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Fighting behaviour in territorial male roe deer *Capreolus capreolus*: the effects of antler size and residence

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Abstract In all areas where they have been studied, male roe deer are believed to have a territorial mating system, although few quantitative studies have been conducted and there remains considerable debate about the function of male roe deer territories. We observed 139 aggressive interactions between male roe deer in Storfosna Island (Norway) during one territorial season (March–August). We recognised seven rank levels of escalation according to the potential danger of the behaviour. On the basis of the number of escalation levels included in the interactions, the complexity of the fights was also scored. We recorded the presence of other individuals during the interaction, the age, the antler size, the territorial status and the residency status of the two contestants and tested how these variables affected escalation, complexity and outcome of the fights. Most of the interactions ended with low levels of escalation, and physical contact occurred only in fights between two territorial bucks. The escalation was also affected by the difference in antler size index (the bucks escalated more when the difference in antler size was smaller) and increased with an increasing number of female deer present during the interaction. The resident buck won in 81% of the fights. When it drew or lost, it was generally both inferior in age and antler size, and the duration and escalation of the

interactions were higher. However, even when a fight was lost, no territory loss occurred. These results are consistent with the evolutionary game theory and the proposed low risk–low gain strategy of roe deer bucks.

Keywords *Capreolus capreolus* · Fighting behaviour · Roe deer · Norway · Ungulate

Introduction

Many species have territorial mating systems, where certain areas are aggressively defended against same-sex intruders. However, fighting is potentially expensive, due to the risk of being injured or dying. Therefore, the animals should decide whether to fight or not according to a cost–benefit trade-off (Maynard Smith 1974). Natural selection should accordingly favour the use of cues to assess the fighting ability of contestants.

Parker (1974) introduced the term resource holding power (RHP) to describe the correlated asymmetry which depends on size, health and weapons. The potential danger of a fight (degree of escalation) is related to the asymmetry in RHP between the contestants (Parker 1974; Maynard Smith and Parker 1976), but it could also depend on the value that they put on the resource, for example, because one of them (the holder; Parker 1974) spent more time and energy in its defence (Davies 1978; Krebs 1982) or is the one who knows its real value (Barnard and Brown 1982; Enquist and Leimar 1987).

Long fights with high escalation are therefore expected when the value of the resource is high (e.g. Robinson 1985) or when failure to fight implies the immediate or future loss of potential gains in fitness (Brodsky and Montgomerie 1987). In fact, pay-off asymmetry might be more important than fighting asymmetry in influencing a male's tendency to escalate (Maynard Smith and Parker 1976). The more similar two contestants are in size, rank, fighting ability and body condition (RHP) and place the same value on the resource, the longer the fight should go on and escalate (Maynard Smith and Parker 1976; Mattiangeli et al. 1998,

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1999). Different signals, such as size, weapon development (e.g. antlers; Clutton-Brock et al. 1980; Clutton-Brock 1982; Markusson and Folstad 1997) or behaviours reflecting vigor, can be used to show the individual RHP (Clutton-Brock et al. 1979).

Although territoriality is common among antelopes, it is less widespread among cervids. The European roe deer *Capreolus capreolus* L. is a territorial cervid (Bramley 1970), where male animals actively defend a territory months ahead of the rut (July–August; Liberg et al. 1998). The territories are occupied in March/April and maintained throughout the summer, while in winter roe deer often form groups to feed in open habitat where available (e.g. Zejda 1978; Maublanc et al. 1987; Cibien et al. 1989; San José et al. 1997). The territorial system, proposed to carry low risk and low gain (Linnell and Andersen 1998), could be viewed as a strategy to reduce the frequency of dangerous fights (Owen-Smith 1977), and most bucks show lifetime fidelity to the area where they established their first territory (Bramley 1970; Ellenberg 1978; Linnell and Andersen 1998).

Because of the cryptic habits of roe deer and their preference for forested habitats, no previous published study has described in detail or quantified the sequence of behaviours in the interactions between roe deer bucks (Bramley 1970). The territories are defended through a combination of scent marking (Johansson et al. 1995) and aggression (Bramley 1970). Because roe deer antlers are relatively simple in structure and ‘dagger-like’, there are potentially great risks of injury associated with combat. Furthermore, the degree of polygyny is believed to be low (Liberg et al. 1998), and the relationship between victory in a fight and access to female deer may be somewhat uncertain (territoriality has an onset several months before the mating season, and female deer may leave their normal home-range to mate with a distant male; Liberg et al. 1998). It is therefore expected that the bucks should carefully assess their rivals before engaging in any aggression.

Thus, we tested the evolutionary game theory (Maynard Smith 1974; Parker 1974; Maynard Smith and Parker 1976) through the following predictions: (a) bucks with similar territorial status and antler sizes (RHP) should escalate more, and bucks with different territorial status and antler sizes should not escalate; (b) the buck with better knowledge of the territory value (i.e. the resident one) should fight more (escalation and duration) and win; and (c) when the territory owner loses, he is inferior in RHP.

Materials and methods

Study area and roe deer

The study was carried out in Storfosna island (10.5 km², 63°40' N), which is a mosaic of moorland (33.4%), rough grassland (18.3%), cultivated pasture (35.3%) and woodland (12.1%). The climate is characterised by mild winters and cool summers, with 160–180 growing days per year. The mean total annual rainfall in 1990–1994 was

1,048 mm, with an average monthly temperature of 5.8°C. Day length varies between 4 h in winter and 20 h in summer. In 1994, snow was present until the end of March (for a more detailed description of the study area, see Linnell and Andersen 1995).

Between 1990 and 1994, the population increased from 15 to more than 50 individuals/100 ha. During the winters of 1991–1994, we captured or recaptured animals on 142 occasions in either cannon nets or drop nets and on six occasions using short drive nets. The animals were manually restrained, weighed and equipped with ear tags and a radio-collar. We radio-collared, ear-tagged and ear-notched about 50% of the animals.

We observed the aggressive and combat behaviour of bucks throughout the 1994 territorial season, from February to mid August. We knew the minimum age of most of the animals (marked as fawns, yearlings or adults in the preceding years) and we considered three age groups: yearling ($n=12$), subadult (2 years old, $n=12$), and adult (3 years and older, $n=25$) after 1 May 1994.

Observations

In the term ‘interaction’ (used as synonym with ‘fight’), we include all of the behaviours observed during territorial disputes between two bucks, including maintenance behaviours such as feeding, because these may actually be part of the display routine. The observations were obtained on an ad hoc basis, mainly from a vehicle, a high observation tower or from vantage points in the terrain, by using binoculars (magnification 8×40). The distance between the observer and the animals varied between 50 and 200 m. There was a clear bias towards observations in open habitats; however, as woodland only covered 12% of the island, this bias is not so extreme. We only recorded data from behavioural sequences where our presence had no discernable effect on the bucks. We recorded the date, time, place, presence of other animals and all behaviours that the contestants used in the interaction.

The repertoire of recognised behaviours involved in an interaction consisted of:

- *Feeding* The buck is eating from the ground or from a bush, standing or moving with the head down.
- *Staring* The buck is standing still, observing another buck, with the head raised and with a rigid stance.
- *Approaching* The buck is moving deliberately toward another buck, looking straight at him.
- *Chasing* The buck follows an escaping buck, usually running.
- *Fraying* Marking behaviour, first performed in March/April, when the bucks remove the velvet from their antlers (shedding) using tree stems and bushes. They continue to do this throughout the summer, probably for visual and scent-marking of their home range and it is also used in interactions between bucks, possibly as a display behaviour (Johansson et al. 1995).

- *Scraping* Marking behaviour, performed by pawing on the ground with a forefoot. Roe deer have glands between their toes providing both a scent and a visual mark (Johansson et al. 1995).
- *Rubbing* Marking behaviour, often performed in association with fraying, rubbing the forehead glands on stems of trees or bushes.
- *Stiff walk* The buck lifts his feet and puts them down firmly in a demonstrative way. It is mostly performed with the side toward the other buck and from a longer distance as compared to parallel walk.
- *Parallel walk* Two bucks walk side by side watching each other closely.
- *Lateral display* The buck turns and shows his side to the opponent.
- *Head shaking* The buck twists his head from left to right repeatedly, directed straight toward its opponent.
- *Lunge* The buck jumps forward from a short distance (ca 5 m), with the antlers toward the opponent, but stops before contact, usually retreating to the original distance.
- *Prod* The buck hits the opponent on his side or back with his antlers.
- *Lunge/contact* The buck jumps forward from a short distance, with the antlers toward the opponent, and hits him. The opponent usually, but not always, manages to engage him with his antlers.
- *Pushing* The bucks are head to head, trying to push each other backwards.
- *Wrestling* The bucks lock their antlers and twist their heads from side to side, often moving around each other, possibly to make the opponent lose his balance.

The length of each antler, compared to the length of the ear, was reported as ‘antler size’. We also counted, for each antler, the number of points (one to three points per antler). We made several observations for each individual, both in the field and from an extensive photo gallery, and we calculated an antler index through the method described by Wahlström (1994).

In this study, we conceptually considered ‘territory’ to be the area in which a resident buck reacts aggressively to intruders, which does not imply its exclusive use (Owen-Smith 1977). We defined a ‘territorial’ buck operationally as one able to establish residence within a clearly defined and compact area (Maher and Lott 1995). In the field, this was usually determined by visual observation and intensive radio-tracking of bucks during the entire season (Andersen et al. 1995). In contrast, the movements of non-territorial bucks (mainly yearlings) were characterised by very large home ranges and erratic movements (Andersen et al. 1995).

We gave a ranked score of the escalation of each interaction, taking into consideration its risk and likely energetic cost:

- 1 Feeding <2 Residency maintenance (staring, approaching and chasing) <3 Marking (fraying, scraping and rubbing) <4 Display (stiff walk, parallel walk, lateral

display and head shaking) <5 Charge and lunge <6 Prod <7 Contact (lunge with contact, pushing and wrestling)

We also defined the ‘complexity’ of interactions as the number of different escalation levels included in the total escalation, with a rank varying from 1 to 7, when all groups of behaviours were displayed.

Statistical procedures

The sample sizes are the number of matched pairs or single animals and vary among the tests according to the number of animals or dyads for which we have the relevant variables. Of the dyads, 58% were encountered only once, 28% encountered twice, 8% three times and 6% five times. Therefore, the level of pseudoreplication was not high, and it is important to notice that the outcome of a dyad’s interaction was not always the same. As we did not record all the fights that might have occurred, it was not possible to account for pseudoreplication and for the effect of winning or losing a previous fight on the future performance of a given buck.

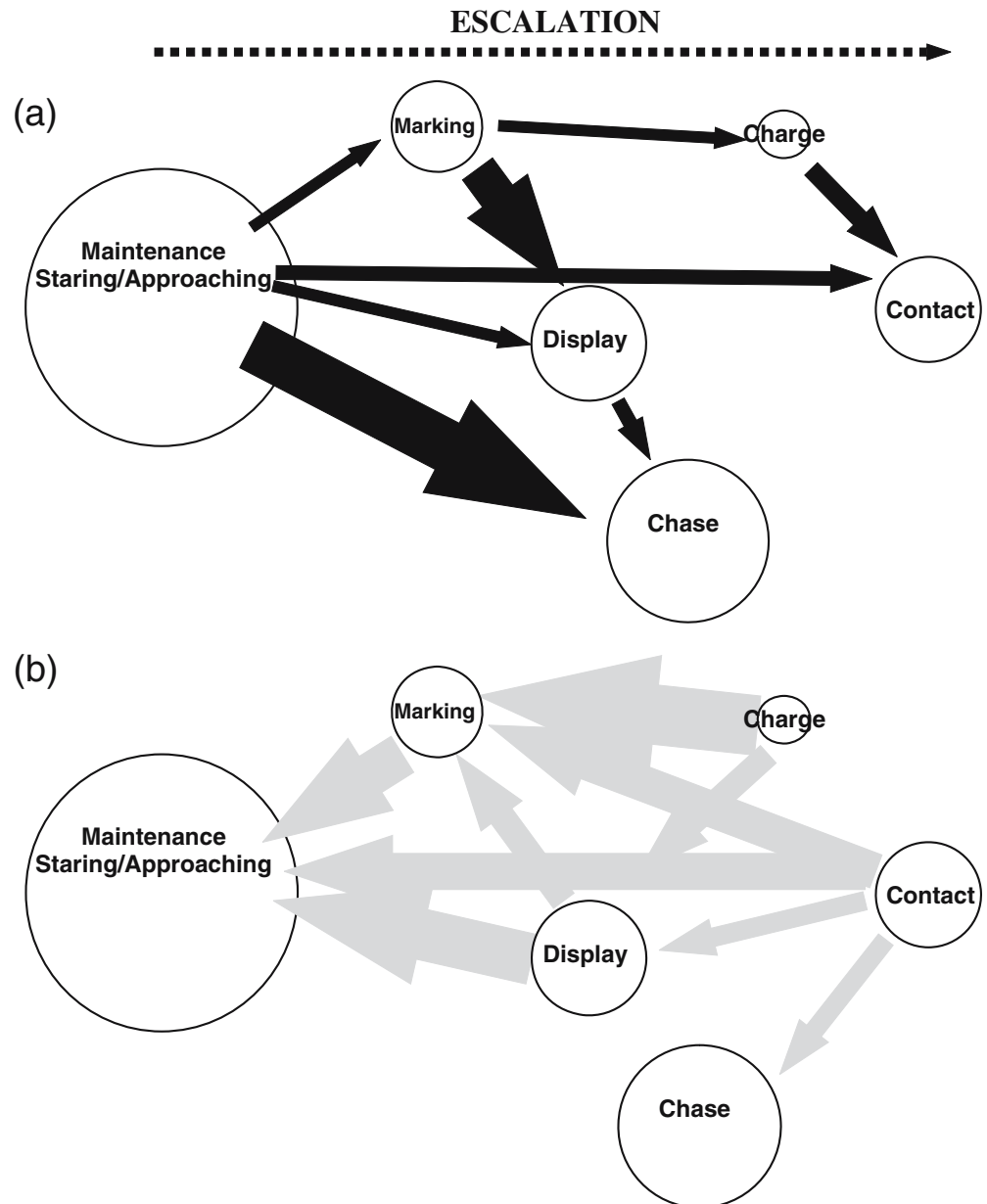
A generalised linear model (GLM) of the binomial family (Hardy and Field 1998; Dalggaard 2002) was used to investigate the influence of several variables, e.g. the difference in antler size, difference in age and so on, on several binary dependent variables. The escalation levels were grouped in two categories to perform a more robust analysis (high escalation, with contact=escalation levels 6–7; low escalation, without contact=escalation levels 1–5). The significance value was $P<0.05$ throughout. All statistical tests were two-tailed. We used the corrected Akaike Information Criterion (AIC_c) for small samples (Burnham and Anderson 2002) to select the most parsimonious model describing territorial status, escalation level and outcome of the fight. Statistical analyses were performed using R 2.01 Software (R Development Core Team 2004).

Results

We observed a total of 139 aggressive interactions between March 2 and end of August 1994. Most of them occurred around sunrise and sunset, with a small peak at noon. The duration of an aggressive interaction varied between 20 s and 10 min, with a median length of 1 min and 10 s. Taking all fights together, we were able to make a chart of the typical fighting patterns (Fig. 1).

Among the 132 interactions of which we could decide the outcome, 103 ended with a clear winner; the rest ended with either a chase or with the contestants slowly walking away from each other. Twenty percent of the interactions were outside any of the competitors’ estimated territories.

Fig. 1 Schematic representation of fighting pattern of roe deer in Storfosna (Norway). The level of escalation increases from *left to right*. The radius of the *circles* represents how often an element was included in an interaction. The size of the *arrows* represents the frequency that a behaviour shifts from one element to another specific element, with the *arrows* leaving one element summing up to 100% (the *arrows* representing less than 10% are left out for clarity). **a** Increasing the escalation level; **b** decreasing the escalation level



The best model for territorial status (binary dependent variable) included age, antler size and their interaction as explaining variables, when all the age classes were included in the analysis (Tables 1a and 2a). Age and antler size were not highly correlated ($r_p=0.14$). Although the interaction between antler size and age was not significant ($P=0.07$; Table 2a), the three-dimensional plot in Fig. 2 shows that the model including the interaction not only has the lowest AIC_c but is also the one which has biologically more meaning. In fact, if you have very small antlers, growing older by itself will not increase the probability of being territorial, while once the antlers reach an index value of about 15, then it is especially age that matters. So, it is neither antler size nor age alone that will decide the status of the buck but the interaction between them.

The best model that described the level of escalation (binary dependent variable: high/low, i.e. with contact/

without contact between the contestants) included the difference in antler size between the two contestants, which had a negative effect and the territorial status and the number of female deer present as explaining variables with a positive effect (Tables 1b and 2b). However, the difference in AIC_c between the first and the second model (including the presence of other bucks with a positive effect) is quite small (Table 1b); therefore, both of the models could be considered equally good, but the most parsimonious one, including less parameters, is the first.

Bucks with a similar antler index seemed to escalate more. Taking into consideration the territorial status, in a fight between two territorial or two non-territorial bucks, the escalation was higher than in a fight between one territorial and one non-territorial bucks (Fig. 3a). The higher level of escalation was reached by fights between two territorial bucks (high escalation 41% of the interac-

Table 1 Summary of the models of (a) territorial status (binary dependent variable) with age and antler index as explanatory variables, (b) escalation (binary dependent variable) with territorial status, difference in age, difference in antler index and number of female deer and bucks present as explanatory variables and (c) outcome (binary dependent variable) with residency status, difference in age and difference in antler index as explanatory variables for male roe deer in Storfosna (Norway)

| Model | K | AIC_c | ΔAIC_c | ω_i |
|------------------------------------------|-----|---------|----------------|------------|
| (a) | | | | |
| age + antler + age \times antler | 4 | 33.80 | 0.00 | 0.805 |
| age + antler | 3 | 36.68 | 2.85 | 0.191 |
| antler | 2 | 44.32 | 10.52 | 0.004 |
| age | 2 | 57.63 | 23.83 | 0.001 |
| (b) | | | | |
| terr + dant + female | 4 | 57.95 | 0.00 | 0.398 |
| terr + dant + female + male | 5 | 58.35 | 0.41 | 0.324 |
| terr + dant + male \times female | 6 | 59.86 | 1.19 | 0.152 |
| terr + dant + dage + female | 5 | 60.25 | 2.30 | 0.125 |
| (c) | | | | |
| resid + dant | 3 | 65.75 | 0.00 | 0.598 |
| resid + dant + dage | 4 | 67.92 | 2.17 | 0.202 |
| resid | 2 | 68.72 | 2.97 | 0.135 |
| resid + dant + dage + dant \times dage | 5 | 70.20 | 4.45 | 0.064 |

The models were ranked by the corrected Akaike Information Criterion. The most parsimonious model is on the top of the list *age* Age, *antler* antler index, *terr* territorial status, *dage* difference in age, *dant* difference in antler index, *female* number of female deer present, *male* number of bucks present, *resid* residency status, K number of parameters, ΔAIC_c difference in AIC_c between the current and the most parsimonious model, ω_i Akaike's weights (i.e. normalised likelihood of the models)

tions). When only one of the bucks in an interaction was territorial, high escalation levels were reached in only 16%

Table 2 Parameter estimates for the most parsimonious model of (a) territoriality, (b) escalation and (c) outcome for male roe deer in Storfosna (Norway)

| Coefficients | Estimate | SE | z | P |
|---------------------|----------|-------|-------|-------|
| (a) | | | | |
| Intercept | 0.89 | 6.30 | 0.14 | 0.887 |
| antler | -4.22 | 2.71 | -1.56 | 0.118 |
| age | -0.33 | 0.46 | -0.73 | 0.463 |
| age \times antler | 0.37 | 0.21 | 1.18 | 0.076 |
| (b) | | | | |
| Intercept | -1.46 | 1.16 | -1.26 | 0.207 |
| terr | 1.35 | 0.64 | 2.12 | 0.034 |
| dant | -0.62 | 0.28 | -2.21 | 0.027 |
| female | 0.95 | 0.42 | 2.26 | 0.024 |
| (c) | | | | |
| Intercept | -0.01 | 0.33 | -0.01 | 1.000 |
| resid | 0.17 | 0.083 | 3.55 | 0.001 |
| dant | 2.00 | 0.056 | 2.03 | 0.042 |

age Age, *antler* antler index, *terr* territorial status, *dant* difference in antler index, *female* number of female deer present, *resid* residency status

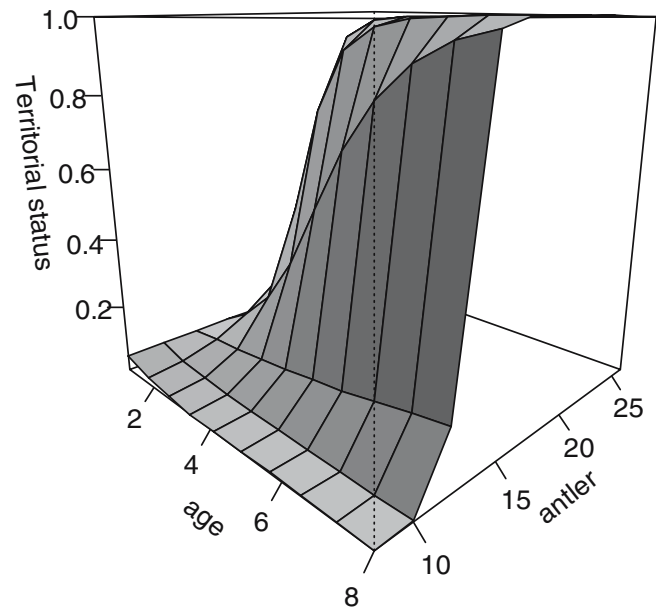


Fig. 2 Three-dimensional plot of the binomial GLM explaining territorial status with age, antler size and their interaction

of the cases. When both of the bucks were non-territorial, high escalation levels were reached in only 19% of the cases. The complexity of the fight was also higher between two territorial bucks (Fig. 3b).

We were able to classify the outcome of 62 interactions of which we knew the ownership of the territory: in ten fights, it ended with a draw; in 50 fights, the resident buck won; and the intruding buck won in only two fights. Moreover, the duration and the escalation were significantly higher when the resident drew or lost as opposed to when it won (Mann-Whitney U test, $n_1=7$, $n_2=38$, $U=51.5$, $Z=-2.567$, $P=0.01$; $n_1=12$, $n_2=52$, $U=204$, $Z=-2.028$, $P=0.043$, respectively). In the two cases when a resident animal lost a fight, he was still able to retain his territory. The best model describing the outcome (binary dependent variable) showed that being resident and having bigger antler size were the most important factors to determine who wins, while a difference in age was not significant (Tables 1c and 2c). The probability (based on the logistic regression model) of a buck winning when he was resident against intruder or intruder against resident or when both bucks are outside their territory is plotted in Fig. 4 for the 40 fights of which we had data on both the residency status and the antler size of the contestants.

Discussion

Our results indicate that antlers appear to be used for mutual assessment of RHP in roe deer and therefore can potentially serve to reduce both the escalation and complexity of inter-buck interactions. Antlers could potentially give information about the age class of the opponent (Strandgaard 1972) and the potential quality of the yearlings (Wahlström 1994). Other ways to inform the

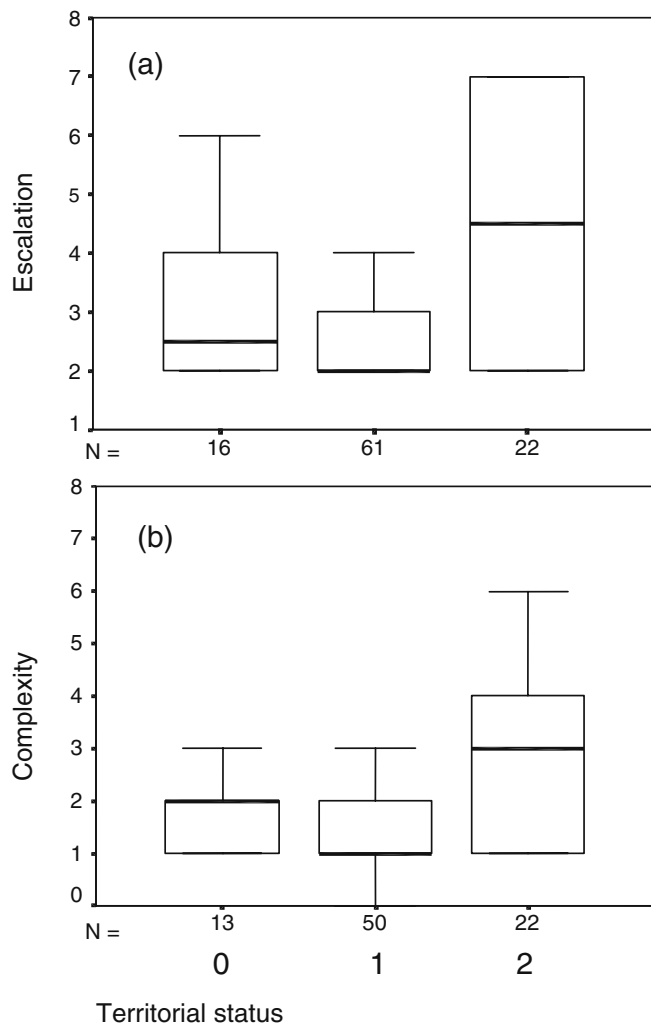


Fig. 3 Highest level of escalation (a, seven levels ranked according to the potential danger and energetic investment of the behaviour) and complexity (b, i.e. the number of different escalation levels included in the total escalation, with a rank varying from one to seven) reached by a roe deer fight in Storfosna (Norway) in relation to the territorial status of the two contestants. 0, both non-territorial; 1 one of them territorial; 2 both territorial

opponent about RHP could be through marking behaviour and display behaviour. Roe deer bucks leave visible signs and scents on the ground or on trees and shrubs, which could provide information to other bucks (and female deer) about the age and the health status of the buck (Johansson et al. 1995). Display behaviours, like parallel walk, stiff walk, head shaking and so on, could also inform the opponent about relative body size, physical condition and motivation to fight.

The difference in antler size index was a good cue to predict the level of escalation, as bucks with similar antler index seemed to escalate more. Moreover, when two territorial or two non-territorial bucks fight, the escalation was higher than in a fight between one territorial and one non-territorial male, probably because the asymmetry between the two bucks in the second case is more marked

and they do not need to escalate to assess their relative RHPs.

The higher level of escalation reached by fights between two territorial bucks could depend on the lower asymmetry between the opponents, but it is also consistent with the higher potential benefit that could be obtained. When only one of the bucks in an interaction was territorial, the asymmetry probably did not rely on antlers but rather on the territorial status itself, which is the consequence of many correlated factors like age, antler size and RHP. When both of the bucks were non-territorial, it is likely that the potential benefit of escalating was not enough to risk potential injury.

The presence of female deer during the interaction seems to have an influence on the level of escalation, which indicates that also roe deer, as other species (e.g. Zahavi 1979; Oliveira et al. 1998), show what is called the 'audience effect' (McGregor and Peake 2000). In fact, in the presence of conspecifics, the two contestants might be more motivated to fight and give information to the 'audience' about their fighting ability. In the case of bucks, this could affect the outcome of future fights, while in the presence of female deer it might affect their future mating choice.

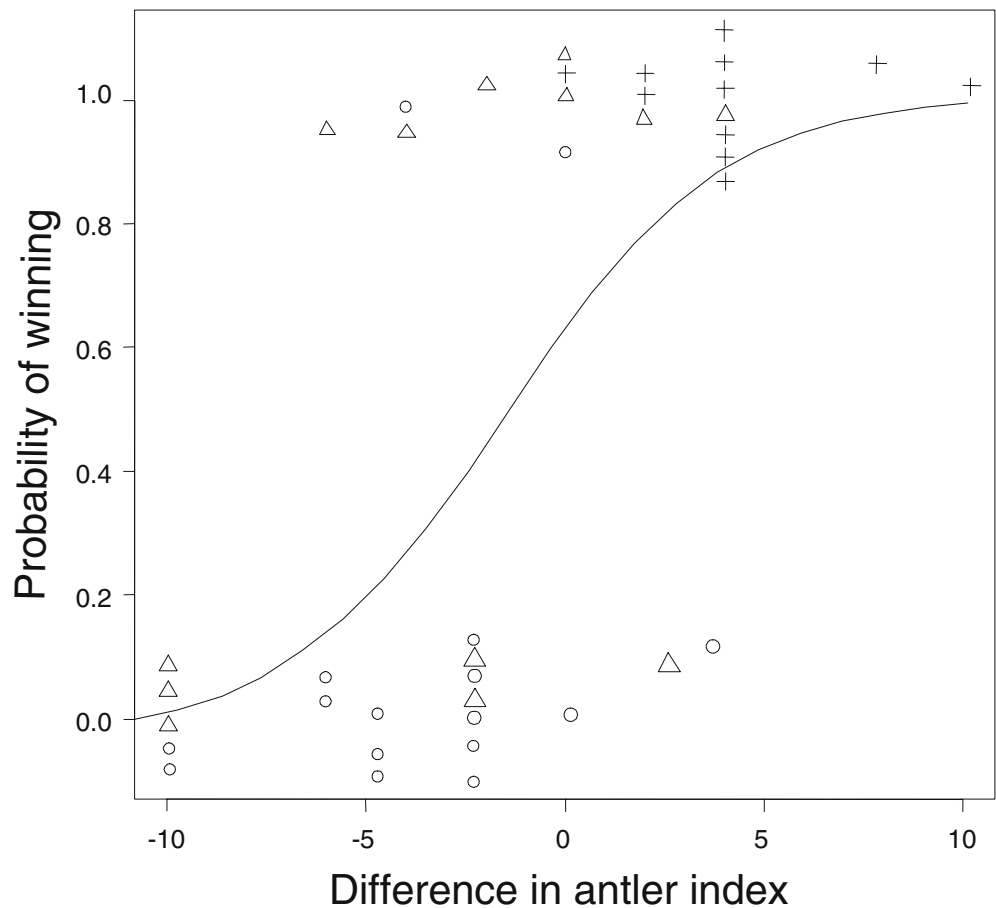
A previous study in the same area found not only that the absence of substantial differences in age-specific reproductive behaviour, because of relatively high degrees of reproductive activity by young bucks, but also that territorial adult bucks invested relatively little time in mating and territorial activities with respect to other ungulates (Melis et al. 2005).

Looking at the outcome of the fight, the territorial system seems to function like a conditional strategy in which the resident buck wins (Kemp and Wiklund 2004). In fact, the territory owner won 81% of the fights, and when it drew or lost it was inferior in antler size (Fig. 4). This is consistent with the long-term site fidelity reported in roe deer bucks (Linnell and Andersen 1998), which could affect the pay-off of the older territorial buck, who has invested more time in defending his site throughout the years.

When the resident lost or drew a fight, the duration and the escalation of the interaction were higher in comparison to when the resident won, also when it had bigger antlers. This could mean that, even if the territory owner had a higher RHP, the intruder could be more motivated to fight. Besides, antler size could be an honest signal of the quality of the male roe deer at the beginning of the territorial season when they are growing but might not be immediately affected by further changes in the health status of the buck after the velvet is shed in late spring.

It is important to notice that in no case did the loss of a fight between two territorial bucks led to territory abandonment by the loser. This would seem to indicate that neighbouring territorial bucks are not so much fighting over access to a territory (as happens in many territorial antelope; e.g. Waser 1975) as fighting for dominance where the territory serves as a spatial reference for this dominance (Owen-Smith 1977). Although we were not

Fig. 4 Data on the outcome of the roe deer contests in Storfosna (Norway) and estimated probability (predicted by the logistic regression model) of the male roe deer winning when he is: resident against intruder (*plus sign*), intruder against resident (*circle*) or when both bucks are outside their territory (*triangle*). The data have been visually adjusted to avoid over-plotting



able to analyse the data on an individual level, it is quite possible that the neighbouring roe deer bucks show the dear enemy effect (Jennings et al. 2004). Given that some female roe deer are highly mobile during the rut (Liberg et al. 1998; San José and Lovari 1998) and that few male roe deer territories totally enfold any female roe deer home ranges, there may be a poor relationship between territory size and access to female deer. Therefore, the result of successful territory establishment is more likely to be an area in which bucks can court and mate without interference (and where the buck can satisfy his own nutritional needs for 6 months), rather than direct and automatic access to female deer. In this way, roe deer territoriality may differ somewhat from conventional models of territoriality but is similar to that found in pronghorn *Antilocapra americana* and springbok *Antidorcas marsupialis* (Jackson et al. 1993; Byers 1997).

We conclude that (a) fights between bucks with similar territorial status and RHP escalate more; (b) the resident wins most of the fights, and when it draws escalation and duration are higher; and (c) when the territory owner loses, he is inferior in RHP. This is consistent with the evolutionary game theory (Maynard Smith 1974; Parker 1974; Maynard Smith and Parker 1976) and the proposed low risk–low gain strategy of roe deer bucks (Linnell and Andersen 1998).

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