EXPLORATION, AGGRESSIVE BEHAVIOUR AND DOMINANCE IN PAIR-WISE CONFRONTATIONS OF JUVENILE MALE GREAT TITS

by

MONICA E.M. VERBEEK, ANNE BOON and PIET J. DRENT[1)]
(Centre for Terrestrial Ecology of the Netherlands Institute of Ecology, P.O. Box 40, 6666 ZG Heteren, The Netherlands)

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Summary

In the development of social dominance, constitutional behavioural characteristics may play an important role apart from morphological traits. Previous work has shown that juvenile male great tits *Parus major* differ consistently in their early exploratory behaviour and can be classified as fast and superficial explorers or slow and thorough explorers. This study investigated whether these individual differences in exploratory behaviour are related to aggressive behaviour, and whether this affects dominance. In an experimental set-up, pair-wise fights were observed. The obtained data were corrected for possible influences of morphological traits. Consistent individual differences in aggressive behaviour were found, indicating that juvenile great tits can be characterised by that behaviour. Fast explorers started more fights than slow explorers, and birds that started more fights also won more fights. An additional experiment with pairs of fast and slow explorers confirmed that fast explorers won more fights than slow explorers. In conclusion, we demonstrated that individual differences in exploratory behaviour are related to aggressive behaviour, which affects dominance. The striking agreement of these findings with studies of rodents and pigs is discussed. It is suggested that the behaviour of fast explorers agrees with an active style of coping with stress, while the behaviour of the slow explorers resembles a passive coping style.

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Introduction

Social dominance has important consequences for fitness since it may affect territory acquisition, mating success, reproduction and survival (*e.g.* Arcese & Smith, 1985; Hegner, 1985; Houston & Davies, 1985; Ekman, 1990). In contests, dominance is determined by several asymmetries between the opponents in fighting ability and value of the resource to each over which the fight takes place (Maynard Smith & Parker, 1976). In great tits, fighting ability is affected by body size, weight, age and sex (*e.g.* Garnett, 1981; Drent, 1983; Dhondt & Schillemans, 1983; De Laet, 1985; Sandell & Smith, 1991). The size of the breast stripe of great tits has been proposed to signal fighting ability (Järvi & Bakken, 1984; Järvi *et al.*, 1987; Pöysä, 1988, but see Lemel, 1989; Sandell & Smith, 1991; Wilson, 1992a) and thus to affect the outcome of a fight when contestants lack information about the social status or fighting ability of the opponent (Lemel & Wallin, 1993).

Apart from morphological traits, behavioural characteristics can affect dominance. For example, mice (Oakeshott, 1974; van Oortmerssen *et al.*, 1985; Blanchard *et al.*, 1988) and rats (Fokkema, 1985) show consistent individual differences in their independently measured level of aggression, which are positively related to social rank in a group. These individual differences in aggression extend to other behavioural systems such as exploratory behaviour (Benus *et al.*, 1987). Non-aggressive mice and rats spend a great deal of time on exploration in a novel environment and remain alert to stimuli in a known environment, whereas aggressive individuals spend less time on exploration, and soon lose their attention to details in the environment and rely on their previous experience (van Oortmerssen *et al.*, 1985; Benus *et al.*, 1987, 1990). Similar correlations between exploratory behaviour and aggressive behaviour were found in pigs (Hessing *et al.*, 1994). In open field tests non-aggressive pigs hardly try to escape, and approach a novel object slowly but explore it intensely, spending much time on exploration, whereas aggressive pigs have a tendency to escape a novel environment and approach a novel object fast, but explore it short and superficially.

In great tits, behavioural characteristics may also affect dominance. Hierarchies are already established in flocks of juveniles, which have important consequences for later dominance and territoriality (Drent, 1983). Juvenile male great tits show consistent individual differences in exploratory behaviour (Verbeek *et al.*, 1994). Juveniles that approached a strange object fast and explored a novel environment fast but superficially, had more rigid foraging habits and did not rapidly adjust their behaviour to a change in the feeding situation. On the other hand, juveniles that approached a strange object slowly and explored a novel environment slowly and thoroughly, quickly adjusted their foraging behaviour to an environmental change. The individual differences in exploratory behaviour found in rodents, pigs and juvenile great tits show striking similarities.

The aim of this study was to investigate whether differences in exploratory behaviour are related to aggressive behaviour in great tits, as has been found in rodents and pigs, and whether this affects social dominance. In this study, aggressive behaviour and the outcomes of pair-wise fights were tested between juveniles of which the early exploratory behaviour was known.

Methods

Subjects

In 1990, 1991 and 1992 nestlings of great tits were collected from the wild when they were eight to twelve days old, and hand-reared (for details see Verbeek *et al.*, 1994). We restricted ourselves to males, since agonistic behaviour differs between the sexes during development (Drent, 1983). All underwent the same procedures and experiments.

After hand-rearing (at an age of 4 weeks), the males were housed individually in standard cages of $0.9 \times 0.4 \times 0.5$ m, with solid bottom, top, side and rear walls, a wire-mesh front and two perches. The birds were kept under natural light conditions, and had auditory and visual contact with other individually housed juveniles, but not with the ones they would be confronted with in later dominance measurements. They were provided with food and water *ad libitum*.

When the juveniles were 4 weeks old, we observed their exploratory behaviour for 10 min in a novel environment with five artificial trees. We recorded the time it took a bird to visit all five trees, the number of tree visits, the number of branch hops during a tree visit, and the time a tree visit lasted. Based on the results we classified the birds as fast and superficial, moderate, or slow and thorough explorers. In another exploration test at the age of 9-12 weeks, the time the birds took to approach a strange object that was placed in their own cage was recorded during repeated 2 min trials, and they were classified as fast or slow approachers (for details see Verbeek *et al.*, 1994). Birds that were fast in both tests, or fast in one and moderate in the other, were classified as fast. Birds that were fast in one test and slow in the other, were classified as moderate. Birds that were slow in both tests, or slow in one and moderate in the other, were classified as slow. In 1990, 20 juveniles were used; nine slow, one moderate, and 10 fast explorers were classified. In 1991, 24 individuals were tested, yielding five slow, two moderate, and 17 fast explorers. For the experiment conducted in 1992, we randomly selected 14 fast explorers and 14 slow explorers.

Experiments

When the birds were 12-15 weeks old, we measured the aggressive behaviour and social dominance (expressed in terms of who won) in pair-wise confrontations. During a confrontation the birds could have several interactions in which one bird showed agonistic behaviour towards the other, and the other reacted to that with agonistic behaviour. An interaction began as soon as both birds showed agonistic behaviour, and ended when both birds showed other than agonistic behaviour. All interactions together that are shown during one confrontation are referred to as a fight.

The juveniles were tested in a similar cage as the one in which they were housed. For the test the cage was separated into two compartments of $0.4 \times 0.4 \times 0.5$ m by a wooden slide, with two perches in each compartment. All observations were made between 10:00 and 15:00 hours. An hour before the confrontation, one juvenile was put into each compartment, which allowed adaptation to the environment and entailed deprivation of food and water. The confrontation started by removing the slide. An interaction was won if one bird showed aggressive behaviour and the opponent reacted by fleeing or crouching. As soon as one bird was the obvious winner, that is when he won ten interactions more than his opponent, the confrontation was concluded by reinserting the slide. After the confrontation, the birds were returned to their own cage. Each confrontation lasted for at least 10 interactions and at most 15 minutes. This maximum time limit was introduced to reduce the influence of gained fighting experience on the behaviour in subsequent fights. If the confrontation lasted 15 minutes because there was not an obvious winner or there were less than 10 interactions, the winner was appointed afterwards if that bird won at least two third of the interactions.

In 1990, each bird was individually confronted with three randomly chosen other males. Between confrontations, the birds had one day of rest. Confrontations between the same birds were repeated in random order after one week of rest. In 1991, each bird was confronted with each of five randomly chosen other birds. Each bird had one confrontation each day. In 1992, the hypothesis was tested that exploratory behaviour predicts the outcome of a fight. This hypothesis arose from the results produced in 1990 and 1991. Fourteen pairs, each consisting of a fast and a slow explorer, were confronted with each other once.

The confrontations were observed from behind a one-way screen and recorded on videotape. In viewing these tapes, the behaviour of each bird in each confrontation was analyzed separately during the first two minutes after the first agonistic behaviour exhibited by the bird. Two minutes were chosen to have enough data to describe the behaviour of the birds, without including the whole confrontation since we were only interested in the first interactions, when the relation between the birds was still unclear. The behaviour was recorded continuously using an event recorder according to the definitions described by Blurton Jones (1968).

To assess initial aggressiveness, we used the time spent in the horizontal posture, expressed in percentage of the two minutes during which the behaviour was recorded. In this posture the legs are deeply bent and the body, head and beak form one horizontal line. The eyes are fixed on the opponent, the neck may be stretched towards the opponent, and the wings may be spread sideways. Often the beak is held open and a hissing sound is made. This behaviour is aggressively motivated, and commonly shown in feeding contests between wild first-year great tits when the opponents have little prior experience with each other (Wilson, 1992b). The horizontal posture is quite distinct from other behaviour and thus easy to recognise, and the subjects spent much time on it during the tests. To minimize the influence of the various opponents on the behavioural data of each individual used in the analyses, we used the average percentage of time spent in the horizontal posture by an individual over the different confrontation tests it had. We will refer to this measure as the time in horizontal.

A second measure of aggressiveness was the fraction of the total number of confrontations of each bird, in which it was the first to initiate an interaction showing one of the following behaviours: approach, the head-up posture (aggressive posture with the body upright, the neck and legs stretched and the beak pointed upwards in line with the body, showing the breast stripe to the opponent), the horizontal posture or an attack (approach followed by physical contact, *i.e.* gripping, pecking and/or pulling or biting). We will refer to this measure as the fraction of fights started.

Morphological characteristics

When the nestlings were 15 days old and the tarsus was fully grown (Garnett, 1976), its length was measured to the nearest 0.1 mm using sliding callipers. Preceding the first and following the last confrontation, body mass was measured to the nearest 0.05 g using a laboratory balance, and stage of moult was scored on a scale of 0-10 (0 = no moult, 10 = moult complete) on the basis of the regular sequence of moult in different parts of the plumage. For both body mass and stage of moult, the average of the two measurements was taken. We selected the age of each bird on the day that half of all confrontations it had, had taken place for use in the data analyses. In 1991 and 1992, we also measured the size of the breast stripe after the last confrontation by taking a standard photograph from a fixed distance. The bird was placed on its back on a mm scaled paper. Using a digital image analysis system we measured the area of the stripe to the nearest 0.1 mm^2 between a line perpendicular to the anterior end of the sternum and a parallel line running 57 mm posteriorly.

Data analyses

In 1990 and 1991 only three individuals from the 44 birds tested were classified as moderate. This is not surprising since there is a correlation between the two measures of exploratory behaviour (Verbeek *et al.*, 1994), indicating consistent individual differences in exploratory behaviour. Whether the three birds that showed inconsistency in their exploratory behaviour are a separate class of birds that really differs from the other birds, or whether this classification is due to artifacts, is not clear. However, this number is too small for proper statistical analysis, and we therefore had to omit these cases from our analysis.

In 1990, the three confrontations of each individual were repeated. The data of the second series of fights in 1990 were used only for analysis of the consistency in aggressive behaviour, not for any analysis using data from both 1990 and 1991 in order to have comparable data.

For analysis of the time in horizontal we used linear multiple regression. To obtain a normal distribution, the time in horizontal was arcsin transformed for such regressions (Kleinbaum *et al.*, 1988). We used logistic regression for the analysis of the fraction of fights started and the fraction of fights won. In the analysis of the time in horizontal and the fraction of fights started (both measures of aggressiveness) we included exploratory behaviour, age, tarsus length, weight, stage of moult and breast stripe and their interaction terms due to their possible influence. To test whether trends in aggressive behaviour differed between years, we also included the factor year and all interactions with it. In the analysis of fraction of fights won, we included both measures of aggressiveness in addition to exploratory behaviour, morphological variables and their interactions, and the factor year. Exploratory behaviour was treated as a dummy variable with two categories: fast and slow (Hosmer & Lemeshow, 1989). In the logistic regressions the significance of predictor variables was tested using the change in deviance and degrees of freedom when the variable was dropped from the model (Hosmer & Lemeshow, 1989). In all regression analyses, we followed a stepwise backward procedure (Kleinbaum *et al.*, 1988), after first checking all associations univariately ($\alpha = 0.05$, two-tailed). We present the final models, and some more results where appropriate.

Results

Consistency and coherence in aggressive behaviour

Forty percent of the total recorded time was spent on agonistic behaviour, most of which (30.1%) was in the horizontal posture. Analysis of the

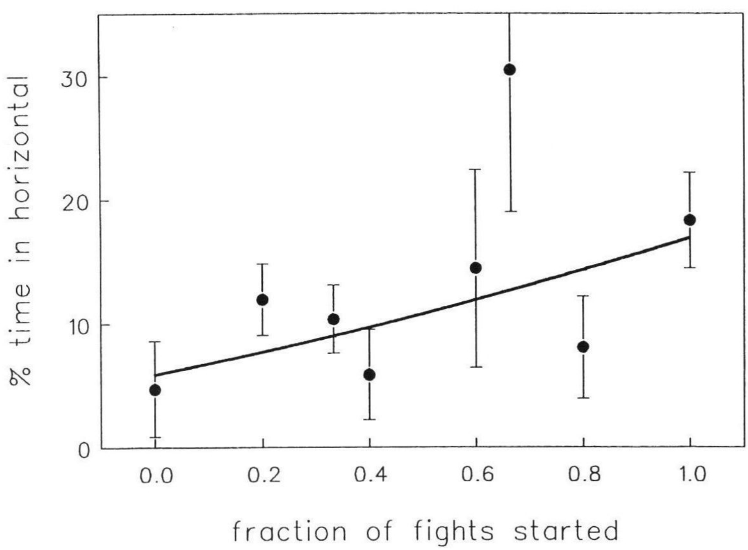

Fig. 1. The percentage of time spent in the horizontal posture (%hor) in relation to the fraction of fights started (fstart). Means and SE for each fraction of fights started are shown. Results of the regression: $\arcsin\sqrt{\%\text{hor}} = 0.25 + 0.1 \times \text{fstart}$; $N = 41$, $R^2 = 0.1$, $p = 0.04$.

repeated contests with the same (randomly chosen) pairs in 1990 showed that the difference in the time in horizontal was significantly higher between juveniles than between the repeated contests of one individual (One-way ANOVA; $N = 60$, df $= 59$, $F = 5.11$, $p < 0.01$). This indicates that the juveniles differed consistently in the time in horizontal. The repeated contests were most frequently initiated (sign test; $N = 30$, $z = 1.77$, $p < 0.04$) and won (sign test; $N = 30$, $z = 3.47$, $p < 0.01$) by the same bird, indicating, once again, consistent behavioural differences between individuals.

A linear regression with the data from 1990 and 1991 showed a positive correlation between the fraction of fights started and the time in horizontal (Fig. 1), which did not differ significantly between the years. This relation indicates coherence in the structure of aggressive behaviour.

Morphology, exploration and aggression

Predictors of the fraction of fights started

The fraction of fights started correlated significantly with exploratory behaviour (Fig. 2). Fast and superficially exploring birds were in confrontations more often the first to show aggressive behaviour than slow and thoroughly exploring birds. This indicates that individual differences in early exploratory behaviour are related to agonistic behaviour. Age, tarsus length, weight, stage of moult or size of breast stripe and their interaction terms were not significantly related to the fraction of fights started, nor was there a significant difference between the years.

Predictors of the time in horizontal

Weight, age and stage of moult were significantly related to the time in horizontal in the final multivariate model. The time in horizontal increased with body mass (Fig. 3a) and age (Fig. 3b), whereas it decreased with stage of moult (Fig. 3c). This means that heavy juveniles spent more time in horizontal than lighter juveniles, older more than younger, and juveniles that had just begun to moult more than juveniles that were about halfway through their moult. The interaction terms of these variables revealed no significant relation to the time in horizontal, indicating that these findings were not the result of correlations between weight, age and stage of moult.

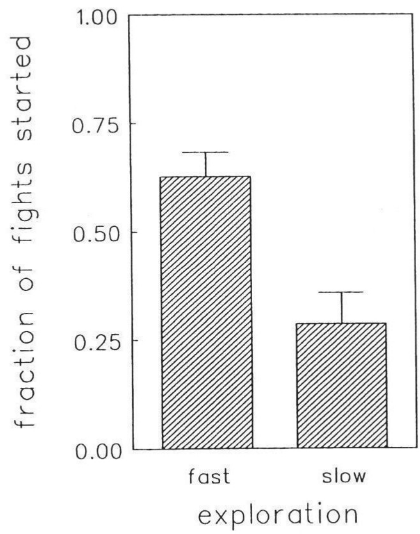

Fig. 2. The fraction of fights started in relation to early exploratory behaviour. Bars represent the mean and SE. The model is expressed as:

$$\text{logit (fraction of fights started)} = 0.52 - 1.51 \times \text{(dummy: slow explorers)};$$

deviance = 66.35, df = 39. Comparison with a model with the intercept only, shows that this model is significant with a $p < 0.01$ (Δdeviance = 18.75, Δdf = 1).

Tarsus length or size of breast stripe were not significantly related to the time in horizontal, nor was there a significant difference between years.

The univariate analysis showed a relation between early exploratory behaviour and the time in horizontal: fast explorers spent more time in horizontal than slow explorers ($t = -2.08$, $p = 0.04$). However, after correction for weight, age and stage of moult, exploratory behaviour was not significantly related to the time in horizontal (although there was a strong tendency: $t = -1.94$, $p = 0.06$) and was therefore not included in the final model (Fig. 3).

Exploration and morphology

Since both exploratory behaviour and morphological traits predict aggressive behaviour, there could be a relation between these factors. The existence of such a relation could also imply that the relation between exploratory behaviour and fraction of fights started was actually caused

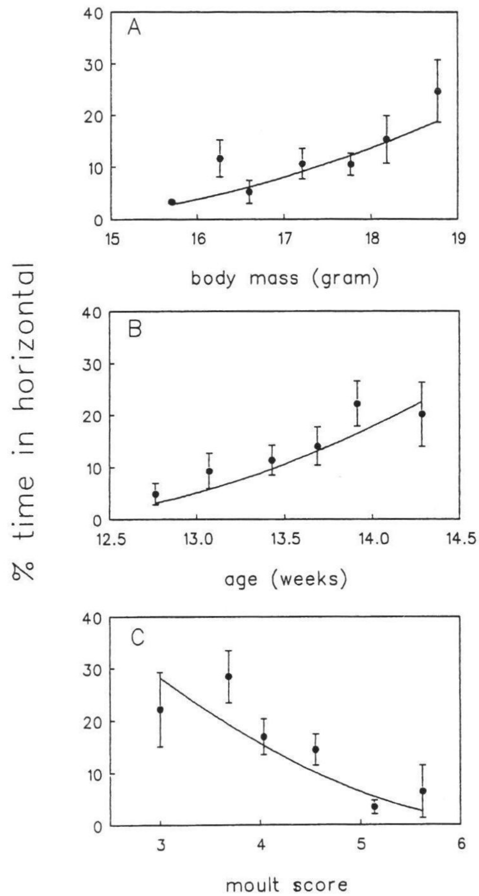

Fig. 3. The percentage of time spent in the horizontal posture (%hor) in relation to body mass (A), age (B), and stage of moult (C), given for a constant average value of the other two parameters. Means and SE are shown over each class of 0.5 gram (A), over each class of 2 days (B), and over each class of 0.5 score of moult (C). The final model is expressed as: $\arcsin\sqrt{\%\text{hor}} = -3.39 + 0.09 \times \text{body mass} + 0.21 \times \text{age} - 0.15 \times \text{moult}$; $N = 41$, $R^2 = 0.26$, $p = 0.01$.

by a morphological trait that was related to both exploratory behaviour and aggressive behaviour. However, a two sample t-test showed that there was no significant difference between fast and slow explorers in weight (mean weight in grams $\pm$ SD: slow explorers: 17.5 ± 1.1; fast explorers: 17.6 ± 0.7; $N = 41$, $p = 0.67$) and tarsus length (mean length in mm $\pm$ SD: slow explorers: 19.9 ± 0.6; fast explorers: 19.9 ± 0.7;

$N = 41$, $p = 0.96$), or size of breast stripe (mean size in $\text{cm}^2 \pm$ SD: slow explorers: 3.08 ± 1.1; fast explorers: 2.91 ± 0.8; $N = 22$, $p = 0.69$). Nor were there significant differences between fast and slow explorers in stage of moult as shown by a Mann Whitney U-test (U-statistic: slow explorers: 200.5; fast explorers: 177.5; $N = 41$, $p = 0.76$) or age (U-statistic: slow explorers: 155.5; fast explorers: 222.5; $N = 41$, $p = 0.36$). Summarizing, there was no relation between exploratory behaviour and any of the morphological traits.

Exploration and dominance

Predictors of chances of winning

Analysis of the fraction of fights won from random opponents showed a significant relation with the two variables representing initial aggressiveness. The fraction of fights won increased with the fraction of fights started (Fig. 4A), and with the time in horizontal (Fig. 4B).

When tested univariately, exploratory behaviour was significantly related to the fraction of fights won; fast and superficially exploring birds won more fights than slow and thoroughly exploring birds (this relation compared with a model with the intercept only: Δdeviance $= 5.41$, Δdf $= 1$, $p = 0.02$). After correction for the fraction of fights started and the time in horizontal, however, the significant relation disappeared (Δdeviance $= 0.73$, Δdf $= 1$, $p = 0.39$). Therefore exploratory behaviour is not included in the final model.

Morphological traits were not significantly related to the fraction of fights won, either when tested univariately or multivariately.

Exploration and winning: an experiment

In the contests between random opponents, fast explorers started more fights than slow explorers, and birds that started more fights also won more fights. Besides, fast explorers won a larger fraction of fights than slow explorers when tested univariately. We expected therefore fast explorers to win from slow explorers in pair-wise fights. We tested this hypothesis in an experiment with 28 birds in which 14 pairs, each consisting of a fast and a slow explorer, had one confrontation. The outcome of the fights was analyzed with a logistic regression, in which we included exploratory

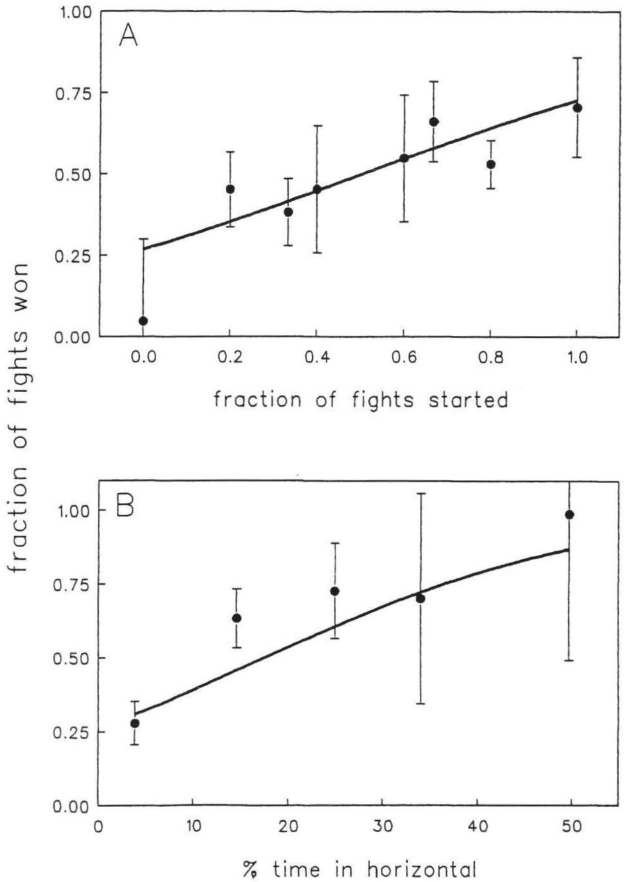

Fig. 4. The fraction of fights won in relation to the fraction of fights started (fstart), and the percentage of time spent in the horizontal posture (%hor), given for a constant average value of the other parameter. Means and SE are shown over each fraction of fights started (A), and over each class of 10 percent time in horizontal (B). The final model is expressed as:

$$\text{logit (fraction of fights won)} = -2.14 + 1.97 \times \text{fstart} + 0.09 \times \%\text{hor};$$

deviance $= 60.18$, df $= 38$. Comparison with a model with the intercept only, shows that this model is significant with a $p < 0.01$ (Δdeviance $= 44.28$, Δdf $= 2$).

behaviour and morphological traits. We did not include both measures of aggressiveness in the analysis; since the birds only fought once, the influence of the opponent on the aggressive behaviour shown was presumed to be large. In the final model only exploratory behaviour is included; none

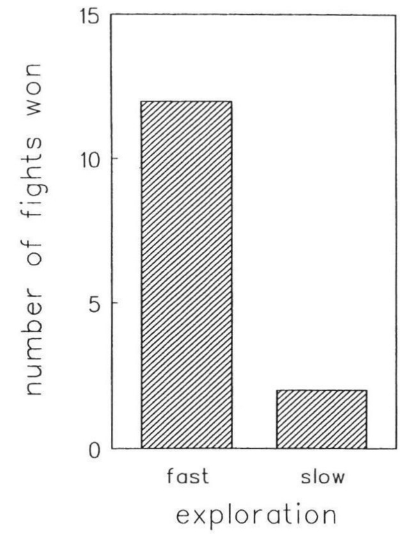

Fig. 5. Fights between pairs, each consisting of a fast and a slow explorer, are significantly more often won by fast explorers than by slow explorers. This result of a logistic regression can also be tested with a χ^2-test: $N = 14$, $\chi^2 = 7.14$, df $= 1$, $p < 0.01$.

of the morphological traits was significantly related to the outcome of the fights. The result of the regression analysis is expressed as:

$$\text{logit (winning)} = 1.79 - 3.58 \times \text{(dummy: slow explorers);}$$

deviance $= 22.97$, df $= 26$. Comparison with a model with the intercept only, reveals that this model is significant with a $p < 0.01$ (Δdeviance $=$ 15.85, Δdf $= 1$). The model shows that, as expected, fast explorers won significantly more fights than slow explorers (see also Fig. 5). We conclude that early exploratory behaviour predicts future dominance in pair-wise fights.

Discussion

Behavioural differences and dominance

Figure 6 shows an overview of our results. We found consistent individual differences in aggressive behaviour, and a positive relation between both measures of initial aggressiveness (A in Fig. 6). This means that juvenile

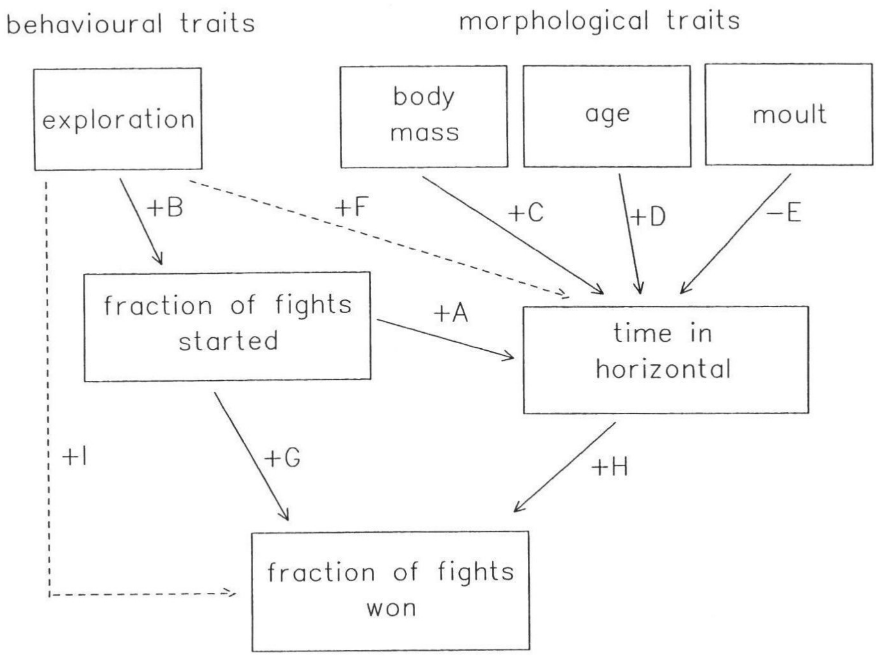

Fig. 6. Summary of the results in a flow diagram. All independent relations we found are indicated with solid arrows. Arrow A refers to the relation shown in Fig. 1, arrow B to Fig. 2, arrows C, D and E to Fig. 3, arrow G and H to Fig. 4, and arrow I to Fig. 5. This latter arrow is dotted, because the relation is not independent from those indicated by arrow B and G. Arrow F is also dotted and not shown in a figure, because the relation is significant when tested univariately, but not any more after correction for body mass (C), age (D) and moult (E). + indicates a positive relation, – a negative. For relations with exploration, + indicates that fast explorers showed a higher value of the related variable than slow explorers.

great tits can be characterised both by their exploratory (Verbeek *et al.*, 1994) and aggressive behaviour.

In the pair-wise contests between randomly chosen birds, fast explorers started more fights (B in Fig. 6), and showed a strong tendency to spend more time in horizontal during the fights (F in Fig. 6). This shows a relation between individual differences in exploratory behaviour and aggressive behaviour, which indicates that individual differences in juvenile great tits are consistent in two different behavioural systems.

The birds that started more fights also won more fights (G in Fig. 6). This suggests that the first blow is half the battle, which has also been shown in several other species (*e.g.* sticklebacks: FitzGerald & Kedney, 1987; evening grosbeaks: Bekoff & Scott, 1989; dark-eyed juncos: Jackson, 1991). The univariate correlation between early exploratory behaviour and the fraction of fights won disappeared after correction for both variables of aggressive behaviour. This is not surprising, since aggressive behaviour at the start of a fight is closer to the outcome, in time and function, than exploratory behaviour measured weeks earlier, and exploratory behaviour and fraction of fights started are correlated. The univariate relation between early exploratory behaviour and fraction of fights won in randomly chosen birds, however, was confirmed by the experiment with selected pairs of fast and slow explorers (I in Fig. 6): fast explorers won from slow explorers. This implies that early behavioural characteristics are important predictors for dominance.

In pigs (Hessing *et al.*, 1994) and rodents (Benus *et al.*, 1987, 1990) aggressive individuals were found to be fast and superficial explorers and non-aggressive individuals were slow and thorough explorers, which strikingly agrees with our findings. Based also on other experiments both Benus (1988) and Hessing (1994) conclude that these differences represent different behavioural strategies, that become particularly overt in stressful situations, like novel environments, fights, inescapable shocks *etc.* Also in other species (*e.g.* dogs: Corson & Corson, 1976; tree shrews: von Holst, 1986; baboons: Sapolsky, 1990) different behavioural and physiological responses to a challenge have been found. In general two strategies to cope with stress have been described: an active or a passive strategy. Active copers show the tendency to actively manipulate the situation that causes stress, whereas passive copers try to adjust to the situation. In the mentioned studies of rodents and pigs, aggressive individuals showed an active coping strategy; their behaviour was aimed at getting away from the source of stress or at removal of the source of stress itself. They initiated fights faster (Benus, 1988) and more often (Hessing *et al.*, 1993), and when defeated they fled more often (Benus, 1988) than passive copers. Non-aggressive individuals showed a passive coping strategy; their behaviour was aimed at adjusting themselves. They did not initiate fights fast or often, and when defeated they showed much immobility.

In juvenile great tits, the early exploratory behaviour and aggressive behaviour in pair-wise fights of the fast explorers seem to agree with an active coping style, while the behaviour of the slow explorers resembles a passive coping style.

Morphology and aggressive behaviour

Body mass, age, and stage of moult (independently of each other) predicted the time in horizontal (C, D, E in Fig. 6), which in turn predicted the fraction of fights won (H in Fig. 6). We did not find a direct relation between body mass, age or stage of moult and the fraction of fights won, although this has been observed by several authors (Kluyver, 1951; Garnett, 1976; Drent, 1983; Järvi & Bakken, 1984; Sandell & Smith, 1991).

The relation between body mass and the time in horizontal (C in Fig. 6) suggests that the positive correlation between social status and body mass found in the field situation is mediated by differences in level of aggressive behaviour.

Developmental differences between the combatants may be underlying the relation between age and time in horizontal (D in Fig. 6). At the time of testing the gonadal system was probably still developing (Balthazart, 1983). This would cause the plasma concentration of testosterone to still be rising to a peak value that is normally reached in September (Röhss & Silverin, 1983), corresponding with an increase in aggressive behaviour in juveniles from June to November (Drent, 1983; De Laet, 1985). It is possible that older juveniles had higher testosterone levels and, therefore, higher levels of aggressive behaviour, expressed in time in horizontal.

The relation between moult and time in horizontal (E in Fig. 6) is probably mediated by levels of thyroid hormone (Huntingford & Turner, 1987). This hormone induces moulting and has a negative influence on the gonadal system, causing a reduction in testosterone and thus in level of aggression (Assenmacher, 1973). This might explain why juveniles that had just started moulting were more aggressive than juveniles that were halfway through the moult. Moulting causes increased vulnerability, making high levels of aggressive behaviour inappropriate (Huntingford & Turner, 1987).

We found no relation between aggressive behaviour or fraction of fights won and the width of the breast stripe, although we expected to corroborate the results of Lemel & Wallin (1993). Great tits show their breast stripes to each other through the head-up posture. On average, of the total time spent on agonistic behaviour, very little was spent in the head-up posture (5.3%). This may indicate that the breast stripe was not an important signal in the context of our experiments. Drent (1983) noticed that juveniles show the head-up posture less frequently before moulting than after moulting. Our (unpublished) recordings of time spent in the head-up posture by juveniles before and after moult confirm this observation (Wilcoxon Matched Pair test: $T = 3$, $N = 8$, $p = 0.04$). It is possible that the breast stripe becomes an important signal only after the first moult, when the male juveniles develop a clear dark stripe.

Processes underlying aggressive behaviour

Since the fraction of fights started was predicted exclusively by early exploratory behaviour (B in Fig. 6, $p < 0.01$), and the time in horizontal mainly by body mass, age, and stage of moult (C, D, E in Fig. 6), this suggests that different processes underlie the two measures of aggressive behaviour. This suggestion is supported by the fact that the relation between both measures of aggressive behaviour was relatively weak (A in Fig. 6). It is possible that at the start of the fight, differences in organisation of behaviour prevail over the behaviour shown. However, during the fight, when the birds communicate with each other through their agonistic behaviour, the influence of the opponent on this behaviour may become more important. The horizontal posture could be a signal to the opponent about the bird's assessment of its own motivation and fighting ability relative to that of his opponent. In that case, the bird's assessment was supported by its physical and developmental condition (body mass, age and stage of moult). Tests with detailed sequential analysis of actions and subsequent reactions of contestants may shed more light on the underlying processes.

The relatively simple way of determining dominance in pair-wise fights did enable us to demonstrate that individual differences in exploratory behaviour are related to aggressive behaviour, which affects dominance. In the wild juvenile dominance relations develop in flocks, which is a more complex situation. Further experiments with aviary groups and measurements in the field are therefore needed.

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