important. This was not the case; pairing with a familiar or unfamiliar companion, or with a calm or an alarmed companion did not alter the freezing duration. The final question asked if there was a possible sex difference in freezing duration in the experimental setting. This was confirmed in that males were more reactive, i.e., male rats showed more freezing behaviour than females when exposed to five, 90-decibel noise bursts in a novel environment.

One problem in using a repeated-measures design was that rats exhibited rapid habituation across experimental conditions. Therefore, a second experiment was conducted in which each subject was only exposed once to the procedure. This resulted in partially replicating the above outcomes, there was a sex difference, males exhibited more freezing than females and no 'companion effect' for males was found. For females, it was important if they were paired with a companion. Females tended to notice a companion although finding no statistical significance between alone and naive, there was a statistically significant difference between the behaviours displayed towards an alarmed or a naive companion. Female rats exhibited more freezing when accompanied with an alarmed companion than when joined with a naive one. The significant difference

between pairing a target rat with an alarmed or a naive rat suggested that females attended to the behaviour of the companion.

8.1 Social facilitation.

The results of these two experiments (i.e., large sex difference, no ‘companion effect’ for males, and some companion effect for females) only marginally support the social facilitation theories discussed in the introduction. The three established theories were, the ‘Mere’ presence theory as supported by Zajonc (1965, 1980), the Learned Drive theory proposed by Cottrell, (1972) and the Distraction Conflict theory proposed by Sanders (1981).

8.2 Zajonc’s Mere Presence Theory

Zajonc’s ‘Mere’ presence theory stated that the mere presence and the predictability of the companion were sufficient to induce a behaviour change. This theory was only partially supported. Male rats did not significantly alter their freezing behaviour when paired, compared to alone. Female rats modified freezing behaviour depending upon the type of companion. Thus, the females supported Zajonc’s theory in that the unpredictability of the companion influenced the behaviour of the target rat. When paired with a naive rat that was conceivably showing predictable behaviour, the target rat showed less freezing as opposed to paired with an alarmed rat which was displaying fearful, and presumably unpredictable behaviour.

In summary, it appears that male rats were not easily influenced by conspecifics whereas females were. Hence, Zajonc’s ‘mere’ presence was only partially supported.

8.3 Cottrell's Learned Drive Theory

The Learned Drive theory also has difficulty explaining the results of the males. The Learned Drive theory postulated that a reaction to a companion was a learned response and this enhanced or inhibited performance. Thus, an animal learned that the presence of a conspecific predicted a certain outcome. Since the rats have never been alone and so have no previous experience of being alone the most likely, reaction would be apprehension and more freezing; however, there was little difference in freezing behaviour between alone and paired. Furthermore, the behaviour of the companion that was calm, naïve or alarmed, was of no consequence. Female rats on the other hand did alter freezing duration when paired. Female rats were raised and tested in an identical manner to the males and so presumably had the opportunity to learn and express the same behavioural interactions as males. However, they exhibited a difference in freezing behaviour towards a companion suggesting that they learned other behavioural interactions than males. Therefore, the Learned Drive theory is not a completely plausible explanation for these results.

8.4 Sander's Distraction Conflict Theory.

The Distraction Conflict theory assumes animals have a limited attentional capacity. Thus, for simple tasks attention can be divided between task and conspecific. For difficult tasks, full attention is required so as not to impair performance. Freezing behaviour is a well-learned if not innate behaviour and thus should be easily distracted by a conspecific. However, this was disconfirmed in these two experiments: males were not influenced by the presence of a conspecific. Conversely, female rats were partially

influenced by the presence of a companion thus lending partial support to the Distraction Conflict model.

Neither the 'Mere' presence, Learned Drive, nor the Distraction Conflict theories were able to explain fully the results of both experiments.

8.5 Taylor and Latané

The aforementioned lack of response of the male rats to a companion is contrary to results reported by Taylor (1981). Taylor found that grouped animals reduced their freezing behaviour when exposed to noise bursts. Four animals were employed in Taylor's groups, compared to two in the current experiment. Having four animals would increase the opportunity to interact, distract and hence reduce overall freezing duration. Furthermore, Taylor made measurements over a period of five consecutive days. This allowed for more interaction between animals and more opportunity for habituation. The results of Taylor's experiment clearly show that. On the first day of testing there was little difference between the social groups. Similar to the findings in this study Taylor found no significantly different companion responses to familiar or unfamiliar companions.

Latané (1969) studied whether rats are gregarious or not, and noted that two rats had less inter-animal space than by chance when placed in an open-field. However, these rats were also tested over consecutive days in which gregariousness increased. The animals were not exposed to other stressful situations, such as noise, other than being positioned in a round open-field. Both Taylor and Latané indicated that paired or grouped rats reduce fear but this fear reduction occurred over several days. Fear reduction in the

target rat did not appear immediately in Taylor and Latané's studies - similar to the findings presented in this thesis.

Furthermore, fear reduction is suggested to be a great motivator for companionship. If this is true, why do these rats not congregate or show freezing reduction immediately when paired together but do so over time? There appears to be a habituation factor. Habituation is the reduction of a response to environmental stimuli. Thus, over time the attention to novel stimuli abates which allows the animal to attend to other less threatening stimuli. For example, animals placed in novel environments are less likely to consume sustenance until they become familiar with the environment; there may be an order of importance in which stimuli are attended to. Conceivably in the current two studies, rats first attended to the most important stimuli which in this case was the environment and noise bursts, and then to the other less threatening stimuli such as the companion. The behaviour exhibited by the companion was not strong enough to override the effects of the environment. Possibly the behaviour of the alarmed animal was 'unnatural' as well.

The alarmed rats were conditioned by pairing light to inescapable shock in order to exhibit freezing and fear during test conditions when exposed to a light-noise combination. It is plausible that the light /shock pairings were too unnatural to elicit the appropriate behavioural changes to induce freezing in the target rat. It may be that rats are not biologically prepared to respond to light as equally as they would to a natural predator. Startle and potentiated startle are reflex reactions to sudden noise bursts, thus occur without cognitive intervention. On the other hand, locating and reacting to a predator involves cognitive procedures. There may be a difference in the physical and

auditory expression between the reflex reaction and the cognitive reaction. Since freezing behaviour is the behaviour of choice when confronted with predators and not startle (Fanslow and Lester 1988). Thus in this experiment the cues available to the target rat were possibly not sufficient to elicit the most reliable response of freezing.

8.6 Isolation prior to experimentation.

More conclusive results might have been found if the animals were individually housed prior to experimentation since isolation increases open-field sociability (Meaney & Stewart, 1979). Aloneness is a problem when searching for effects of conspecific interaction. Animals raised in isolation may not develop the skills to interact appropriately when paired together, and so confound the results. Conversely, animals separated prior to testing may not display 'true' behaviour for they are not only coping with the experimental procedure but also with the loss of a mate. A possible solution would be to habituate the animals to isolation by exposing them to isolation and thus encourage them to develop coping skills. However, for a potential model of alarm signalling for conservation purposes, it is necessary to replicate potential threats and solutions to approximate natural situations. Normally, captivity-bred animals are not kept in isolation and nor do social animals live isolated in natural settings. Therefore, social isolation was not appropriate for this experiment.

8.7 Genetics

If all rats reacted to the noise bursts with identical freezing duration, then this behaviour is potentially detrimental - not only to individual survival but also to group

survival. Thus if all rats freeze for the same duration then they may all incur losses on other survival opportunities such as foraging, mating and sleeping. On the other hand, it is just as detrimental if all rats showed no freezing behaviour when confronted with unfamiliar stimuli, i.e., if rats exhibited no freezing behaviour, then the predator is likely to catch some or all prey, therefore reducing the group number to a less viable level. Thus, it is likely that a proportion of rats do not react equally to all stimuli (natural selection). For example, if 30% of the rats exhibited diminished reactions to stimuli, then these animals may have gained an advantage in resources. They may have made a choice that exploring the environment is more likely to lead to profitable results than freezing behaviour. Trullar and Skolnick (1993) found that a large part of the variance in fear-associated behaviour is genetically related. Mainardi and Mainardi (1988) genetically developed mice of which a small percentage when confronted with a novel problem could solve this. A larger percentage was capable of learning through social learning, but some never learned the tasks, again indicating genetic variance to various environmental problems. They explained these results, as successful information needs to be spread rapidly and economically through a population. This can be achieved through genetics but also by environmental factors and social contacts.

8.8 Learned Predator Responses

In this study, it was assumed that the response to the alarmed rat was innate. Conceivably responses would be stronger if the rats were exposed more often to fearful cage-mates and had exposure to various displays of alarm behaviour. For example Ramakrishnan and Coss (2000) found that bonnet macaques recognised a range of calls

but they had to learn to differentiate between various types of alarm calls. Specifically, juvenile animals responded to more non-alarm calls than experienced adults, thus reacted with more false alarm responses. Similar findings were reported in juvenile birds, which flew further and changed position amongst the branches more often compared to adults when exposed to conspecific alarm calls (Rajala, Rätti & Suhonen 2003). Accordingly, there seems to be a behavioural plasticity that allows innate recognition skills to become more finely tuned with experience.

8.9 Environmental Enrichment

In natural habitats animals experience many varied environmental cues - natural environmental enrichment. Laboratory rats in the current study were housed in simple cages; therefore lacking exposure and opportunity to interact with many diverse stimuli. This 'sterile' environment may have resulted in more general fear to the open-field that could have compromised the specific fear response of the target rat to the alarmed animal. For example, environmental enrichment reduces stress in singly housed rats (Belz, Kennell, Czambel, Rubin & Rhodes 2003) reduces open-field inactivity in Japanese Quail (Jones, Mills & Faure, 1991), and less faecal boli are deposited and faster habituation occurs to the open-field test (Larsson Winblad & Mohammed 2002). Additionally, environmental enrichment enhances goal specific searching, thus reducing the need to waste valuable resources on non-directional searching (Larsson et al., 2002). Therefore, lending support that environmental enrichment reduces overall fear thus attention to other more salient stimuli may be possible.

In natural environments, most animals are below maximum bodyweight. Slight food deprivation has been found to be a great motivator that in turn may encourage risk-taking behaviour (Sogard & Bori 1997, Barta 2004). Satiated animals on the other hand are less likely to show risk behaviour (Borge and Lawrence 1998). Since laboratory rats used in this study were not food or water deprived prior to experimentation there is little reason to believe that risk assessment was influenced by nutritional deprivation.

8.10 Possible other species for alarm signalling research.

Even though the results found in the current study were somewhat inconsistent with previous research, it is possible that rats are not an optimum animal for studying alarm signalling between conspecifics. Birds such as Japanese Quail (*Coturnix coturnix japonica*) might be appropriate as they are capable of learning from conspecifics (White, & Galef, 1999) This is especially so when learning involves locating and manipulating food sources (Palameta & Lefebvre, 1985), avoidance learning (Mason 1988) predator recognition calls (Curio 1988) and also cannibalistic behaviour (Cloutier Newberry, Honda & Alldredge 2002) can be socially transmitted

Fish are also capable of learning from alarmed conspecifics that certain odours are noxious. (Suboshi, Bain, Carty, McQuoid, Seelen, & Seifert, 1990; Mathis, Chivers, & Smith 1996). These experienced fish could pass new information onto others. The learning was facilitated by the release of pheromones or alarm signals released by injury to the fish (Wisenden, Vollbrecht & Brown 2004).

Fish and birds either shoal or flock together, i.e., they are allelomimetic rats are not. Allelomimetic animals are conceivably more aware of behaviours emitted by

conspecifics. This may be a reason why alarm signalling is possibly more successful in these species than in rats.

For conservation purposes this not a flaw, since New Zealand lacks native mammals but has many endangered native birds. Therefore, a model using birds may find more conclusive results, which are transferable to endangered species.

8.11 Conclusion.

Male rats exhibited little behavioural differences when paired with a conspecific but females did. The females to a degree reduced their freezing behaviour when paired, but more importantly, they significantly increased their freezing duration when paired with an alarmed animal. The naïve females continued to freeze when exposed to an alarmed rat. It appeared that for males fear of the environment competed with the attractiveness of the conspecific, this was not so evident in the behaviour of the females. Some points rose to improve the opportunity for social transmission of fear between animals these were, reduce environmental fear through possibly environmental enrichment and habituation, allow for genetics, and social exposure between juveniles and adults. Female animals may be better transmitters of fear signals between animals than males. They mainly raise the young who then have the opportunity to learn from their mothers. Even though rats are possibly not the species of choice for this type of research, the notion that animals can learn from each other must not be disregarded. There is ample evidence that animals can and do learn from conspecifics.

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