# Individual strategies of aggressive and non-aggressive male mice in encounters with trained aggressive residents

RENSINA F. BENUS, JAAP M. KOOLHAAS & GEERT A. VAN OORTMERSSEN

*Department of Animal Physiology, University of Groningen, P.O. Box 14, 9750 AA Haren,*
*The Netherlands*

**Abstract.** To determine whether individual differences in offensive behaviour are related to differences in defensive behaviour, the responses of male wild house mice, *Mus domesticus*, of an aggressive and a non-aggressive line to defeat by physically stronger residents were analysed. Individuals of the aggressive line engaged in more flight behaviour, whereas the males of the non-aggressive line predominantly showed immobility. The higher flight tendency of the aggressive intruders provoked more attacks by the resident, resulting in more fighting between the resident and an aggressive male than between the resident and a non-aggressive intruder. However, if offered an opportunity to escape from the home-cage of the resident, aggressive males more readily made use of it than non-aggressive intruders. Differences between aggressive and non-aggressive male mice are interpreted in terms of fundamentally different behavioural strategies adopted in response to social interaction. The response of aggressive males can be characterized as an active behavioural strategy by which they tend to determine actively their social situation. In contrast, the prevailing lack of overt attempts to manipulate the situation by the non-aggressive mice points to passive confrontation, in an offensive as well as in a defensive context.

Males of a variety of rodent species will attack a strange conspecific entering their familiar, home or territorial area (Crowcroft 1966; Archer 1976; Koolhaas et al. 1980). The intensity of attack depends on the attacker's familiarity with the surrounding area (Jones & Nowell 1973; Mink & Adams 1981; Flannelly et al. 1984) and the type of intruder (Alberts & Galef 1973; Archer 1976; Brain et al. 1981; Whalen & Johnson 1987). Individual differences in aggression measured under standardized conditions have most often been ascribed to genetic and/or hormonal differences between individuals (Lagerspetz 1964; Selmanoff et al. 1976; Simon 1979; Van Oortmerssen & Bakker 1981; Hahn & Haber 1982; Albert et al. 1986; Van Oortmerssen et al. 1987; Whalen & Johnson 1987) and are related to various other characters, such as open-field activity, defecation in an open-field, reactivity to a novel environment, maze performance, etc. (Hall & Klein 1942; Lagerspetz 1964; Brain & Nowell 1969; Svare & Leshner 1973; Annen & Fujita 1983; Benus et al. 1987). Surprisingly, very little has been reported on the behaviour of aggressive versus non-aggressive individuals when attacked by a residential male upon intrusion of its terri-

tory, despite the growing tendency to analyse agonistic behaviour in terms of offence and defence (Blanchard & Blanchard 1977; Lehman & Adams 1977; Flannelly et al. 1984).

The study of individual differences in defensive behaviour has been incorporated in only a few studies. Von Holst et al. (1983) described two distinct types of submissive tree shrews, *Tupaia belangeri*, living in the territory of a resident male. One type actively tries to escape from the resident, whilst the other hardly ever responds to its threats and attacks. In addition, in a confrontation between two conspecifics in an unfamiliar cage, physiological parameters suggest that some males respond to social interaction in a predominantly sympathetic adrenal-medullary pattern, whereas others respond with an increase in adrenocortical function. These two types of response resemble the fight–flight and the conservation–withdrawal response, respectively (Cannon 1929; Engel & Schmale 1972; Henry & Stephens 1977). The fight–flight response is a behavioural and neuroendocrine pattern highly suited to either attack or flight (Cannon & La Paz 1911). It contrasts with the conservation–withdrawal response (Engel &

Schmale 1972) which is characterized by release
of adreno-corticotropic hormone, an increase in
adrenal-cortical activity and behavioural inhi-
bition. Selye (1950) saw passive withdrawal as
being connected with defeat and frustration,
whereas the fight–flight response is associated with
increased activity. However, the results obtained by
Von Holst et al. (1983) on male tree shrews indicate
that the same situation (i.e. defeat) can elicit both
types of response, albeit in different individuals.

Thus, during defence animals may either be more
sympathetically or more parasympathetically
dominated. The same distinction has been found in
individual differences in offence. It has long been
recognized that aggression is positively correlated
with sympathetic tone (Guyton 1956; Schwartz et al.
1976; Fokkema et al. 1988). Accordingly, one can
hypothesize that individuals show a consistent
physiological and behavioural differentiation in
response to social interaction. Individuals with a
fight–flight response will be aggressive in their own
territory and have a high flight tendency when
defeated. In contrast, individuals with a conser-
vation–withdrawal pattern will not be aggressive in
their own territory and will withdraw passively,
whenever possible, during defeat. Fokkema's (1985)
study on social behaviour and blood pressure in rats,
*Rattus norvegicus*, partly supports this hypothesis. In
addition to differences in sympathetic tone between
aggressive and non-aggressive male rats, he has
demonstrated a significant positive correlation
between how much aggressive behaviour an individ-
ual shows in a victory test and how much active
defence and flight behaviour it performs during de-
feat. However, since less flight does not necessarily
imply more immobility, and vice versa, a more
detailed description of the behavioural patterns of
aggressive and non-aggressive males during attack
by a residential male is important to test the validity
of a supposed consistent relation between individual
differences in behavioural response during both
offence and defence.

In the present experiments the behavioural
response of individuals of an aggressive and non-
aggressive mouse, *Mus domesticus*, line to defeat
was recorded. During defeat special attention was
paid to flight and immobility, since these two
behavioural elements are considered to represent
the most salient manifestations of an active (fight–
flight) and a passive (conservation–withdrawal)
response, respectively. The latency to escape from
the territory of the resident was also measured,

since we expected the aggressive, active intruder
to escape more readily than the non-aggressive,
passive one.

The data given in parts a, b, c of Fig. 3 and the
data on the duration of immobility bouts given in
Table II have been published in a review article
(Benus et al. 1991).

## METHODS

### Subjects

We used male wild house mice of selection lines
for short and long attack latency (SAL and LAL
mice; Van Oortmerssen & Bakker 1981). The ani-
mals were housed in Plexiglas cages (17 × 11 ×
13 cm) in a room with an artificial 12:12 h light:
dark cycle (dark from 1230 hours). The litters were
weaned at 3–4 weeks of age. At the age of sexual
maturity (6–8 weeks) the animals were paired male–
female. At the age of 14 weeks the males were tested
for their attack latency score. This is the mean time
in three tests between the moment a territorial
mouse meets an opponent and the moment it shows
the first sign of attack, after which the animals are
separated immediately, thus reducing physical con-
tact to an absolute minimum (for details of the
procedure see Van Oortmerssen & Bakker 1981).
Subsequently, the males were used in either the
defeat-test or the escape-test. Residents were
aggressive male mice that had been given numerous
brief confrontations with both unaggressive male
albino mice and young (8–10 weeks old) wild
opponents. It was necessary to train the residents,
because they had to be able to withstand intruders
of the aggressive line. Numerous brief confron-
tations were used, since it is known that terminating
a fight after a short time by removing the opponent
produces a consistent elevation of aggression in
male laboratory mice (Lagerspetz 1961; Leshner &
Nock 1976) and, moreover, such short confron-
tations (ending after two attacks by the resident)
are not too stressful for the opponents. Residents
were always older (mean age 30 weeks), and usually
heavier, than experimental intruders (mean age 16
weeks), which enhanced the likelihood that resi-
dents would defeat the intruders (cf. Lore et al.
1984; Van Oortmerssen et al. 1985).

### Defeat-test

The residents were given at least a week to
become territorial in observation-cages. These
cages were divided into three compartments (A, B
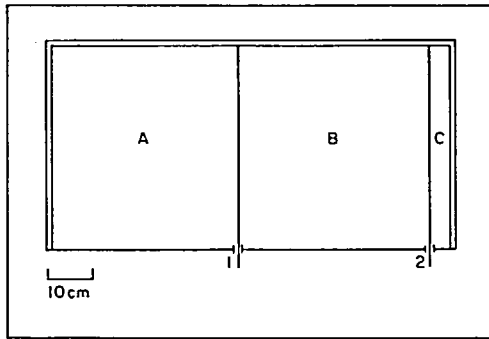and C) by Plexiglas sliding doors 1 and 2 (Fig. 1).

Figure 1. Ground-plan of an observation-cage used in the defeat-test (for explanation see text).

Compartment A (40 × 46 × 40 cm) functioned as the home-cage of the resident and compartment B (40 × 46 × 40 cm) as the border area of the territory. At the time of the experiment (always between 1300 and 1600 hours) the resident was locked up in C (4 × 46 × 40 cm), an opponent was introduced into B, sliding door 2 was opened and the confrontation time started. After 30 s, the behaviour of the intruder was observed for 5 min, after which the animals were separated. However, if an animal was visibly wounded, we terminated the confrontation immediately. During the confrontations we recorded behaviour on a keyboard processor or on tape. The behavioural elements distinguished are listed in Table I. To analyse the behavioural response to defeat, the incidence of the behavioural elements per confrontation and the total percentage of time spent on these elements were determined. To present the data clearly, in this analysis upright, sniffing and locomotion (other than approach and withdrawal) were taken as one behavioural element, i.e. exploration. Attack, chasing, side display and boxing belonged to the behavioural category aggressive behaviour. Only the behaviour of animals that were actually defeated by a resident were included in the analysis. In this way the behaviour of 31 LAL (mean attack latency $\pm$ SE = 448·0 $\pm$ 42·9 s) and 46 SAL (mean attack latency = 21·3 $\pm$ 2·1 s) male intruders was analysed.

## Escape-test

Residents lived in a Plexiglas cage (compartment I and II; Fig. 2). At the time of the confrontation (always between 1300 and 1600 hours) the resident was locked up in I (17 × 11 × 13 cm) and the opponent was introduced into II (38 × 35 × 38 cm). Subsequently sliding door 1 was raised and the confrontation started when the resident entered II, after which the door was lowered again. On days 1 and 2 the confrontation lasted 10 min; on days 3, 4 and 5 an escape opportunity was offered to the intruder. This escape opportunity (III, Fig. 2) was a Plexiglas tube with a diameter of 4·5 cm and a length of 100 cm, leading to the home-cage of the intruder (IV, 34 × 22 × 13 cm). The escape tube was made accessible by raising sliding doors 2 and 3 at the moment of the first attack by the resident. Escape latency was the time between the opening of the escape tube and the entrance of this tube by the intruder. If an intruder failed to escape within 10 min, the resident was locked up in I and the intruder was left in II until it voluntarily entered the escape tube and its home-cage. The experiment was performed with 11 LAL (mean attack latency $\pm$ SE = 600 $\pm$ 0 s) and nine SAL (mean attack latency = 18·8 $\pm$ 5·5 s) male intruders.

## Ethical Considerations

As it would have been impossible to obtain details of defensive behaviour without allowing contact between the animals, we tried to reduce damage during encounters. The escape-test and defeat-test were both needed to be able to determine whether the behaviour of intruders was mainly influenced by the specific circumstances or was indeed part of a behavioural strategy that is generally adopted by the animal. Our original intention was to get data on escape and defeat from one set of experiments, in which days 1 and 2 of the escape-test could be used as the defeat-test. However, a relative lack of offensive behaviour by the residents on these days (possibly owing to the design of the cage) made it impossible to use the data for analysis of behaviour in a defeat situation, because these confrontations did not represent such a situation. As a consequence an additional defeat-test (in different cages) was needed. The confrontations were kept relatively short. On days 1 and 2 of the escape-test encounters lasted 10 min, because of the relative lack of offensive behaviour by the residents. On days 3–5 the duration depended on the escape latency of the intruder, ranging from about 180 s on day 3 to about 20 s on day 5. In the defeat-tests, it became clear that a period of 5·5 min was sufficient to get the information needed. To minimize potential suffering, the duration of the

**Table I.** Behavioural elements distinguished in intruder mice when confronted with a physically stronger resident (after Van Oortmerssen 1971 and Van Zegeren 1980)

| Behaviour | Description |
| --- | --- |
| Fighting | The behaviour shown by each of the contestants when locked together in violent kicking, biting and wrestling behaviour |
| Flight | Rapid movement away from the resident, generally accompanied by squeaks, leaps and sudden changes in direction |
| Submissive upright | Sitting upright, head into the air, forepaws rigidly stretched out forward |
| Immobility | Absence of any movement |
| Approach | Directional locomotion towards the resident |
| Withdrawal | Locomotion directed away from the resident |
| Attack | Rushing and leaping at the resident with kicks and bites |
| Chasing | Chasing a fleeing resident |
| Side display | Approaching the resident in a sideways stance accompanied by intention movements of boxing and biting |
| Boxing | Alternated kicking with the forepaws, combined with intention movements of the body towards the resident, the intruder remaining in its place |
| Tail-rattling | Fast waving movements in the tail, which makes a rattling noise when the tail is held against hard objects |
| Investigation | Sniffing any part of the resident's body |
| Jumping | Jumping up, often to a wall |
| Upright | Standing or sitting on hindlegs, mostly making sniffing movements, with the nose up in the air |
| Sniffing | Standing still with nose in substrate |
| Locomotion | Diagonal and quadrupedal locomotion, no high speed, no apparent direction |
| Grooming | Wiping, licking and nibbling the fur with forepaws and tongue |
| Rest | Any other behavioural element |
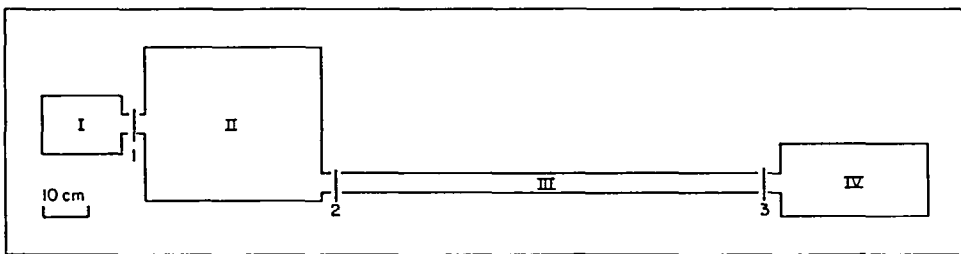


**Figure 2.** Ground-plan of an observation-cage used in the escape-test (for explanation see text).

tests was reduced from 10 to 5·5 min. Whenever an animal was visibly wounded (which was very rare) the confrontation was terminated immediately. Residents were trained fighters, so even SAL intruders could be defeated without excessive fighting. When residents are not trained, SAL males tend to fight back intensively. However, the more aggressive a resident is, the less actual fighting occurs, since the sooner the intruder shows a submissive posture, the sooner the fight is ended. Thus, training of the residents was necessary to minimize the amount of severe fighting. It was possible to train the residents with minimal suffering for the 'target' animals by using young wild or adult albino mice. Since such animals never fight back, the attacks were mild and brief, and wounds were never observed. Training encounters lasted approximately less than 30 s, ending after two attacks by the resident. Each 'target' animal was used only once. In this way, although real physical training was very restricted, it was possible to increase the aggressiveness of the residents substantially. Indications that we managed to minimize suffering are the following observations: (1) no weight loss could be measured the day after the confrontation; (2) the intruder, including 'target' animals, behaved

normally as soon as we put it back in its home-cage; (3) the mean percentage of time spent fighting was 6%, which corresponds to a time of 18 s and most of this time was spent on wrestling/boxing and not biting. Relatively large numbers of animals were used in the defeat-tests, because we used this experiment to investigate other questions (the effect of defeat on subsequent behaviour), thereby reducing the total number of animals used in all experiments.

## Statistics

Data are expressed as $\bar{X}\pm$SE. Differences in behaviour between the various types of intruders were tested using the Mann–Whitney $U$-test. To measure the degree of association between behavioural elements the Spearman rank correlation coefficient was calculated. The $P$-values are two-tailed, unless otherwise stated.

## RESULTS

### Defeat-test

In 16·4% of the confrontations with SAL males the resident was attacked by the intruder and subsequently defeated. None of the LAL males attacked and defeated a resident. SAL males that defeated the resident were omitted from the analysis of the behavioural response to defeat. However, seven SAL intruders took the initiative to attack first, which resulted in a simultaneous attack by both the resident and the intruder, and two showed some aggressive behaviour towards the resident. These nine individuals, which were clearly defeated by the resident, were included in the analysis. Both LAL and SAL intruders were readily attacked by the residents, the attack latencies being $9\cdot4\pm2\cdot8$ s and $7\cdot2\pm1\cdot7$ s, respectively. SAL intruders more frequently engaged in flight behaviour than LAL mice (Fig. 3). Instead, the LAL intruders were more immobile than SAL males, although the frequency of immobility bouts was significantly higher in SAL than in LAL intruders (Fig. 3). There was no difference in the quantity of exploratory behaviour, although SAL males initiated an exploration bout more often than LAL males (Fig. 3). SAL intruders were more frequently attacked, as is indicated by the significantly higher number of fights (Fig. 3), than LAL mice. In addition, the total percentage of time spent on fighting was significantly higher for confrontations with SAL than LAL intruders (Fig. 3).
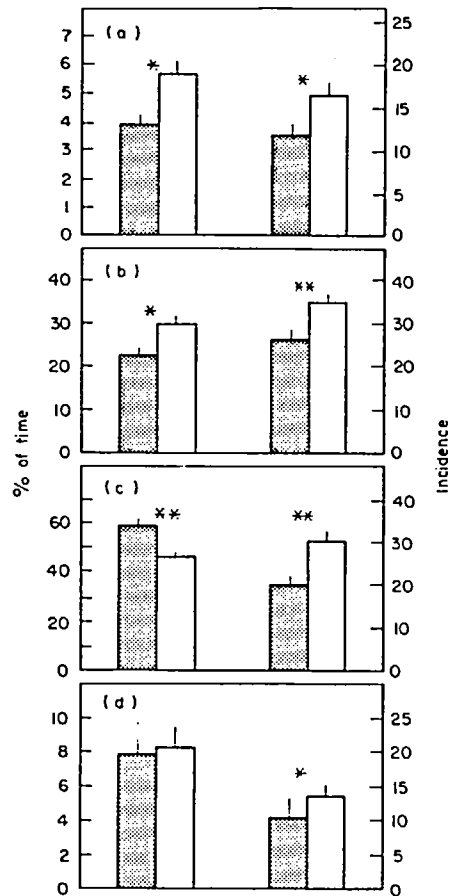


**Figure 3.** Percentage of observation time and frequency per observation period ($\bar{X}\pm$SE) spent (a) fighting, (b) in flight, (c) immobile and (d) exploring by unaggressive or LAL (▨) and aggressive or SAL (□) mice when defeated by a trained fighter. $*P=0\cdot03; **P<0\cdot01$, Mann–Whitney $U$-test.

The mean durations of fight, flight and exploration bouts were remarkably similar for LAL and SAL mice (Table II), but on average an immobility bout lasted more than 5 s longer for LAL than for SAL mice.

LAL intruders jumped less than SAL ones ($0\cdot9\pm0\cdot2$ and $4\cdot8\pm0\cdot9$ times per confrontation, respectively; Mann–Whitney $U$-test: $P<0\cdot01$). The incidence of rattling was $7\cdot5\pm1\cdot0$ for SAL and $4\cdot5\pm1\cdot2$ for LAL mice (Mann–Whitney $U$-test: NS). There was no difference in the amount of submissive upright (LAL: $6\cdot1\pm1\cdot1$ and SAL: $7\cdot2\pm0\cdot8$%). Other behavioural elements, such as aggressive acts, social investigation, approach, withdrawal and grooming, were only rarely observed and took

**Table II.** Duration ($\bar{X}\pm$ SE; s) of fight, flight, immobility and exploration bouts of unaggressive (LAL) and aggressive (SAL) mice in a 5-min confrontation with a trained fighter

|  | LAL | SAL | P* |
|---|---|---|---|
| Fight | 1·1±0·1 | 1·1±0·1 | NS |
| Flight | 2·6±0·1 | 2·6±0·2 | NS |
| Immobility | 11·2±1·3 | 6·1±0·6 | <0·01 |
| Exploration | 2·8±0·7 | 3·2±0·8 | NS |

*Mann–Whitney U-test.

0·5 and 1·0% of the total time in confrontations with LAL and SAL intruders, respectively.

The number of fight and flight bouts were positively correlated, with the correlation coefficient being higher for LAL than SAL males (Fig. 4). The percentage of time spent on fighting and fleeing were also positively correlated (LAL: $r_s = 0.53$, $P < 0.01$; SAL: $r_s = 0.40$, $P < 0.01$). The number of fight and immobility bouts were not significantly correlated (LAL: $r_s = 0.33$; SAL: $r_s = 0.01$), but the percentages of time spent on fighting and immobility were (Fig. 5), with the correlation coefficient being higher for SAL than for LAL mice.

### Escape-test

When, after two defeat-confrontations, the intruder could escape from the territory of the resident, SAL males did so more promptly than LAL mice (Fig. 6), the difference in escape latency being significant on the third day (day 5 of confrontation). On day 3 of a confrontation (first provision with an escape opportunity) two SAL mice did not escape. However, the next day, when they were acquainted with the escape route, they escaped rapidly. All LAL mice used the escape route within 10 min on all test days.

### DISCUSSION

Analysis of the behaviour of male mice during defeat in the home-cage of a strange conspecific revealed crucial differences in defensive behaviour between, previously assessed, aggressive (SAL) and unaggressive (LAL) individuals. SAL intruders engaged in more flight behaviour than LAL mice, whereas the latter were more immobile. In addition, SAL mice escaped more readily from the territory

of the resident than LAL males. These data extend the previous reports that male tree shrews and rats respond to defeat in one of two ways (Von Holst et al. 1983; Fokkema 1985) and support the hypothesis that individuals respond with consistent behavioural differences to social interaction (in offensive as well as in defensive situations), analogous to the fight–flight (active) and the conservation–withdrawal (passive) responses. Because the residents were very aggressive, intruders did not have much opportunity to explore their environment. Therefore, the percentage of exploratory behaviour was low and did not differ for SAL and LAL mice. However, SAL individuals more often initiated an exploration bout than LAL mice, which again indicates their different strategies: SAL mice were more ready to initiate activity than LAL mice.

The active strategy of SAL intruders is expressed not only in their higher flight and escape tendency, but also in their readiness to attack residents. Almost 20% of them attacked the resident and another 20% defeated it. These attacks cannot be considered as retaliatory (and hence as defence), as the intruders took the initiative to attack. Normally, territorial males are not attacked by conspecific intruders (Adams 1976; Thor & Flannelly 1976a). Therefore, the relatively large proportion of SAL intruders that did attack the resident seems to reflect an extreme expression of the fight–flight response in these animals. Also, the highly aggressive residents respond consistently to social interaction. They either fight, when capable of defeating the intruder, or flee, when severely attacked by it. This flight behaviour tends to be very extreme. Such exaggerated flight is seen among SAL males that have failed to defeat less aggressive mice on unfamiliar ground (Van Oortmerssen et al. 1985). The extreme flight behaviour of SAL males is probably also reflected in their larger number of jumps.

The greater propensity of aggressive mice to be active is probably the cause of their shorter escape latencies. Aggressive male rats also escape more readily from the territory of a resident than unaggressive rats, because the latter freeze, which is a passive strategy (Koolhaas et al. 1986). However, the difference in escape latencies between SAL and LAL males is rather small, which may result from LAL males being more attentive to details in the environment (Van Oortmerssen et al. 1985; Benus 1988; Benus et al. 1988). Once they initiate active behaviour they use the escape route more efficiently
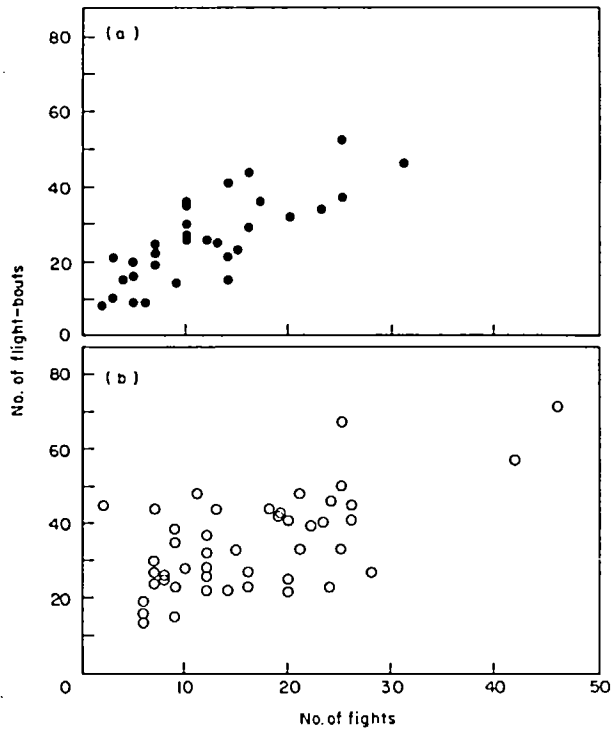
Figure 4. Correlation between the number of fights between a trained fighter and a conspecific male intruder and the number of flight bouts shown by the intruder. (a) Unaggressive or LAL ($\bullet$; $r_s = 0.79$, $P < 0.01$) and (b) aggressive or SAL ($\bigcirc$; $r_s = 0.49$, $P < 0.01$) intruders.

than SAL mice. This idea is strengthened by the fact that some SAL males did not detect the escape route the first time, whereas all LAL mice did.

Although SAL intruders more often initiated attacks towards residents than LAL mice, this fact cannot account for the significant difference in the amount of fighting between resident-SAL male and resident-LAL male confrontations, since still at least 99% of these fights were initiated by the resident. Moreover, the lengths of fight bouts were similar in both types of confrontation, indicating that SAL and LAL mice are equally likely to fight back, once defeated. This leaves us with the question of why residents initiated more fights against SAL than LAL intruders. We need to answer this question to determine whether the difference in response between aggressive and unaggressive mice indeed reflects different strategies, or results from a difference in the intensity of the resident's response. It is known that many characteristics of the intruder, such as previous social experience, dominance status, and age, may

influence the response of the resident (Brain et al. 1981; Lore et al. 1984). However, in our study rearing conditions were similar for all the mice, and, moreover, we measured aggression levels as attack latency scores, thereby avoiding actual fighting. With regard to age, it has been reported that only sexually mature intruders appear to elicit attack by mature males (Thor & Flannelly 1976b), which may be related to the androgen-dependence of the attack-eliciting properties of intruders (Thor & Flannelly 1976a; Adams 1979). The intruders used in the present study were of similar age, but baseline plasma testosterone levels differ between the two lines (with the SAL line having the higher levels; Van Oortmerssen et al. 1987). This may cause a difference in the intensity of the resident's response towards them. However, since SAL and LAL intruders were both attacked quickly and for as long as each other (as indicated by the similar lengths of flight bouts) it is unlikely that the resident's response was influenced by differences in testosterone levels between the two lines. In addition,
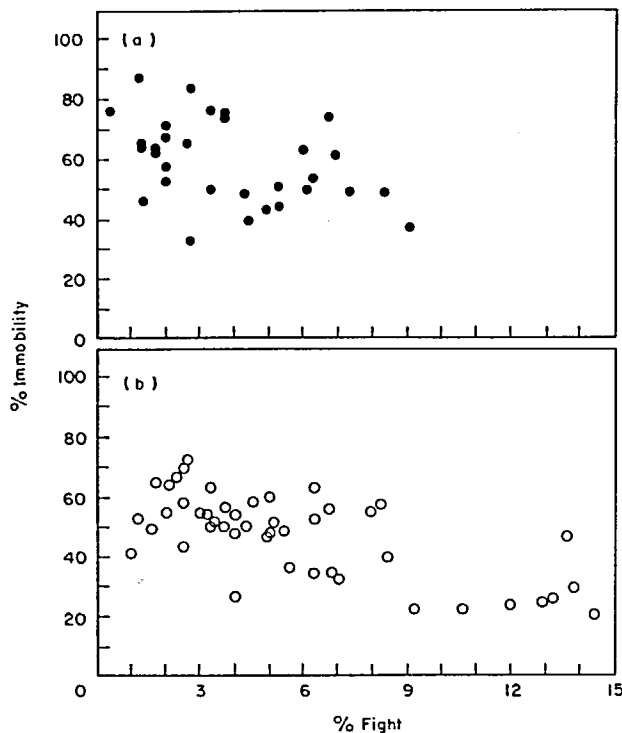
**Figure 5.** Correlation between the percentage of time spent fighting between a trained fighter and a conspecific male intruder and the percentage of time spent immobile by the intruder. (a) Unaggressive or LAL (●; $r_s = -0.45$, $P = 0.01$) and (b) aggressive or SAL (○; $r_s = -0.59$, $P < 0.01$) intruder.

because experienced residents attack even their own female when she is introduced as an opponent (Benus 1988), it is unlikely that they will respond to more subtle differences in stimulus characteristics between male opponents. However, clear differences in mobility between intruders may readily influence the number of attacks by the resident. In house mice attack is triggered by moving objects (Lagerspetz 1964) or the sight of an animal running away (Scott & Fredericson 1951) and rats will bite an intruder attempting to flee (Blanchard et al. 1977; Adams & Boice 1983). In contrast, immobility is an effective inhibitor of attack because of the removal of the facilitatory cues of movement (Alberts & Galef 1973). The positive correlation between fight and flight on the one hand and the negative correlation between fight and immobility on the other support the view that differences in mobility between intruders affect the resident's response. Therefore, we conclude that the difference in the intensity of the resident's response towards aggressive and unaggressive intruders was

caused by the different behavioural strategies adopted by the two types of intruder.

Because of their passive strategy LAL intruders predominantly stayed immobile in response to the resident's presence. However, despite their immobility they were regularly attacked by the resident; a fact that has more commonly been reported for experienced (aggressive) residents (Lagerspetz 1964; Blanchard et al. 1975). Therefore, the flight behaviour of the LAL intruders is probably induced by severe attacks by the experienced resident, since flight remains the major defensive behaviour of a severely attacked animal (Blanchard et al. 1975). The very close association between fight and flight in confrontations with LAL males supports this view. In confrontations with SAL males this association is much looser, indicating that SAL males flee not only in direct response to severe attacks, but also, for instance, in response to the resident approaching. In fact, only the behaviour that is not elicited in direct response to attacks by the resident (i.e. behaviour that is not forced)
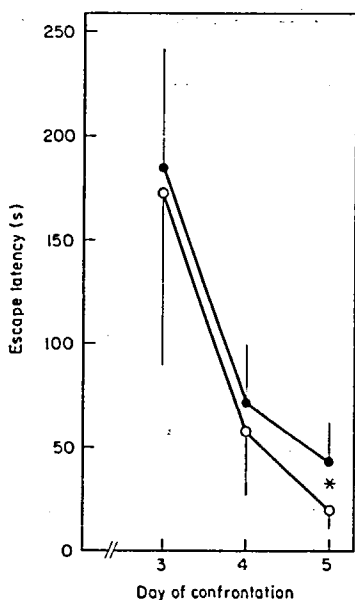
**Figure 6.** Escape latencies ($\bar{X} \pm$ SE) of unaggressive or LAL (●) and aggressive or SAL (○) male intruders when given the opportunity to retreat from the home-cage of a trained fighter on days 3, 4 and 5 of confrontation. On days 1 and 2 the intruders were defeated without having an opportunity to escape. $*P = 0.05$, Mann-Whitney $U$-test, one-tailed.

can be considered as an expression of the behavioural strategy adopted. Therefore, under more natural circumstances the difference between unaggressive and aggressive intruders would probably be even more salient.

The results of this study are thus consistent with the hypothesis that individuals respond in one of two fundamentally different ways to social interaction. These two types of individuals employ a different kind of strategy. One type tends to determine its social situation and hence is aggressive in its own territory and predominantly flees and/or escapes when defeated (i.e. it has an active strategy); the other type endures social interaction and, thus, is non-aggressive and engages in immobility (i.e. it has a passive strategy).

## ACKNOWLEDGMENTS

## REFERENCES

Adams, D. B. 1976. Relation of scent-marking, olfactory investigation, and specific posture in isolation-induced fighting of rats. *Behaviour*, **56**, 286–298.

Adams, D. B. 1979. Brain mechanisms for offense, defense, and submission. *Behavl Brain Sci.*, **2**, 201–241.

Adams, N. & Boice, R. 1983. A longitudinal study of dominance in an outdoor colony of domestic rats. *J. comp. Psychol.*, **97**, 24–33.

Albert, D. J., Wash, M. L. & Gorzalka, B. B. 1986. Testosterone removal in rats resulted in a decrease in social aggression and a loss of social dominance. *Physiol. Behav.*, **36**, 401–407.

Alberts, J. R. & Galef, B. G. 1973. Olfactory cues and movement: stimuli mediating intraspecific aggression in the wild Norway rat. *J. comp. physiol. Psychol.*, **85**, 233–242.

Annen, Y. & Fujita, O. 1983. Intermale aggression in rats selected for emotional reactivity and their reciprocal $F_1$ and $F_2$ hybrids. *Aggress. Behav.*, **10**, 11–19.

Archer, J. 1976. The organization of aggression and fear in vertebrates. In: *Perspective in Ethology. Vol. 2* (Ed. by P. P. G. Bateson & P. H. Klopfer), pp. 231–298. New York: Plenum Press.

Benus, R. F. 1988. Aggression and coping: differences in behavioural strategies between aggressive and non-aggressive male mice. Ph.D. thesis, University of Groningen.

Benus, R. F., Bohus, B., Koolhaas, J. M. & van Oortmerssen, G. A. 1991. Heritable variation for aggression as a reflection of individual coping strategies. *Experientia*, **47**, 1008–1019.

Benus, R. F., Koolhaas, J. M. & van Oortmerssen, G. A. 1987. Individual differences in behavioural reaction to a changing environment in mice and rats. *Behaviour*, **100**, 105–122.

Benus, R. F., Koolhaas, J. M. & van Oortmerssen, G. A. 1988. Aggression and adaptation to the light–dark cycle: role of intrinsic and extrinsic control. *Physiol. Behav.*, **43**, 131–137.

Blanchard, R. J. & Blanchard, D. C. 1977. Aggressive behavior in the rat. *Behav. Biol.*, **21**, 197–224.

Blanchard, R. J., Blanchard, D. C., Takahashi, T. & Kelley, M. J. 1977. Attack and defensive behaviour in the albino rat. *Anim. Behav.*, **25**, 622–634.

Blanchard, R. J., Fukunaga, K., Blanchard, D. C. & Kelley, M. J. 1975. Conspecific aggression in the laboratory rat. *J. comp. physiol. Psychol.*, **89**, 1204–1209.

Brain, P. F., Benton, D., Childs, G. & Parmigiani, S. 1981. The effect of the type of opponent in tests of murine aggression. *Behav. Proc.*, **6**, 319–327.

Brain, P. F. & Nowell, N. W. 1969. Some behavioral and endocrine relationships in adult male laboratory mice subjected to open field and aggression tests. *Physiol. Behav.*, **4**, 945–947.

Cannon, W. B. 1929. *Bodily Changes in Pain, Hunger, Fear and Rage*. New York: Appleton.

Cannon, W. B. & de la Paz, D. 1911. Emotional stimulation of adrenal secretion. *Am. J. Physiol.*, **27**, 64–70.

Crowcroft, P. 1966. *Mice All Over*. London: Foulis.

Engel, G. L. & Schmale, A. H. 1972. Conservation-withdrawal: a primary regulatory process for organismic homeostatis. *Ciba Found. Symp.*, **8**, 57–76.

Flannelly, K. J., Flannelly, L. & Blanchard, R. J. 1984. Adult experience and the expression of aggression: a comparative analysis. In: *Biological Perspectives on Aggression* (Ed. by K. J. Flannelly, R. J. Blanchard & D. C. Blanchard), pp. 207–259. New York: Alan R. Liss.

Fokkema, D. S. 1985. Social behavior and blood pressure: a study of rats. Ph.D. thesis, University of Groningen.

Fokkema, D. S., Smit, K., van der Gugten, J. & Koolhaas, J. M. 1988. A coherent pattern among social behavior, blood pressure, corticosterone and catecholamine measures in individual male rats. *Physiol. Behav.*, **42**, 485–489.

Guyton, A. C. 1956. *Textbook of Medical Physiology*. Philadelphia: W. B. Saunders.

Hahn, M. E. & Haber, S. B. 1982. The inheritance of agonistic behavior in male mice: a diallel analysis. *Aggress. Behav.*, **8**, 19–38.

Hall, C. S. & Klein, S. J. 1942. Individual differences in aggressiveness in rats. *J. comp. Psychol.*, **33**, 371–383.

Henry, J. P. & Stephens, P. M. 1977. *Stress, Health, and the Social Environment: a Sociobiologic Approach to Medicine*. New York: Springer-Verlag.

Jones, R. B. & Nowell, N. W. 1973. The effect of familiar visual and olfactory cues on the aggressive behavior of mice. *Physiol. Behav.*, **10**, 221–223.

Koolhaas, J. M., Fokkema, D. S., Bohus, B. & van Oortmerssen, G. A. 1986. Individual differences in blood pressure, reactivity and behavior of male rats. In: *Biological and Psychological Factors in Cardiovascular Disease* (Ed. by T. H. Schmidt, T. M. Dembroski & G. Blümchen), pp. 517–526. Berlin: Springer-Verlag.

Koolhaas, J. M., Schuurman, T. & Wiepkema, P. R. 1980. The organization of intraspecific agonistic behaviour in the rat. *Prog. Neurobiol.*, **15**, 247–268.

Lagerspetz, K. 1961. Genetic and social causes of aggressive behaviour in mice. *Scand. J. Psychol.*, **2**, 167–173.

Lagerspetz, K. M. J. 1964. Studies on the aggressive behaviour in mice. *Ann. Acad. sci. fenn. B.*, **131**, 1–131.

Lehman, M. N. & Adams, D. B. 1977. A statistical and motivational analysis of the social behaviors of the male laboratory rat. *Behaviour*, **61**, 238–275.

Leshner, A. I. & Nock, B. L. 1976. The effects of experience on agonistic responding: an expectancy theory interpretation. *Behav. Biol.*, **17**, 561–566.

Lore, R., Nikoletseas, M. & Takahashi, L. 1984. Colony aggression in laboratory rats: a review and some recommendations. *Aggress. Behav.*, **10**, 59–71.

Mink, J. W. & Adams, D. B. 1981. Why offense is reduced when rats are tested in a strange cage. *Physiol. Behav.*, **26**, 567–573.

Schwartz, R., Sackler, A. M. & Weltman, A. S. 1976. Some adrenal correlates of aggression in isolated female mice. *Aggress. Behav.*, **2**, 1–9.

Scott, J. P. & Fredericson, E. 1951. The causes of fighting in mice and rats. *Physiol. Zool.*, **24**, 273–309.

Selmanoff, M. K., Maxson, S. C. & Ginsburg, B. E. 1976. Chromosomal determinants of intermale aggressive behavior in inbred mice. *Behav. Genet.*, **6**, 53–69.

Selye, H. 1950. *The Physiology and Pathology of Exposure to Stress*. Montreal: Acta Medica.

Simon, N. G. 1979. The genetics of intermale aggressive behavior in mice: recent research and alternative strategies. *Neurosci. Biobehav. Rev.*, **3**, 97–106.

Svare, B. B. & Leshner, A. I. 1973. Behavioral correlates of intermale aggression and grouping in mice. *J. comp. physiol. Psychol.*, **85**, 203–210.

Thor, D. & Flannelly, K. 1976a. Intruder gonadectomy and elicitation of territorial aggression in the rat. *Physiol. Behav.*, **17**, 725–727.

Thor, D. & Flannelly, K. 1976b. Age of intruder and territorial-elicited aggression in male Long-Evans rats. *Behav. Biol.*, **17**, 237–241.

Van Oortmerssen, G. A. 1971. Biological significance, genetics and evolutionary origin of variability in behaviour within and between inbred strains of mice. *Behaviour*, **38**, 1–92.

Van Oortmerssen, G. A. & Bakker, T. C. M. 1981. Artificial selection for short and long attack latencies in wild *Mus musculus domesticus*. *Behav. Genet.*, **11**, 115–126.

Van Oortmerssen, G. A., Benus, R. F. & Dijk, D. J. 1985. Studies in wild house mice: genotype-environment interactions for attack latency. *Neth. J. Zool.*, **35**, 155–169.

Van Oortmerssen, G. A., Dijk, D. J. & Schuurman, T. 1987. Studies in wild house mice. II. Testosterone and aggression. *Horm. Behav.*, **21**, 139–152.

Van Zegeren, K. 1980. Variation in aggressiveness and the regulation of numbers in house mouse populations. *Neth. J. Zool.*, **30**, 635–770.

Von Holst, D., Fuchs, E. & Stöhr, W. 1983. Physiological changes in male *Tupaia belangeri* under different types of social stress. In: *Biobehavioral Base of Coronary Heart Disease* (Ed. by T. M. Dembroski, T. H. Schmidt & G. Blümchen), pp. 382–390. Basel: Karger.

Whalen, R. E. & Johnson, F. 1987. Individual differences in the attack behavior of male mice: a function of attack stimulus and hormonal state. *Horm. Behav.*, **21**, 223–233.