When are females dominant over males in rats (Rattus norvegicus)?

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ORIGINAL ARTICLE

When are females dominant over males in rats (*Rattus norvegicus*)?

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Abstract

In group-living animals, males are assumed to be dominant over females when they are larger than females. Despite this, females have sometimes been proven to be dominant over some males via the winner-loser effect, which becomes stronger when the intensity of aggression in the group is higher. To test whether the winner-loser effect leads to (partial) female dominance in a species with a pronounced sexual dimorphism, we studied the hierarchy in 12 rat colonies (*Rattus norvegicus*) in which the rats could freely interact with their group members within a spacious area. To investigate the underlying mechanisms, we compared the empirical data to hypotheses generated by the agent-based model 'DomWorld'. We show that females dominated on average 55% of the males, and occupied the alpha position in four colonies, in three of them they shared it with one or several males. Moreover, in line with the predictions of the computational model, females dominated a higher percentage of males when the intensity of aggression of the colony was higher. This shows that although females are only half as heavy as males, they dominate part of the males probably through the winner-loser effect. We suggest that this effect may be widespread in many other species and can be tested experimentally.

Significance statement

It is often assumed that males automatically dominate females because males are bigger and stronger than females in many species. However, the present study shows that females can dominate males due to the winner-loser effect. We used an agent-based computational model to generate specific hypotheses that we empirically tested in a large sample of rat colonies. Despite this species having a pronounced male-biased sex dimorphism, some females dominated males – with one female even occupying an unshared alpha position. Such partial female dominance was stronger in colonies with higher intensity of aggression. Here, defeated males may suffer a drastic decrease in their fighting capability and consequently give females more opportunities to surpass them in the hierarchy.

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Introduction

In group-living animals, agonistic interactions often lead to a dominance hierarchy (Drews 1993). Compared to subordinates, dominant individuals have easier access to resources like food, shelter and mates (Bernstein 1981). Several processes have been suggested to lead to the formation of dominance hierarchies, like being larger (Clutton-Brock and Huchard 2013), forming coalitions with kin and other group members (Chapais 1992; Cords and Thompson 2017), and the self-reinforcing effects of winning or losing fights (Chase et al. 2003; Hemelrijk and Wantia 2005; Chase and Seitz 2011). This winner-loser effect implies that, after losing a fight, the loser is more likely to lose again

and, after winning, the winner is more likely to win again. Males are typically assumed to be dominant over females in species with male-biased sexual dimorphism (Smuts 1987; Clutton-Brock 2016), because they are heavier and physically superior. Yet, in these species females have sometimes been shown to be dominant over some males, even though they are physically inferior to males (Chase et al. 2002). This so-called partial female dominance over males has been reported in macaques (Hemelrijk et al. 2008; Surbeck and Hohmann 2013), vervet monkeys (Young et al. 2017; Hemelrijk et al. 2020), capuchin monkeys (Izar et al. 2021), lemurs (Kappeler 1990; von Engelhard et al. 2000), spotted hyenas (Vullioud et al. 2018), and rock hyraxes (Hemelrijk et al. 2022). How the winner-loser effect may be responsible for dominance of females over some males has been shown in the computational model DomWorld (Hemelrijk 1999). The model represents a "world" with individuals that live in a group and fight. DomWorld represents the different winning capability of the sexes by making "male" agents start with a higher initial dominance value than "female" agents, and by making the impact of fights initiated by "males", i.e. the intensity of their aggression higher than initiated by "females" (Hemelrijk et al. 2003). As a result, when males are defeated by other males rather than females, they sink in rank more and thus are more likely to lose again even against females; consequently females may eventually dominate those defeated males (Hemelrijk 1999; Hemelrijk et al. 2003, 2008). In spite of the initially male-biased fighting capability, the model shows that (i) dominance of females over males may emerge via the winner-loser effect; (ii) female dominance over males becomes greater when the intensity of aggression is higher; and (iii) female dominance over males increases with the fraction of males in the group, but only in groups or species with high intensity of aggression (Hemelrijk et al. 2008; Izar et al. 2021). Hemelrijk and co-authors (Hemelrijk et al. 2003) argue that dominance of females over some males increases as a consequence of the intensity of aggression of the group. They show also that a spatial structure arises with dominants in the center and subordinates at the periphery as a consequence of the fleeing by losers, causing them to end up more and more at the periphery of the group. This structure becomes stronger the higher the intensity of aggression is (Hemelrijk et al. 2003).

Hypotheses generated by the model DomWorld have been confirmed in empirical data, mostly in non-human primates (Kappeler 1990; von Engelhard et al. 2000; Hemelrijk et al. 2008; Surbeck and Hohmann 2013). Specifically, females have been shown to be dominant over a higher percentage of males in macaques (i) when the intensity of aggression is higher (Hemelrijk et al. 2008), and (ii) in macaques (Hemelrijk et al. 2008), in vervet monkeys (Hemelrijk et al. 2020) and in capuchin monkeys (Izar et al. 2021) when the percentage of males in the group is larger in the group. Although the

abovementioned hypotheses have been suggested to explain (partial) female dominance over males in some non-human primates based on observational data, it has so far not been studied experimentally. Furthermore, adding taxonomically distant species to the literature is useful to understand how widespread the mechanism is.

Predictions from DomWorld are expected to apply to a broad range of species as long as the species fulfil certain assumptions from the model, such as that the individuals live in groups with a dominance hierarchy, sexual dimorphism is male-biased, aggression is intense with males showing more intense aggression than females, and outcomes of fights are reinforced through the winner-loser effect.

We chose the Norway rat (*Rattus norvegicus*) for several reasons. First, rats meet the assumptions of DomWorld. They form dominance hierarchies (Blanchard et al. 1988; Tamashiro et al. 2007), the size of adult females is less than half of that of the males (Whishaw and Kolb 2005; Suckow et al. 2006), aggression is intense, i.e. potentially leading to wounds, especially among males (Blanchard and Blanchard 1977), and the winner-loser effect has been shown (Lehner et al. 2011). Second, in groups of rats hardly anything is known about intersexual dominance, even though millions of rats are used each year for research and billions are subject to pest control (Schweinfurth 2020). So far, laboratory studies on dominance have focused almost exclusively on males to assess hierarchies (Blanchard et al. 1993, 1995; Macdonald et al. 1995), and even when mixed-sex groups were used, hierarchies have been assessed intrasexually only (Blanchard et al. 1984, 2001). Third, in rats a large sample size can be reached because they are bred and kept in the lab easily, thus, several groups can be tested. Further, we have control over the sex ratio (i.e. the proportion of males), number of individuals per group, size of the housing space, and the spatial distribution of food. We chose wild-derived rats rather than other laboratory strains because wild-derived rats show higher levels of aggression (in frequency and intensity) than domesticated strains like Wistar and their behaviour resembles that of wild rats more than other laboratory strains because they have not been bred for specific purposes like other strains have been (de Boer et al. 2003).

Therefore, we quantified the dominance of female over male rats to our knowledge for the first time, and studied the following predictions from DomWorld: (i) The higher the intensity of aggression of the group is, the higher the percentage of males that females are dominant over, and (ii) the higher the intensity of aggression of the group is, the stronger the spatial centrality of dominants. In addition, we tested in both DomWorld and our rat colonies whether stronger spatial centrality of dominants in the group was associated with higher dominance of females over males. We used 12 mixed-sex colonies with a sex-ratio of four males and four females, housed in a spacious social environment.

We compared these empirical data with predictions from the model DomWorld, which was adjusted to represent both the group composition and the male-biased sexual dimorphism of our rats.

Methods

Computational model: DomWorld

We used the computational model DomWorld (Hemelrijk 1999; Hemelrijk et al. 2008) to investigate which variables are related to the dominance of females over males in rats. DomWorld is a simple agent-based model in which individuals move freely and have only two behavioural rules: aggregate and fight. In DomWorld, if an agent sees no one close by (PersSpace), it searches for others at larger distances (NearView, MaxView). If it detects others in NearView, it keeps moving forward. Otherwise, it looks in MaxView for others, and if so, it moves one step in the direction of the other. If the agent doesn't detect others in MaxView, it turns over a SearchAngle. If it meets another agent in close proximity (Perspace), the agents may fight (see Table 1). Before starting a fight, it assesses its chances to win (this is referred to a "mental battle" (Hemelrijk 2000; Hemelrijk et al. 2017)). If the agent assesses it will win the fight (during its mental battle), it will engage in it, otherwise it will move away. In both the "mental battle"

Table 1 Parameters used in the theoretical model DomWorld for females and males

Parameter	Females	Males
Initial Dominance	16	32
StepDom high	0.1	1
StepDom medium	0.055	0.55
StepDom low	0.01	0.1
Number of mental battles	1	
Field of View	120	
PersSpace	4	
NearView	24	
MaxView	48	
FleeDist	2	
WithdrawDist	0	
ChaseDist	1	
MoveDist	1	
WiggleTurn	0	
WiggleTurnError	10	
SearchTurn	90	
SearchTurnError	10	
WonTurn	0	
WonTurnError	0	

and the actual battle, the chance to win is greater when the individual's dominance value (DOM-value) is relatively larger than that of its opponent. When the outcome of the fight has been decided, the winner chases the loser (Chase-Dist), the loser flees (FleeDist), and the dominance values are updated, i.e., the value of the winner increases and that of the loser decreases by the same amount. Sexual dimorphism is represented by the initial dominance value and the intensity of aggression (StepDom). They are set higher in male-agents than female-agents. We examined three levels of intensity of aggression, namely high, medium, and low (see Table 1) and conducted 120 runs for each. In our analysis we omitted the transient data by analysing data for the stable phase, from period 240 to 260. For more information on the model see Hemelrijk (1999), and Hemelrijk et al. (2008).

Empirical data: Subjects and experimental procedure

We used 48 male and 48 female wild-type Norway rats (*Rattus norvegicus*), bred at the animal facility of the Groningen Institute of Life Sciences in the Netherlands. Females were sterilized on day 28 by surgical oviduct ligation to avoid pregnancy while maintaining their oestrous cycles. At approximately four months of age, i.e. when all individuals had reached sexual maturity (Suckow et al. 2006), the animals were first housed in standard cages ($58 \times 35 \times 20$ cm) in same-sex groups of three or four animals, for three weeks. Subsequently, they were housed for one week in male–female pairs to get sexual experience. After this, animals were placed in colonies during the experiment (see details below), lasting ten days. At the onset of the experiment, males weighed on average almost twice as much as the females (average weight of males: 449.9 g, SD: 42.96; average weight of females: 234.5 g, SD: 17.79, see Fig. S1). Throughout the entire study period, the animals received standard chow and water ad libitum. They were kept at a 12-h reversed light/dark period with lights off at 5:00AM. The temperature was 21 °C $\pm$ 2° with a humidity of 50% $\pm$ 5%.

To identify the rats individually, they were treated with hair dye (Garnier Olia Super Blond B + +). For this, rats were anesthetised by a 30-min induction to isoflurane. The marking was done seven days before the beginning of the experiment to avoid any behavioural changes due to the process. To monitor their health, their body weight was recorded daily before and after the experiment. During the ten days of the experiment, body weight was recorded on days 0 (baseline, the day before the start of the experiment), 2, 5, 8 and 10.

Visible burrow system

During the experiment, the social behaviour of rats was observed when they were housed in colonies. They were housed in an adaptation of the Visible Burrow System (hereafter called VBS) (Blanchard et al. 1995; Herman and Tamashiro 2017). The VBS is a housing system that partially resembles the living conditions of rodents in nature (Blanchard et al. 2001). It facilitates the assessment of dominance hierarchies of animals in groups because we observe dyadic fights that can be affected by bystanders (Chase et al. 2003). Furthermore, the assessment of dominance hierarchies in groups of freely moving animals is proven to be more reliable than testing dyads in social isolation (Lindzey et al. 1966; Howells and Kise 1974; Benton et al. 1980; Stricklin et al. 1985; Chase et al. 2003).

The VBS consists of an open arena and a burrow (Fig. 1). The open arena ($90 \times 100 \times 100$ cm) was illuminated by LED lights on its walls (at a height of 80 cm) for 12 h a day (lights on at 5:00PM). The open arena was connected to the burrow ($50 \times 100 \times 25$ cm) through two round openings of 7 cm diameter. The burrow contained a tunnel system leading to four nest boxes, i.e., two small ones in the middle of the burrow ($15 \times 15 \times 18$ cm) and two larger ones at the outer sides ($25 \times 15 \times 18$ cm). The walls and floors were made of grey 5 mm thick PVC. The burrow was covered with a black Plexiglas lid (Perspex 96IR; Talboom, Breda, the Netherlands), enabling infrared video recording, but keeping the burrow dark for the rats. Two water bottles were mounted to one of the walls of the arena and a third bottle next to one of the nest boxes in the burrow (see Fig. 1A). Standard chew was distributed on the floor of the open arena and the nests once every other day, to avoid food depletion.

Animals were housed in the VBS in colonies of eight animals, i.e., four males and four females, for ten days. In four VBS's, we tested sequentially three batches of four colonies each. Males as well as females were matched in weight intrasexually as closely as possible, for each colony. Rats within a colony were unfamiliar with each other prior to the start of the experiment. Digital monochrome GigE cameras with infrared vision (Basler acA 1300-60mNIR) were used to monitor the colonies 24/7.

Behavioural measurements

Observations in the VBS were done with The Observer® XT v.14 (Noldus Information Technology, Wageningen, the Netherlands) and were based on an ethogram of agonistic acts (Table 2). For each agonistic act, we scored its frequency, the interaction partner, and whether it happened in the open arena or the burrow. Blind scoring was not possible in our experiment because we need the individual identities to determine hierarchies. We determined the loser of a fight as the one who moved away from the opponent, and the winner as the one who showed offensive acts and caused the opponent to move away. We classified agonistic acts as "intense" when they involved potential or actual physical damage (attack jump and clinch attack; see Table 2) and as "mild" when they did not involve potential or actual physical damage (all acts other than those classified as "intense"; see Table 2) (Kemble et al. 1993; Miczek et al. 2001). Data were collected on days 1 and 2 because dominance hierarchies in rats are formed during the first two days in a colony (Blanchard et al. 1985), and on days 5 and 10 to check for stabilization of the hierarchy in the middle and the end of the experiment (see Table S2, Fig. S3). During each day of observation, we scored behaviour for 10 min at seven time points (when animals showed the highest peaks of activity), which means six during the dark phase and one just after the light phase started.

Fig. 1 Top view of the Visible Burrow System, schema (**A**) and photo (**B**), used for the experimental period. The system consists of two major compartments: An open arena and a closed burrow which comprises a tunnel system with four nest boxes (two small and two large). The arena has a reversed day-night photoperiod, and the burrow is always completely dark. Rats move freely between the open arena and the burrow.
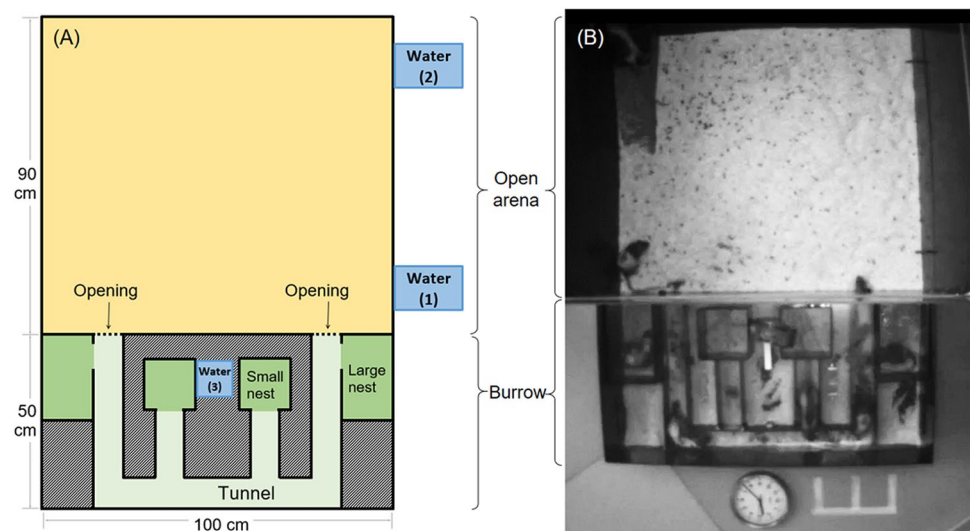
Table 2 Description of behaviour observed in rat colonies

BEHAVIOUR	DESCRIPTION
OFFENSIVE	Aggressive behaviour directed towards a conspecific, including sideways (lateral) threat, upright posture, attack jump, clinch attack, and chase.
DEFENSIVE	Defensive or submissive display directed to a conspecific in response to being aggressed, including upright posture, move away, run away, keep down posture (submissive-supine posture or "pinning"), and freezing.

PATROLLING
(offensive)
During a confrontation with a tunnel-guarding animal (see below), the attacker moves laterally against the wall adjacent to the tunnel entrance with an arched back, similar to the lateral threat.

TUNNEL GUARDING
(defensive)
A rat remains inside one of the tunnels, oriented toward its entrance to the surface of the open arena, and in close proximity (within 2cm) to the tunnel entrance.
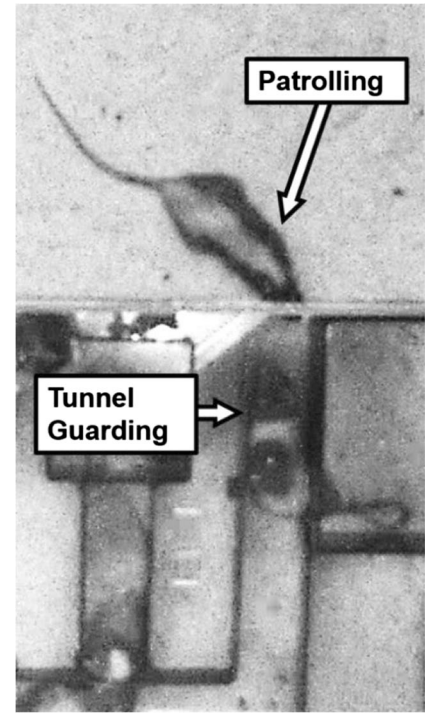
Measures of the dominance hierarchy

We determined the rank order of individuals in the dominance hierarchy by the Average Dominance Index, and the degree of dominance of females over males by the Female Dominance Index. The centrality of dominants and the intensity of aggression of the colony were also calculated. We describe these measures below.

Average Dominance Index. To determine the dominance hierarchy, the frequency of decided fights (i.e., fights leading to a clear winner and loser) of each individual against all colony members were organised in square matrices. Dominance hierarchies were inferred from the Average Dominance Index (Hemelrijk et al. 2005), which is the average proportion with which an individual wins from all its opponents, thus excluding colony members with whom the individual did not interact. According to this, high-ranking individuals won a higher average proportion of fights against opponents than low-ranking individuals. We used the Average Dominance Index instead of other ranking methods like David's score or the so-called I&SI because the Average Dominance Index is mathematically simpler than the David's score, but

equally efficient to assess dominance order of individuals in hierarchies (Hemelrijk et al. 2005; Saccà et al. 2022) and, further, both methods reproduce the dominance order more precisely than the I&SI (Hemelrijk et al. 2005).

Female Dominance Index. We calculated the degree of dominance of females over males in a colony using the Female Dominance Index (Hemelrijk et al. 2008, 2020). It is the proportion of males over which females are dominant on average.

Centrality of dominants. We calculated the degree of centrality of dominants in the model DomWorld per run by correlating the individual's rank computed as the Average Dominance Index and the average spatial distance from the individual to others (Hemelrijk et al. 2003; Puga-Gonzalez et al. 2009), both taken as an average over period 240 to 260. We expected the distance from an individual to others to be shorter, the higher the rank of the individual. Regarding the experimental data, previous research in rodents has shown that dominants remain more time in the open arena of the Visible Burrow System than subordinates (Blanchard et al. 1995). As a measure of the centrality of individuals, we used the proportion of time spent in the open arena of the VBS, and we correlated it with the individual rank.

Intensity of aggression of the colony. In the model Dom-World, three levels of intensity of aggression were distinguished: high, medium, and low (see Table 1). In our colonies of rats, we classified per agonistic act the intensity of aggression as either high or low. The intensity of aggression of the whole colony was represented by the proportion of agonistic acts of high intensity from all agonistic acts.

Statistical analysis

Statistical analyses were performed using R (v. 4.2.2) with the packages "lme4" (Bates et al. 2015), "dplyr" (Wickman et al. 2021), and "ggplot2" (Wickham 2016), and the MatrixTester add-in for Excel (v3.0.1; CKH, available on request) to calculate the Average Dominance Index and the Female Dominance Index. A probability level of $p \leq 0.05$ was considered significant. For the empirical data, non-parametric tests were used because the data were not normally distributed.

For the statistical analyses of the data from the Dom-World simulations, we used a one-way ANOVA with a Tukey post-hoc test to check for differences in the Female Dominance Index (FDI) values, as well as for differences in the degree of centrality of dominants, between the levels of intensity of aggression in the colony. For the relation between female dominance index and centrality across the levels of intensity of aggression in the colony, we used a generalized linear mixed model (GLMM), assuming a negative binomial distribution for the female dominance index (zero-inflated).

For the statistical analysis of the empirical data, Kendall rank correlation tests were used (bootstrapped 1,000 times)

to test the correlation between (i) female dominance index and intensity of aggression of the colony, (ii) female dominance index and centrality of dominants, and (iii) centrality of dominants and intensity of aggression of the colony. We used Kendall because our sample size is small, and data are not normally distributed.

Results

Female dominance over males in colonies of rats

Despite males being almost twice as heavy as females (Fig. S1), females were dominant over 13% to 75% of the males. On average females dominated 55% of the males (the average value of the Female Dominance Index was 0.55, SD = 0.17; median = 0.58). In one colony, a female occupied the alpha position solitarily, in three colonies she shared the alpha position with at least one male, and in eight colonies she ranked directly below the alpha male (see Fig. 2).

Testing hypotheses from DomWorld in rat colonies

In DomWorld, the degree of female dominance over males was greater, the higher the intensity of aggression of the colony was (one-way ANOVA: $F_{2, 357} = 55.76$, $p < 0.001$; Fig. 3a). We confirmed this prediction in our rat colonies, as the female dominance index was positively correlated with the intensity of aggression of the colony (Kendall rank correlation: $r_\tau = 0.54$, $p = 0.008$; Fig. 3b). Studying each sex separately shows that the intensity of male attacks is more strongly related to the female dominance index than that of attacks by females is, however, the correlations are statistically significant for both sexes (Kendall rank correlation,

Fig. 2 Schematic representation of the dominance hierarchy in 12 colonies of rats. The hierarchy was calculated based on the Average Dominance Index (ADI) of members of both sexes. Female Dominance Index (FDI) values are shown; males in black squares, females in red circles; the alpha position is highlighted by a bold border
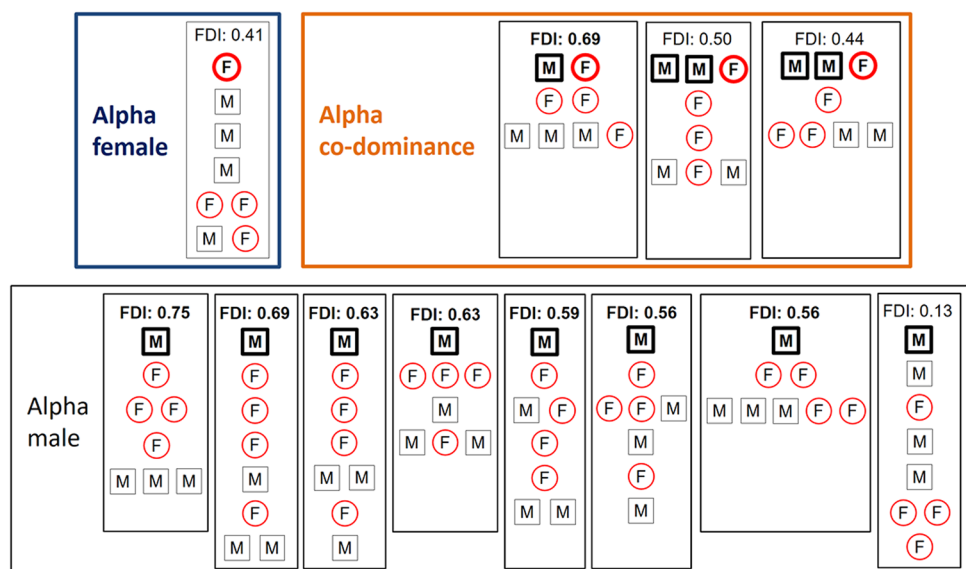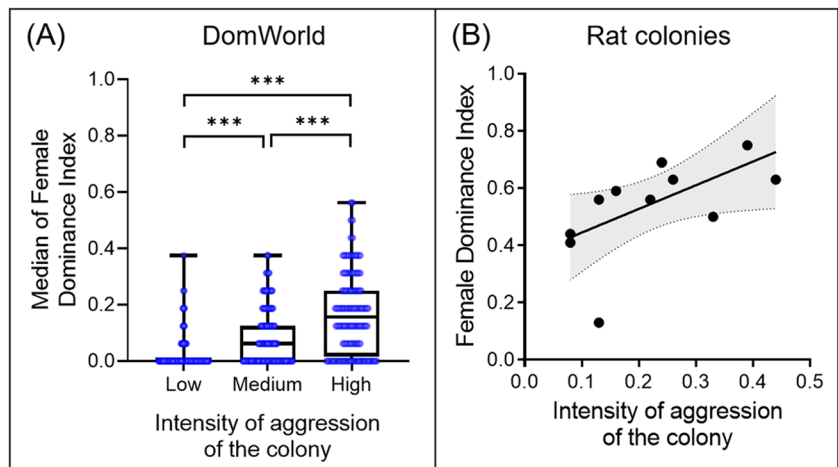
Fig. 3 Relation between the female dominance index and the intensity of aggression of a colony. The relation between the Female Dominance Index (FDI) and the intensity of aggression of the colony is shown for the model DomWorld (**A**) and the rat colonies (**B**). The boxplot shows the median, quartiles and maximum and minimum values, and brackets in the boxplot indicate post-hoc analysis (*** $p < 0.001$). The trendline in the scatterplot shows the best-fitting straight line, and the grey band shows 95% confidence interval

males: $r_\tau = 0.45$, $p = 0.023$; females: $r_\tau = 0.38$, $p = 0.048$; Fig. S4).

Second, there was neither an association between the centrality of dominants and the intensity of aggression in a group in the model (one-way ANOVA: $F_{2, 357} = 2.95$, $p = 0.054$; Fig. 4a), nor in the rat colonies (Kendall rank correlation: $r_\tau = 0.219$, $p = 0.166$; Fig. 4b).

In DomWorld for low, medium and high intensity of aggression, the relation between the female dominance index and the spatial centrality of dominants was nonsignificant (Generalised Linear Mixed Model: $\beta = 0.080 \pm 0.52$, $p = 0.88$; Fig. 5a). In the empirical data, however, the female dominance index and the centrality of dominants were positively correlated in colonies where intensity of aggression was high (Kendall rank correlation: $r_\tau = 1.00$, $p < 0.001$), but was correlated neither in the ones with low (Kendall rank correlation: $r_\tau = 0.40$, $p = 0.16$) nor in those with medium aggression intensity (Kendall rank correlation: $r_\tau = 0.18$, $p = 0.36$). When analysing all the 12 rat colonies together,

the female dominance index and the spatial centrality of dominants were positively correlated (Kendall rank correlation: $r_\tau = 0.50$, $p = 0.015$; Fig. 5b). A schematic summary of all findings is shown in Fig. 6.

Discussion

Despite female rats being half the size of males, they dominated on average 55% of the males in our 12 colonies. In one colony a female even took up the unshared alpha position, and in three other colonies females shared the alpha position with one or several males. In line with the predictions of the computational model DomWorld, females dominated a higher percentage of males when the intensity of aggression of the colony was higher. This suggests that more intense fights increase the chance that defeated males sink lower in the hierarchy than the anatomically smaller females. The degree of spatial centrality of dominants did

Fig. 4 Relation between the spatial centrality of dominants and the intensity of aggression of a colony. The relation between the spatial centrality of dominants and the intensity of aggression of the colony is shown for the model DomWorld (**A**) and the rat colonies (**B**). The boxplot shows the median, quartiles and maximum and minimum values, and brackets in the boxplot indicate post-hoc analysis (NS = non-significant). The trendline in the scatterplot shows the best-fitting straight line, and the grey band shows 95% confidence interval
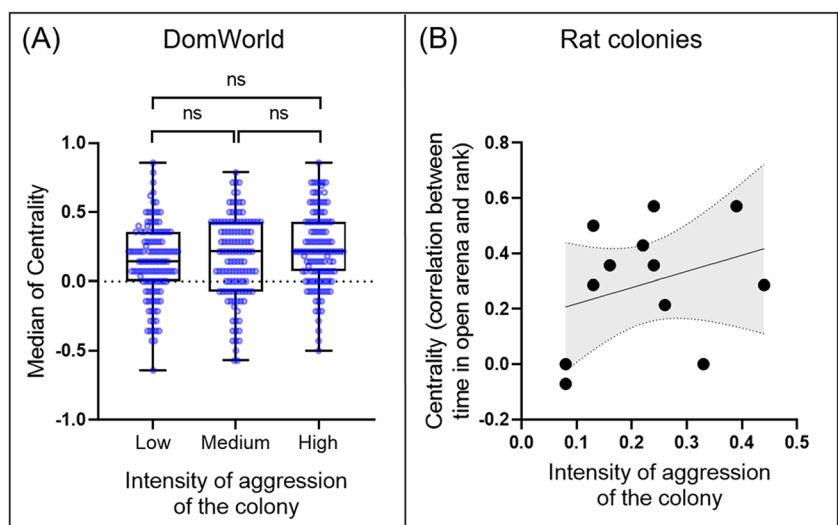
Fig. 5 Relation between the female dominance index and the spatial centrality of dominants. The relation between the Female Dominance Index (FDI) and the centrality of dominants is shown for the model Dom-World (**A**) and the rat colonies (**B**). The trendlines show the best-fitting straight line, and the grey bands show 95% confidence interval
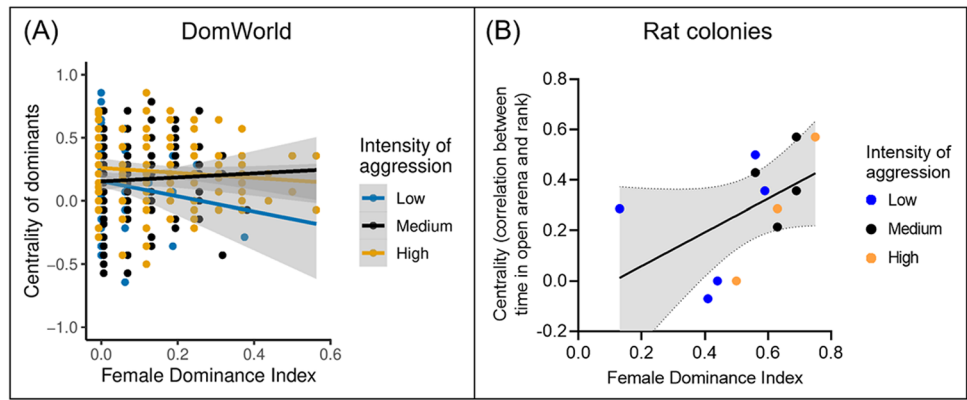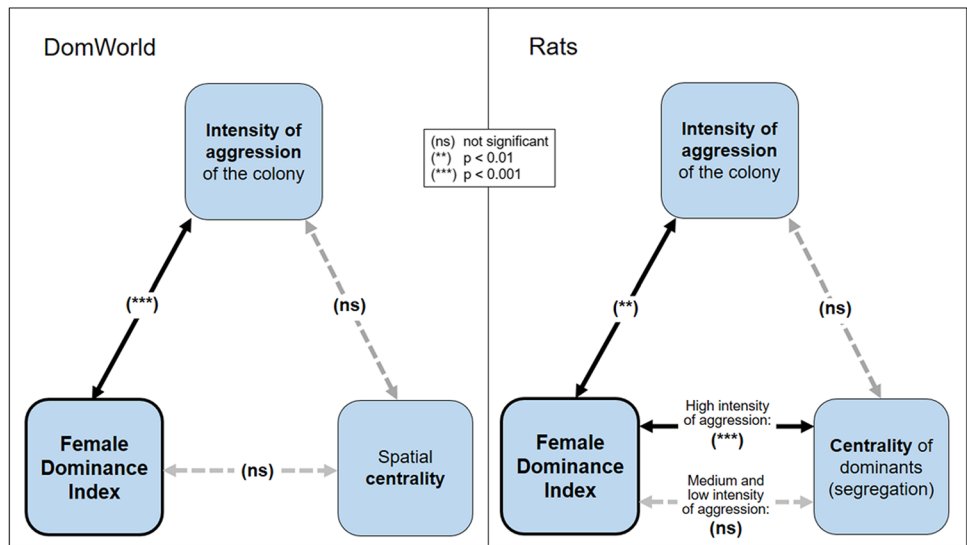

Fig. 6 Schematic results from the model DomWorld and the rat colonies

not correlate with the intensity of aggression, neither in groups in DomWorld nor in our colonies of rats. Finally, in rat colonies with stronger spatial centrality of dominants (i.e., when dominants spent more time in the open arena), females dominated a higher percentage of males, however DomWorld did not show such a relation.

The sexual dimorphism of rats in this study is similar to that reported in wild colonies (Calhoun 1962; Barnett 1976), suggesting that males are physically superior to females. Despite this, females dominated part of the males in all colonies, indicating that dominance status cannot be predicted by body size only (Wright et al. 2020). The presence of alpha females in rat colonies has been reported before in a few studies (Blanchard et al. 1984; Ziporyn and McClintock 1991), but without quantifying the average degree of dominance of females over males. Here we do so for wild Norway rats for the first time to our knowledge.

To investigate what processes underlie female dominance over males in rats, we tested hypotheses from DomWorld in our empirical data. Partial female dominance was correlated

with the intensity of aggression of the colony, meaning that in colonies with more intense fights, females dominated on average a higher percentage of males. In DomWorld, the superior fighting capacity of males versus females is represented by a higher initial dominance value (Hemelrijk et al. 2003) and a higher intensity of aggression of males (represented by a higher value for the scaling factor StepDom, see Methods) than females. Consequently, the impact of interactions initiated by a male is greater than that by a female besides, at a high intensity of aggression, the impact of the outcome of each interaction is larger and the hierarchy is differentiated more strongly than at low intensity (Hemelrijk et al. 2017). Therefore, defeated males suffer a drastic decrease in their fighting capability, giving females more opportunities to surpass them in the hierarchy. Whereas in colonies with less intense aggression, winning or losing a fight has less impact on the fighting capability of individuals, leading to fewer changes in the hierarchy and, thus, resulting in fewer opportunities for females to dominate males. The strong, positive correlation between the Female Dominance

Index and the intensity of aggression of the colony in our rats confirms DomWorld's hypothesis, and is also found in primate species like macaques (Hemelrijk et al. 2008), vervet monkeys (Young et al. 2017; Hemelrijk et al. 2020), capuchin monkeys (Izar et al. 2021), and lemurs (Kappeler 1990; von Engelhard et al. 2000).

Because defeated individuals flee from winners after a fight and all individuals want to group, a spatial structure emerges with dominants in the centre of a colony and subordinates at the periphery. We investigated whether a stronger spatial centrality of dominants is associated with both a greater intensity of aggression of the colony, and a larger degree of female dominance over males. First, our results revealed no association between spatial centrality of dominants and the intensity of aggression of a colony. This contradicts previous studies in DomWorld (Hemelrijk 1999; Puga-Gonzalez et al. 2009) where the degree of centrality of dominants was higher when the aggression was more intense. This discrepancy occurs because dominance was previously measured by the "internal" dominance values (DOM-value) (Hemelrijk 1999), whereas we based it on the outcome of fights (with the Average Dominance Index).

Second, DomWorld showed that females were not dominant over more males when the degree of centrality of dominants was greater, but in our colonies of rats this correlation was significant (i.e., female dominance over males was higher when dominants remained longer in the open arena). However, this correlation in our rat colonies may be mainly driven by three colonies with the highest intensity of aggression (see Fig. 5b). Only these three colonies showed a significantly positive correlation whereas colonies with lower intensity of aggression show nonsignificant results when analysed separately. Furthermore, a more detailed analysis revealed that higher ranked males stayed longer in the open arena than lower ranked males, but this relation is not seen in females (see Fig. S5). This may be a consequence of males attacking more often males than females (see Fig. S6A), and the intensity of attacks being higher in males than females (see Fig. S7), making lower-ranking males stay in the burrow for longer after being defeated, possibly looking for protection from higher-ranking males.

Future empirical studies are needed to detect whether the degree of female dominance over males is higher when the proportion of males in the group is larger. According to DomWorld, in groups with high intensity of aggression, a larger proportion of males increases the frequency of male-male fights (Hemelrijk et al. 2008). This increases the chance that males are defeated by other males, and subsequently the chance for females to beat males and become dominant over them. The association between proportion of males and female dominance over them has been confirmed also in some species of macaques (Hemelrijk et al. 2008), in vervet monkeys (Hemelrijk et al. 2020), capuchin monkeys (Izar et al. 2021), and rock hyraxes (Hemelrijk

et al. 2022). Previous experiments with Long-Evans rats (Tamashiro et al. 2004) found that males showed offensive acts more often the higher the rank of the male in colonies that were male-biased but not in those that were female-biased. This study concerned only two sex ratios (2♂ 4♀, and 4♂ 2♀), and measures of female dominance over males and intensity of aggression were absent. Thus, systematic studies with colonies of different sex ratios are still needed.

Future studies are needed also to determine whether higher dominance of females gives them more freedom in choosing a sexual partner (Moore et al. 2001). In addition, further studies on coalitions are needed to determine whether coalitions exist in rats and, if so, to establish their influence on the formation of dominance hierarchies. Coalitions have been reported in many primate and mammal species, also those with some female dominance, such as bonobos (Tokuyama and Furuichi 2016), spotted hyenas (Strauss and Holekamp 2019), lions (Packer et al. 1991) and ring-tailed lemurs (Kittler et al. 2015). However, there is no evidence to date for coalitions in rodents. In addition, there was no behavioural evidence of coalitions in our study, but further study should be useful.

Our results highlight the importance of studying intersexual dominance (Kappeler et al. 2022; Seex et al. 2022) by revealing female co-dominance with males despite the females' smaller body size, in a species that is phylogenetically distant from primates. We conclude that although female rats are smaller than males, they dominate on average half of the males possibly through the winner-loser effect, and the higher the aggression intensity of the colony the greater the dominance of females over males, in line with the hypotheses from the computational model DomWorld. This shows that testing hypotheses from agent-based models empirically is useful, and suggests that females may be more dominant over males in more species than we think and that body size may not be the only predictor of dominance status.

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Data availability The underlying data are available as supplementary material.

Declarations

Ethics approval All experimental procedures were approved by the Animal Ethics Committee of the University of Groningen (IvD protocol 184844–01-003) and the School of Psychology & Neuroscience under the aegis of the University of St Andrews Animal Welfare and Ethics Committee (approval code 211).

The procedures with animals in this research were implemented in accordance with the guidelines of the Experiments on Animals Act (Wet op de Dierproeven 2014) of the Government of The Netherlands. This law is based on Directive 2010/63/EU of the European Parliament and the Council of the European Union, on the protection of animals used for scientific purposes.

Conflict of interests The authors declare no conflict of interest.

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