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Litter defence and parental investment allocation in house mice

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Abstract

In house mice, post-partum maternal aggression against a potentially infanticidal male conspecific can be considered a parental investment act. As such, it constitutes a suitable experimental paradigm for testing parental investment allocation. In the present study, 60 nulliparous female albino mice were tested for maternal aggression on day 8 of the lactation period (single 5-min test exposure to a male intruder). Four experimental groups were created by manipulating the litter size. In two groups, litters were culled at birth to 4 and 8 pups respectively, without any further pup removal. In the third group, litters were culled at birth to 8 pups, but 4 further pups were removed 3–4 hours before the test. In the fourth group, litters were manipulated as in the third group except that the 4 pups were returned to the litter after a 10-min removal. Dams with 8 pups at the time of testing showed significantly higher scores of aggressive behaviour than dams with 4 pups. The females of the two groups that had 4 pups at the time of testing did not differ in the intensity of maternal aggression. These results indicate that female house mice defend the investment made in their litters according to expected benefits (i.e., offspring number) and not to cumulative past investment.

Key words: House mouse; Litter defence; Litter size; Parental investment

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Introduction

Parental investment theory states that animals should base their investment decisions on expected benefits and not on whether or not past investment will be wasted (Dawkins and Carlisle 1976; Boucher 1977). Otherwise, they would commit the 'Concorde fallacy' (Weatherhead 1979; Dawkins and Brockmann 1980; Weatherhead 1982). However, since parental investment has been defined in terms of costs on an individual's future reproductive success (Trivers 1972), past investment is likely to affect the future reproductive potential of the parent; moreover, past investment and expected benefits are often positively correlated (Maynard Smith 1977; Coleman et al. 1985). Therefore, to base parental investment decision rules on past investment would not necessarily mean to commit the Concorde fallacy (Fagerström 1982; Coleman et al. 1985; Curio 1987).

In order to maximize their lifetime reproductive success, parents should invest according both to the value of their current offspring and to their own future reproductive potential (Williams 1966). The question then arises as to what extent animals incorporate the parameters of either past investment (as an indicator of expected future reproduction) or the value of their offspring (and the probability of a gain in fitness through it) in their parental investment decision rules. This question has already stimulated a great deal of experimental work (e.g., Weatherhead 1979; Weatherhead 1982; Coleman et al. 1985; Windt and Curio 1986) but, unfortunately, this has been conducted on a very narrow range of animal species (exclusively birds and fish).

In several animal species, parental investment theory has been used to investigate patterns of parental defence of the offspring (Barash 1975; Andersson et al. 1980; Lazarus and Inglis 1986; Montgomerie and Weatherhead 1988; Redondo 1990). In particular, in order to test parental investment allocation, an experimental paradigm in which brood size (an index of brood value) and cumulative past investment are manipulated independently, has been designed (Sargent and Gross 1985) and applied to analyse patterns of parental defence of the brood in a fish species (Coleman et al. 1985).

In the present study, the experimental design by Sargent and Gross (1985) was adapted to the house mouse so as to obtain, at a certain point of the lactation period, dams with litters of equal size but unequal amounts of cumulative past investment and, conversely, dams with litters of unequal size but equal amounts of cumulative past investment (see Methods for the details). Parental investment decision rules were tested by means of a litter defence test. In house mice, it is commonly accepted that post-partum maternal aggression serves to protect the offspring, e.g., from potentially infanticidal male conspecifics (Ostermeyer 1983; Maestriperi, submitted for publication). Litter defence by a mouse dam is presumably to be considered a form of unshared parental investment (*sensu* Lazarus and Inglis 1986) since it simultaneously benefits all pups in the litter. Since the risk of receiving serious injuries from a male intruder is relatively low and 'present cost' (Lazarus and Inglis 1986) associated with a reduced chance of survival of the altricial offspring is consequently unlikely, the predicted variation in litter defence as a function of offspring number should be easily observable and, in fact, it has already been observed (Maestriperi and Alleva, 1990; Maestriperi and Rossi-Arnaud 1991, in press). A further aim of the present study was therefore to point out that maternal aggression, as measurable in a simple behavioural

test, can provide a rather sensible indicator of parental investment in house mice and, in particular, can constitute a suitable experimental paradigm for testing parental investment allocation (see also Maestripieri 1991, in press).

Methods

Sixty nulliparous female mice of a Swiss-derived (CD-1) strain (age 50–70 days) purchased from Charles River Italia (22050 Calco Italy) were used. Females were housed in pairs in opaque Plexiglas cages (33 × 13 × 14 cm) covered with a metal top. All animals were maintained in the same air-conditioned room at $21 \pm 1^\circ\text{C}$ and $50\% \pm 10\%$ relative humidity, with a reversed lighting schedule (white lights on from 9:30 p.m. to 9:30 a.m.). Pellet food and water were available *ad libitum*.

After acclimatization, both females of a pair were mated with a sexually experienced adult male which was left in their cage for 10 days. After the removal of the male, pregnant females were housed individually. At delivery, dams were randomly assigned to one of four conditions ($n = 15$). In the Early removal group (E group), litters were culled to 4 pups. In the Late removal group (L group), litters were culled to 8 pups, but 4 further pups were removed on day 8 of their age. In the Control group (C group), litters were culled to 8 pups. In a further control group (Control-Late group, CL), litters were manipulated as in the L group except that the 4 pups were returned to the litter after a 10-min removal. In all groups, litters contained the same number of male and female pups.

Litter defence by dams against a male intruder was scored when the pups were 8 days old (day of delivery was considered as day 0), 3–4 hr after manipulation in the L and CL groups. Tests of aggression were therefore carried out when dams had already considerably invested in their litters (see König and Markl 1987), and maternal aggression was expected to be at a high level (Ostermeyer 1983).

Previously isolated (2–3 weeks) adult male mice of the same strain were used as intruders. All males had previous mating experience 30–40 days before testing. The use of males with a relatively recent (within 12–50 days) mating experience considerably reduces the probability of occurrence of infanticide (vom Saal 1985). The male, marked by a black spot on his back, was introduced for 5 min into the home cage of the female in the presence of her litter. All dams and male intruders were used only once. Tests were carried out between 11:00 a.m. and 2:00 p.m.. Each test session was videorecorded and successively reanalysed for behavioural scoring. Sampling technique was “all occurrence” (Altmann 1974).

The following categories and elements of female behaviour (most of which are defined in Grant and Mackintosh 1963) were considered: (1) proportion of attacking females, that is, the number of pairs in which overt attack by the female occurred; (2) latency to the first attack, that is, the time (in seconds) elapsed from the introduction of the male to the first biting attack by the female; (3) number of attacks; (4) total attacking time (TAT); (5) number of tail rattling episodes; (6) latency to the first submissive posture, that is, time (in seconds) elapsed from the introduction of the male to the first time the female was observed in a crouched submissive posture; (7) number of submissive postures.

Non-parametric tests were used for statistical analysis. Probabilities are two-tailed unless otherwise specified.

Results

The following proportion of females in the four groups displayed overt aggression towards the male intruder: 9/15 in the E group, 8/15 in the L group, 13/15 in the C group, and 12/15 in the CL group (chi square = 5.39, $df = 3$, NS). The total attacking time and the number of attacks and tail rattling episodes differed significantly between the four groups (Kruskal-Wallis analysis of variance: number of attacks, $H = 8.41$, $P < 0.05$; TAT, $H = 9.98$, $P < 0.02$; number of tail rattling episodes, $H = 10.77$, $P < 0.02$). Since the information obtained by the analysis of number of attacks and total attacking time appeared to be to a large extent superposable, only that referring to total attacking time will be presented. Overall, the larger the litter size at the time of testing (in the C and CL groups) the higher the aggression rate. Fig. 1 (a and b) shows TATs and tail rattling episodes in the four groups. TATs in the C and CL groups were higher than those by females of the L (Mann-Whitney U test; C, $U = 60$, $P < 0.05$; CL, $U = 58.69$, $P < 0.03$) and the E group (C, $U = 64$, $P = 0.05$; CL, $U = 54.66$, $P < 0.02$) (Fig. 1a). Tail rattling episodes were more frequent in the C group than in the L and the E groups (L and E, $U = 57.5$, $P < 0.05$). They were also higher in the CL than in the E and L groups even though in the latter case the difference just missed statistical significance (E, $U = 57.5$, $P < 0.05$; L, $U = 64.6$, $P < 0.1$) (Fig. 1b). Both scores were not significantly different between the C and CL groups and between the L and E groups. No significant differences were found with respect to the latency to the first female attack ($H = 0.76$, $df = 3$, NS).

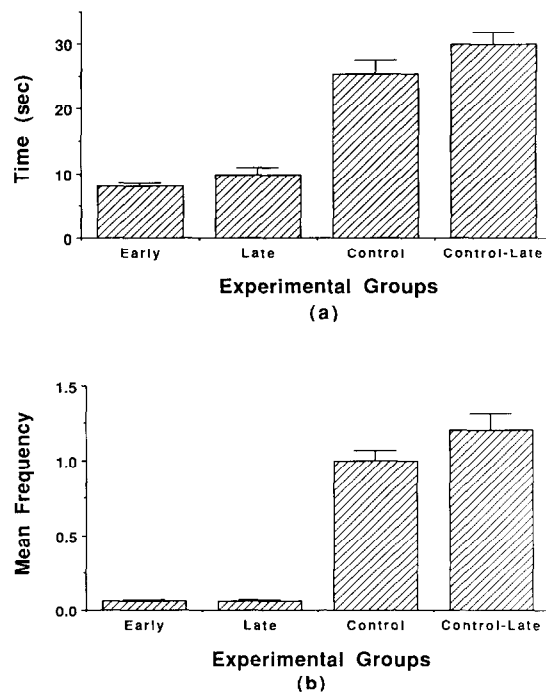


Fig. 1. (a) Total attacking time of the females in the four groups (mean and SEM); (b) mean frequencies (and SEM) of tail rattling episodes displayed by the females in the four groups.

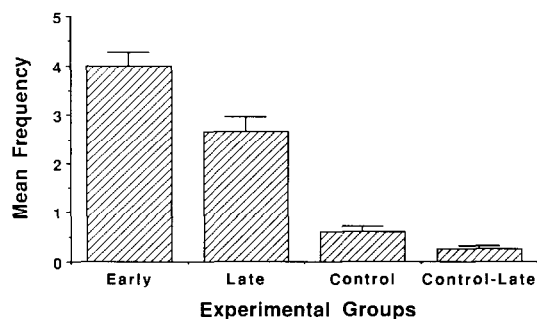


Fig. 2. Mean frequencies (and SEM) of submissive postures displayed by the females in the four groups.

The analysis of submissive postures shown by females confirmed only partially the view that the females with smaller litters at testing were less aggressive than those with larger litters. In fact, this score differed between the four groups ($H = 8.58$, $P < 0.05$; see Fig. 2). E females were more prone to show submissive behaviour than C ($U = 60.5$, $P < 0.05$) and CL ($U = 55.6$, $P < 0.02$) females. No significant differences were found between L females and those of the other three groups, and between the C and CL groups. No significant differences between the four groups were also found in the latency to the first submissive posture ($H = 0.11$, NS).

Males neither committed infanticide during the 5-min tests nor reacted aggressively to the females' attacks. When opposed to aggressive females, the intruders were rapidly attacked, and they only reacted with attempts to flee or by displaying defensive upright postures.

Discussion

The results of the present study show that mouse dams having larger litters at the time of testing displayed more intense maternal aggression towards an unfamiliar male intruder than dams having smaller litters. Noticeably, dams whose litters had been reduced 3–4 hours before testing (L group) showed a lower level of maternal aggression when compared to dams whose litter size had not been altered. Since a comparable reduction in maternal aggression did not occur in the CL group, where the dams and their pups were subjected to a similar degree of manipulation, the experimenter's disturbance of the dams seemed not to be responsible for their differences in behaviour. One cannot, however, rule out the possibility that loss of pups *per se*, besides litter's handling, constituted a stressful experience for L dams with a relatively short-lasting effect of reduction in maternal aggression. The ideal control to this possibility, i.e. to retest L dams later on would, however, have drawbacks in not being totally compatible with the experimental design (e.g., for comparisons of past investment in the different groups) and as the experience of repeated tests of maternal aggression can affect later behaviour (Green 1978).

Mouse dams are known to behave differently towards intruders of different reproductive status and infanticidal potential (Parmigiani et al. 1988; Elwood et al. 1990). However, when these variables are held constant, it has been suggested that

the dam's behaviour affects the male's rather than vice versa (Maestriperi and Alleva, 1991 in press). Thus, in this case where all intruders had the same age and reproductive experience it is unlikely that differences in female behavior have arisen from differences in the males' behaviour towards litters of different size (see Maestriperi and Alleva, 1991 in press). On the other hand, recent research on proximate mechanisms regulating the onset and the maintenance of mouse post-partum fighting has highlighted the role played by direct pup stimulation on the mother's aggressive behaviour. Even though the primary role of suckling stimulus in triggering post-partum aggressive behaviour has repeatedly been acknowledged (see Svare 1977), other nonsuckling tactile (e.g. nuzzling) or nontactile (visual, auditory and olfactory) exteroceptive stimuli provided by pups have been suggested to play a major role, particularly in the midlactation phase (days 6–12; Garland and Svare 1988). A finer regulation of maternal aggression on pup stimuli would be particularly adaptive in such a period, since considerable investment has already been made in the pups, and the latter are still at a considerable risk of infanticide. Quantitative differences in exteroceptive stimulation provided by litters of different sizes thus conceivably provide an effective means for fine tuning the intensity of litter defence to its size.

A functional interpretation of our results suggests that the intensity of maternal defence of the litter is adjusted according to the actual number of offspring being defended, regardless of the number of pups the dams have reared until the time of testing. Therefore, it seems that mouse mothers defend their investment according to the value of their litters rather than to the amount of past investment made in them.

In the house mouse, past investment by dams in litters of different size might be expected to affect the level of optimal litter defence in different ways. On the one hand, defence of larger litters should be enhanced since rearing them brings about higher costs on the dam's future reproduction (i.e., a delay in the subsequent parturition due to prolonged time required for pup weaning; Fuchs 1982). On the other hand, defence of smaller litters should be enhanced since their pups are slightly more developed (and hence, more valuable) when compared to same-age pups from larger litters. Finally, investment made by a female mouse in her litter is expected to be highly correlated to offspring number and it can represent *per se* a good, if indirect, measure of expected benefits.

However, it is remarkable that, following the experimental manipulations carried out in the study, if dams of the L group had defended their pups according to past investment, and hence more than those of the E group, they would have actually committed the Concorde fallacy. In fact, in this case, past investment in the litter did not correlate with litter size at the time of testing. Therefore, to base parental strategies on past investment would be particularly misleading in situations similar to that artificially created by our experimental manipulation (i.e., a relatively early pup loss). On the contrary, the results of this study suggest that house mice are able to use indicators of future reproductive success other than past investment, e.g., a more direct evaluation of the litter value. Moreover, house mice seem to have evolved the capabilities to adjust adaptively their parental strategies in response to unpredictable changes in litter size, as it has been previously reported to occur in similar situations in other vertebrate species (Robertson and Biermann 1979; Carlisle 1985; Ridgway 1989).

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