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Research article

Offspring defence in relation to litter size and age: experiment in the bank vole *Clethrionomys glareolus*

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Abstract. According to parental investment theory, nest defence activity should be related to the reproductive value of the offspring. Alternative hypotheses suggest that defence activity may, for example, depend upon the conspicuousness of the young. Studies concerning this topic have been carried out almost exclusively on birds and experimental data on the diversity of organisms is lacking. Bank voles *Clethrionomys glareolus* were used to study the effects of the number and age of offspring upon the pup defence activity of mothers. Male bank voles are infanticidal and thus an adult male was used as a predator. Defence trials were conducted in the laboratory and filmed for subsequent analysis. Litter sizes were divided into three treatment groups: reduced (−2 pups), control (±0 pups) and enlarged (+2 pups). In order to study the effect of offspring age upon maternal defence activity the trials were conducted twice: when the pups were 3 and 8 days old. Defence activity increased with the number of offspring and enlarged litters were most actively defended. This result supports parental investment theory and conclusions drawn by earlier studies of birds. However, in contrast to the conclusions of earlier studies, older offspring were defended less than the younger ones. Whilst new-born pups are totally defenceless against predators their vulnerability decreases as they age. Therefore, we suggest that maternal aggression in female bank voles is related to the value as well as to the vulnerability of the offspring. The validity of this explanation and the determinants of parental investment decisions in small mammals in general deserve further study.

Key words: harm to offspring hypothesis, infanticide, litter size manipulation, mammals, nest defence, offspring vulnerability, parental effort, parental investment theory, vulnerability hypothesis

Introduction

Parental investment theory predicts that individuals should invest more heavily in larger rather than smaller broods and in older rather than younger offspring in order to maximize their fitness (Trivers, 1972; Barash, 1975; Lazarus and Inglis, 1986; Winkler, 1987). The nest defence behaviour of parents provides one possibility to study the predictions of the theory. The risks of defending the nest fluctuate independently of the characteristics of the brood. However, because the reproductive value of the brood increases with the number and age of the offspring, the benefits of defence should increase with these two traits. During the last few decades, numerous correlational and a few experimental studies, conducted mainly on birds, have examined parental investment from the angle of this 'reproductive value of offspring' hypothesis (review by Montgomerie and Weatherhead, 1988; Wiklund 1990; Winkler, 1991; Rytkönen *et al.*, 1995). Other hypotheses presented include the 'harm to offspring' hypothesis (Montgomerie and Weatherhead, 1988; Dale *et al.*, 1996, Listøen *et al.*, 2000), in which parental investment is related to the harm that offspring would suffer during periods without parental care (e.g. without incubation or feeding) and the 'vulnerability' hypothesis (Harvey and Greenwood, 1978; Onnebrink and Curio, 1991), in which parents adjust their defence behaviour according to the conspicuousness of the nest. Although the predictions of these hypotheses are in some cases the opposite of each other they are not mutually exclusive.

The validity of testing the predictions of parental investment theory has often been questioned (e.g. Nur, 1983; Knight and Temple, 1986a, b; Montgomerie and Weatherhead, 1988). It is particularly important to take into account the following factors when making generalisations about the results of different studies. Firstly, properly controlled experimental manipulations (e.g. of brood size) are necessary in order to demonstrate the cause-and-effect relationships convincingly. Secondly, interpretation of the results may be difficult (not necessarily objective) when many separate behavioural elements are measured during the same study and only few are found to significantly support the predictions. Thirdly, earlier research has concentrated almost exclusively on birds. Only a few experiments have focused upon fish (e.g. Pressley, 1981; Carlisle, 1985; Knight and Temple, 1986a; Lavery and Keenleyside, 1990), and there are no explicitly carried out experiments in mammals.

The study species, the bank vole (*Clethrionomys glareolus*), is a common rodent in the Palearctic region. Aggression of female rodents has been found to increase during pregnancy, peak sharply after the pups are born and then gradually decline until the pups are weaned (e.g. St. John and Corning, 1973; Svare and Gandelman, 1976; Koskela *et al.*, 1997). However, although small mustelids, such as least weasels (*Mustela nivalis*) and stoats (*M. erminea*), are important predators of microtine rodents (e.g. Tapper, 1979; Norrdahl and Korpimäki, 1995), it is very unlikely that an individual female could successfully defend her pups against an attacking mustelid predator. Infanticide (killing of pups by conspecifics) occurs in a wide range of mammals including the bank vole (reviewed in Hrdy, 1979; Hausfater and Hrdy, 1984; Labov *et al.*, 1985). Several lines of evidence support the notion that the function of maternal aggression is to protect the offspring from conspecifics (e.g. Wolff, 1985, 1993; Maestripieri, 1992; Wilson *et al.*, 1993; Wolff and Peterson, 1998). Pup defence also puts defending females at risk of injury, or even death (e.g. Gandelman and Simon, 1980; Mallory and Brooks, 1980; E. Koskela, T. Mappes and T.A. Oksanen, pers. obs.), thus fulfilling the conditions for a study of defence behaviour using a cost-benefit approach (Montgomery and Weatherhead, 1988).

The aim of the current experiment was to test the predictions of parental investment theory using the bank vole as the study species. More specifically, we studied the effects of the number and age of offspring upon the defence activity of female bank voles. Contrary to an earlier study of mammals (Maestripieri and Alleva, 1990), litter size manipulations were performed by taking into account the original litter sizes (see Methods section). This was essential in order to control for differences in individual circumstances which may affect the results (i.e. the individual optimisation hypothesis; Perrins and Moss, 1975; Morris 1985).

Methods

The study was conducted at the Experimental Animal Unit of the University of Jyväskylä. The bank voles used were mature second generation laboratory-bred voles and the females had given birth at least once before the study. The voles were housed individually in standard mouse cages except during the mating and nursing periods, with commercial pellets and water provided in excess. Hay and wood chips were used for bedding.

Individuals were paired by placing a randomly chosen male and female together into the same cage for 7 days. Pregnant females were checked twice a day to determine the time of parturition. Immediately after new-born pups were discovered, they were counted and marked. Bank vole females do not recognise their new-born pups from foreign ones (e.g. Mappes *et al.*, 1995; Koskela *et al.*, 1998), so litter size manipulations were performed within 2 days of the females giving birth. There were three litter size manipulation groups: reduced litters, ‘R’, with two pups removed; control litters, ‘C’, where the original litter size was not altered and enlarged litters, ‘E’, with two pups added. The initial sizes (weight) of the mothers did not differ between the manipulation groups (mean ± SE in grams, R: 19.5 ± 1.0, C: 20.6 ± 0.7, E: 20.5 ± 1.0, One way ANOVA, $F_{2,38} = 0.440$, $p > 0.6$). There were also no differences in the original litter sizes of the mothers assigned to different manipulation groups (mean ± SE, R: 5.0 ± 0.2, C: 4.8 ± 0.3, E: 5.2 ± 0.3, One way ANOVA, $F_{2,38} = 0.454$, $p > 0.6$). All the females were mated readily after the first parturition (with a randomly chosen male) and were pregnant during lactation. This was done because in naturally occurring populations of small mammals, females with postpartum oestrus are usually pregnant whilst lactating (Bronson, 1989).

To study the effect of the age of offspring upon maternal defence activity the defence trials were conducted twice: once when the pups were 3 days old and again at 8 days old. Each time the offspring were also weighed. Behavioural trials were not conducted immediately after parturition, because at that time females are in postpartum oestrus and it may be difficult to categorise their behaviour into separate functional aspects. The trials were carried out in a 1 × 1 m arena, which was covered with transparent Perspex. So that the smell of the arena was familiar to the female during the trial, wood chips and hay from her cage were spread over the floor. All the pups from one litter were taken from their nest, placed, together with their own bedding into a small cage (15 × 10 × 7 cm) and positioned at the centre of the arena. The mother of the pups was then released into the arena and after a 3 min familiarisation period, beginning from when she first noticed the pups, a strange male was also introduced into the arena. The behaviour of the female–male pair was observed for 10 min. Each male was used for only one such trial, was unrelated to the female and was not the father of the pups. During both trials the pups were still completely dependent upon their mothers' care, as bank voles' eyes do not open until around 12 days of age and they are not weaned until about 20 days of age. However, at 8 days old pups already weigh 5–7 g, are grey and move, for example, around their cage when disturbed.

The behavioural trials were filmed and analysed following the completion of the trials. All the tapes were analysed by the same observer who was unaware of the manipulation groups to which the females belonged. The following categories of female behaviour against male were observed during each ten-minute trial: (1) the number of attacks, (2) number of chases, (3) number of fights and (4) total combined time used for the three behaviours (i.e. total defence time). For the male behaviour, the following were recorded: (1) number of approaches towards the female and (2) general activity during the trial (i.e. total time spent patrolling the arena).

Principal component analysis was run to summarise the information of the three female behavioural variables (attacks, chases and fights). Variables (counts per 10 min) were $\ln(x + 1)$ transformed before the analysis to normalise their distributions. One component, accounting for 91.1% of the total variance, was extracted from the data set. As all three variables had very high positive loadings (attacks 0.952, chases 0.969, fights 0.942), the component was described as 'aggressive behaviour'. The defence activity exhibited by the females in relation to litter size and age was studied using a Repeated measures ANOVA on the following variables; aggressive behaviour and total defence time. The latter variable had a positively skewed distribution and was $\mathrm{sqr}(x + 0.5)$ transformed before the analysis. The behaviour of the males did not depend upon litter manipulation groups or the age of the offspring (repeated measures ANOVA, approach: treatment $F_{2,38} = 1.05$, $p > 0.3$, age $F_{1,38} = 0.30$, $p > 0.5$, patrol: treatment $F_{2,38} = 1.05$, $p > 0.4$, age $F_{1,38} = 0.30$, $p > 0.8$). Consequently, male behaviour was not included in the models as a separate factor. Kendall's partial correlations (treatment as a controlling variable) were used to study the effects of the size of the offspring and the mother upon maternal defence. All the tests were two-tailed.

Results

Both the number and the age of offspring affected the defence activity of females. The values of the component, 'aggressive behaviour', increased with the number of offspring but decreased with increasing age of the offspring. There was no interaction between the two variables (repeated measures ANOVA, treatment $F_{2,38} = 3.33$, $p = 0.046$, age $F_{1,38} = 4.69$, $p = 0.037$, treatment by age $F_{2,38} = 0.52$, $p > 0.5$, Fig. 1a). The same pattern was evident from descriptives of all three separate variables (attacks, chases and fights, Table 1). The total defence time of the females was longer for larger litters and younger pups (repeated measures ANOVA, treatment $F_{2,38} = 4.02$, $p = 0.026$, age $F_{1,38} = 7.38$, $p = 0.010$, treatment by age $F_{2,38} = 0.38$, $p > 0.6$, Fig. 1b). The linear term for polynomial contrast was significant both for aggressive behaviour ($t = 2.55$, $p = 0.015$) and total defence time ($t = 2.70$, $p = 0.010$).

Litter size enlargements decreased whilst reductions increased the size of offspring in relation to the control group (Table 2). However, there was no correlation between the sizes of the offspring, at either 3 or 8 days of age, and defence activity of the females (Kendall's partial correlations, controlling for treatment: $0.031 \leq |r_k| \leq 0.080$, $n = 41$, all $p \geq 0.4$). The size of the females (initial weight or head width) also had no effect on the defence activity they exhibited ($0.002 \leq |r_k| \leq 0.119$, $n = 41$, all $p \geq 0.2$).

Discussion

We studied experimentally the effects of the number and age of offspring upon parental investment decisions using the bank vole as a study species. Our aim was to provide a novel study on the subject and try to avoid the drawbacks that, according to Montgomerie and Weatherhead (1988), have made it difficult to interpret some earlier studies. The results show that bank vole females adjust their defence activity according to the characteristics of their offspring and defend larger litters more intensively than smaller ones. This is consistent both with the predictions of parental investment theory and the majority of

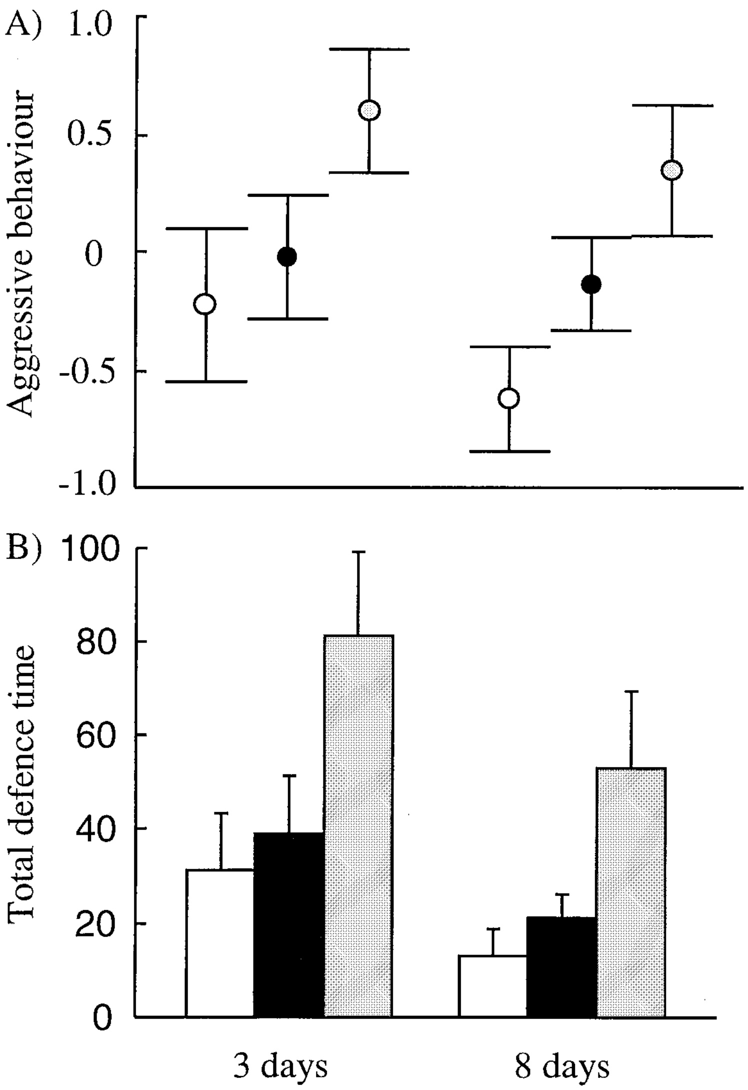

Figure 1. The defence intensity of bank vole females increases with litter size but decreases with the age of offspring. (a) Aggressive behaviour (PCA component, mean ± SE) and (b) Total defence time (in sec, mean ± SE) of females during the 10-min trial. White circles/bars: reduced litters, black circles/bars: control litters, grey circles/bars: enlarged litters.

data collected by earlier studies of birds and fish (reviewed by Montgomerie and Weatherhead, 1988; Lavery and Keenleyside, 1990; Wiklund, 1990; Rytkönen *et al.*, 1995). However, in contrast to the majority of findings by these studies (Montgomerie and Weatherhead, 1988; Rytkönen *et al.*, 1990, 1995), the intensity of defence behaviour exhibited by females decreased as the age of the offspring increased.

Table 1. Descriptive statistics of female behaviour (counts for 10 min) in relation to litter manipulation and offspring age. Numbers for untransformed values, mean ± SE. For statistics see Results

Variable (days)	Litter manipulation group		
	Reduced (n = 12)	Control (n = 16)	Enlarged (n = 13)
Attacks			
3	11.25 ± 4.46	10.63 ± 2.77	20.46 ± 4.43
8	3.25 ± 1.19	8.44 ± 2.13	16.77 ± 5.17
Chases			
3	7.00 ± 2.72	9.13 ± 2.66	16.31 ± 3.93
8	2.83 ± 1.15	5.44 ± 1.57	11.69 ± 3.07
Fights			
3	3.67 ± 1.71	4.44 ± 1.56	7.85 ± 2.19
8	1.58 ± 0.87	2.56 ± 0.75	6.46 ± 2.11

Table 2. The effect of litter size manipulation on the weight of offspring (in grams) in relation to their age. Values represent mean ± SE. Repeated measures ANOVA used

Weight	Reduced (n = 12)	Control (n = 16)	Enlarged (n = 13)
At manipulation	1.87 ± 0.03	1.91 ± 0.03	1.92 ± 0.02
3 days	3.86 ± 0.21	3.05 ± 0.19	2.66 ± 0.17
8 days	6.00 ± 0.20	5.16 ± 0.19	4.75 ± 0.16
20 days (weaning)	12.17 ± 0.28	11.06 ± 0.28	10.27 ± 0.22
Factor	df	F	p
Treatment	2, 36	11.61	< 0.001
Age	3, 34	17532.95	0.003
Treatment × Age	6, 70	3.75	< 0.001

Why do female bank voles defend older pups less intensively than younger ones? Parental investment theory does not provide a simple explanation for this result: although the reproductive value of offspring increases with age, older offspring are defended less by their mothers. One possible reason for this is that it may be difficult to use hypotheses developed (mainly) for birds to generalise about other taxa. However, optimal parental investment should, in addition to the characteristics of the brood, depend upon various environmental variables. In small mammals an obvious threat to newly born pups is infanticide from conspecifics. New-born pups are easily killed without a mother's protection, but as they age they get bigger, leave their nest when disturbed and are thus very likely harder to kill (Wolff, 1985). In the present study, simultaneously when the reproductive value of the offspring increased and the mothers decreased their defence activity, the relative vulnerability of offspring decreased. Thus, our result of negative relationship between defence intensity and offspring age does not necessarily contradict the parental investment theory.

The other hypotheses, that is, the 'harm to offspring' hypothesis (Dale *et al.*, 1996) or the 'vulnerability' hypothesis (Harvey and Greenwood, 1978; Onnebrink and Curio, 1991), do not either provide an easy interpretation for our results. Because new-born pups are probably most vulnerable to infanticide, mothers should take greater risks for younger offspring as the marginal benefit of protection is greatest in such a case. This conclusion follows the predictions of the 'harm to offspring' hypothesis (Dale *et al.*, 1996) but the idea behind it is different. According to Dale *et al.* (1996) older offspring are cared for less (left unattended for longer) because they conserve energy more efficiently, not because they are more difficult to kill. Although this means that mothers should adjust the intensity of defence according to the vulnerability of the pups, the prediction is completely opposite to that of Onnebrink and Curio's (1991) 'vulnerability hypothesis'. According to this hypothesis the conspicuousness of the (bird) nest increases with the age of nestlings and that is why parents have to increase the defence of their brood as their offspring age. To conclude, it seems difficult to use these two hypotheses when interpreting the results from different study objects than birds. However, there are necessarily no qualitative differences in the parental response to offspring age between small mammals and birds. In both groups parents decrease defence activity with offspring age, whereas this just happens already during nursing period in voles. Further, in both groups parents seem to adjust their defence intensity taking into account the vulnerability of the offspring.

The negative relationship between offspring age and defence intensity found in the present study may also depend, at least partly, on other factors than offspring vulnerability. In the experiment the females were mated readily in postpartum oestrus and were pregnant during lactation, which is normal in natural populations of small mammals. Accordingly, the present experiment cannot study whether the costs and benefits of the subsequent litter as well as the reproductive value of the females themselves affect the behavioural decisions of the females. In birds the defence level of the parents in relation to their renesting potential and brood number has received both theoretical and empirical study but the results are not unequivocal (reviews by Montgomerie and Weatherhead, 1988; Redondo, 1989). This is easy to understand as studies are difficult to conduct by simultaneously controlling several correlated factors (e.g. parental age, brood number and changing probabilities of parent and offspring survival). Moreover, the life-histories of small mammals differ greatly from birds. Thus, empirical data is needed before discussing the defence intensity and future reproductive potential in small mammals.

A totally alternative way of interpreting the results would be to argue that they are against the reproductive value hypothesis and support rather the offspring vulnerability hypothesis. Simultaneously when litter size enlargements increased the number of offspring, they decreased the weight of offspring (reproductive value) and probably also their ability to defend themselves. Thus, the observed increase in defence intensity of enlarged litters could be due to their increased vulnerability. However, although we agree that litter manipulation cannot totally separate the effects on offspring number and size, we do not find this interpretation satisfactory. We could not find any within-treatment correlation between offspring size and defence intensity, neither there is evidence of different vulnerability of same-aged but different sized young.

The reproductive value of offspring is often hypothesized to increase with body size and hence heavier pups should be more intensively defended than smaller ones (Carlisle, 1985; Montgomerie and Weatherhead, 1988). In birds the size at fledging often explains future survival or the probability of breeding (e.g. Perrins, 1965; Gustafsson and Sutherland, 1988), but still the defence activity of parents has not been found to increase with the size of offspring (e.g. Curio and Regelmann, 1986; Rytkönen *et al.*, 1995; Dale *et al.*, 1996). In mammals studies concerned with the size and quality of offspring are very scarce but in general the findings support benefits of large size (see e.g. Discussion in Koskela *et al.*, 1999). In the present study we found no evidence of bank vole females adjusting the intensity of their defence according to the size of their offspring. One possible explanation for this negative result may be that parents are unable to detect differences in nestling quality, as previously suggested by studies of birds (Curio and Regelmann, 1986). However, as already mentioned, the study design used in the present study cannot fully separate the effects of offspring number and size on defence intensity of females. This decreases the statistical power of the analyses and calls for more detailed experiments on the subject.

To summarise, our experiment provides new support for parental investment theory, as bank vole females adjusted the intensity of their defence according to the value of their litter (i.e. number of pups). However, in contrast to certain predictions of parental investment theory and the general conclusion from earlier studies, the defence intensity of females decreased as their offspring grew older. In the bank vole infanticidal individuals pose an obvious threat to the pups but as the pups grow older they are less vulnerable. Thus, the need for protection and the benefits of defence, are greater for younger offspring. As infanticide is a common phenomenon in several mammalian species (reviewed in Hrdy, 1979; Hausfater and Hrdy, 1984; Wolff and Peterson, 1998), we propose that female mammals defend older offspring less because they are less vulnerable to male attacks. The validity of this explanation and the determinants of parental investment decisions in small mammals in general deserve further study.

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