

The effect of a single dose of testosterone propionate on activity, and natal dispersal in the meadow vole, *Microtus pennsylvanicus*

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In *Microtus* spp. sex ratio is not important as a determinant of dispersal unlike in the grey-sided vole *Clethrionomys rufocanus* where females that disperse tend to come from male biased litters. In male biased litters the probability that females are exposed to testosterone *in utero* is high and it is thought that the testosterone exposure mediates dispersal. Here we test whether a single dose of testosterone propionate mediates dispersal in meadow voles, *Microtus pennsylvanicus*. Females exposed to testosterone propionate at birth are more active than females not exposed to testosterone but their dispersal tendency measured in large outdoor enclosures is probably not increased. Dispersal tendency of female meadow voles is thus more flexible than that of female grey-sided voles.

1. Introduction

Dispersal is a critical population parameter which may affect density dynamics as well as genetic makeup. Much controversy exists about the mechanism and effects of dispersal (for a general reference see Stenseth and Lidicker 1992). Pusey (1987) has hypothesized that dispersal in mammals, which is male biased, is triggered by testosterone and serves in part, to decrease inbreeding. It is not known how testosterone might work to effect dispersal behavior, but some studies suggest that testosterone exposure early in life can alter dispersal patterns exhibited by juveniles and adults.

Holecamp et al. (1984) found that female Belding's ground squirrels injected with testosterone

propionate (TP) as newborns exhibited dispersal behaviour later in life similar to that of males. Androgens are strongly suggested as control agents of natal dispersal in the Belding ground squirrel because males leave the natal home range while females tend to remain (Holecamp et al. 1984). Testosterone, also, has been shown also to affect many behaviors such as aggression, food intake and sexual activity in laboratory rodents (Beatty 1979; vom Saal et al. 1983; vom Saal 1984).

Testosterone has been administered to animals in the field experimentally to determine its effects on aggression. Gaines et al. 1985 experimented with implanting testosterone in silastic tubing to increase aggressiveness in male prairie voles *Microtus ochrogaster*. Krebs et al. (1977) gave

male *M. townsendii* subcutaneous implants of testosterone but did not find that this treatment increased aggression compared with control animal. However, Taitt and Krebs (1982) found that testosterone implanted female *M. townsendii* showed increased wounding, larger home ranges, and reduced survival.

Females may be exposed to testosterone early in life in the uterus, through what is known as the IUP or intrauterine phenomenon. This theory states that a female positioned between two males in utero is exposed to testosterone secreted by the adjacent males (vom Saal 1984). Therefore, if testosterone effects dispersal behavior, females which are exposed to testosterone in the uterus should exhibit dispersal tendencies.

Ims (Andreassen & Ims 1990, Ims 1987, 1989, 1990) has convincingly shown that a major portion of the variation in dispersal tendency of female grey-sided voles (*Clethrionomys rufocanus*) is explained by litter sex ratio. Females from male biased litters show a high tendency to disperse. In male biased litters there is a high probability for females to be located next to males and thus be exposed to testosterone. Dispersal tendency of female meadow voles *M.*

pennsylvanicus does not appear to be explained by sex ratio (Bondrup-Nielsen 1992).

In this experiment we injected newborn meadow voles with a single dose of testosterone propionate to determine the effect on activity under laboratory conditions and on spacing behaviour in outdoor enclosures. Working in large out-door enclosures has the advantage that several parameters relating to the study animals but not weather and season can be controlled. However, results obtained from studies using enclosures may not directly relate to what animals do under natural conditions but probably points in the direction for what to expect.

2. Material and methods

2.1. Study animals

The meadow voles used in the study of activity were live-trapped in May 1991 and the animals for the field trials were live-trapped in May 1992 in the Gaspereau Valley, Nova Scotia, Canada. Voles caught were brought back to the lab, weighed, sexed and toe-clipped for individual identification. The voles were then paired at random. All voles were housed in plastic cages (15 × 22 × 45 cm) with wire tops. Wood chips and cotton were provided for bedding and nesting material and was changed weekly. The room temperature was maintained at 20°C and the photoperiod was 16L:8D. The voles received ad libitum Purina Rodent Laboratory Chow (#5001) and grass or hay. Also, a vitamin supplement (Biotin Stress Pak) was added to the water throughout the experiment.

Once females had given birth all individuals in a litter received the same treatment and were injected (30G needle) subcutaneously either with a solution of testosterone propionate in sesame oil or pure sesame oil within 36 hrs. Litters deemed control were injected with 0.025 ml of sesame oil. Litters deemed experimental were injected with 500 microliters testosterone propionate (TP) dissolved in 0.025 ml sesame oil. Animals used for the Activity and the Field Study were different (see below).

2.2. Activity study

A total of 44 individuals from 10 litters were injected with TP (27) and oil only (17). We used the same method for determining activity as described by Wong and Bondrup-Nielsen (1992). Individuals between the ages of 5 to 8 weeks were placed in a terrarium and video taped for ten minutes. Tapes were viewed later and the various categories of activity (Tabel 1) were summed and compared within sex between treatments using the Mann-Whitney *U* statistic.

Table 1. Ten behaviour categories defined and used to record the activity of the meadow voles during ten minute behaviour trials.

Behaviour	Description
Huddle	vole motionless, limbs together
Stationary	vole standing or sitting still, eyes open and may or may not be displaying sniffing behaviour
Grooming	vole scratching and/or licking fur
Reaching	vole on hind legs and stretching front legs up wall of the arena
Rearing	vole on hind legs in the centre of arena with nose in air
Walking, Edge	vole moves at moderate pace along edge of arena
Walking, Centre	vole moves at moderate pace through centre of arena
Running	vole moves rapidly from one point to another
Digging	vole scratches at floor or wall of arena with front paws
Other	behaviour not classified by above categories

2.3. Field study

In total, 17 litters were injected, 8 control and 9 experimental, totalling 115 individuals. All animals were released in the field, however, only 98 voles were used in the analysis as 17 animals were never caught or known to have died.

For seven days after birth, the litters were kept in the lab to ensure that all individuals were healthy. They were then moved to a field enclosure in the Gaspereau Valley. The enclosures consisted of a sheet metal fence with 1m sections of corrugated steel buried approx. 40 cm in the ground and bolted together. Fish gill net was suspended 2 meters above the enclosure supported by poles and wire and draping over the sides to prevent any predators from entering (see Bondrup-Nielsen 1992). Each enclosure measured 30 by 40 meters and contained 48 trapping stations, in a 6 × 8 grid, each at 5 m intervals. The metal fence that separated the enclosures had eight small holes (5 × 5 cm) along the bottom to allow voles to move between the two. Although the grass cover within each enclosure varied to a small degree this variation did not appear to affect population dynamics of meadow vole populations studied over four years (pers. obs.).

Each litter and mother was initially placed in a wire cage (30 × 15 × 15 cm) with hay, cotton, Purina Rodent Chow #5001, and vitamin supplemented water. Each cage was placed at one of five locations in the same enclosure. After five days the mother and litter were taken out of the cage (cage removed) to allow the litter and mother to move as they pleased. The cotton nesting material and Rodent Chow were left at the spot. This allowed for a natural weaning process to occur which usually takes place at 18–20 days of age. Only five litters were present in the enclosure at any one given time to keep the density fairly low but relatively constant throughout the experiment.

For a period of 12 weeks, starting in the middle of June, voles released in the enclosures were live-trapped for two days each week. Each trap session consisted of eight checks, approximately 7 am, 12 pm, 4 pm and 8 pm, over two days. The traps were left open during the rest of the week. Each group of voles was live-trapped for three weeks after weaning to allow for natal dispersal data only. Some adults, including mothers, were left in the enclosures to keep the density of adults even throughout the experiment.

The live-traps used were Ugglan multiple capture traps. Each trap was baited using rolled oats and apple. Once caught, a vole's individual number, sex, time, date and station at which it was caught were recorded. Weight was only recorded once per trapping session. At the end of the three weeks the litters were removed from the enclosures. The live-trapping data was analyzed to determine the effect of TP on space use and home range size. We used the minimum polygon method to estimate home range size.

Five main space use patterns were defined: Type 1 — “Home range at release site” — this included voles which set up a home range at the site where they had been released; Type 2 — “Home range within release en-

closure” — voles established a home range within the enclosure where they had been released but not at the release site; and Type 3 “Home range in the adjacent enclosure” — voles established home ranges within the adjacent enclosure. A comparison of space use patterns was analyzed using a Contingency table.

3. Results

3.1. Activity

A single injection of testosterone propionate had a significant effect on activity, particularly in females (Table 2). Experimental females that received one injection of TP at birth showed greater measures for “Walk, centre”, “Reach” and “Running” than control females (Table 2). Experimental males injected with TP were less “Stationary” and were “Running” more than controls (Table 2). For combined activities experimental females were much more active than controls (Table 2). Experimental males showed similar although not as marked trends as experimental females.

3.2. Dispersal and home range size

The survival rate of juvenile meadow voles was measured as the total number of voles surviving from release to the end of the three week study period. There was no significant difference in survival between controls and experimentals ($\chi^2 = 0.68$; $p = 0.41$). Trappability was measured as the total number of times individuals were caught during the three week study period. The mean trappability of each treatment were compared using a Mann-Whitney U test and found to be not significant ($U = 1127.3$; $p = 0.52$).

Growth rate and body size between control and experimental animals was not affected by the neonatal injection of TP (Table 3).

The testosterone injection appeared to have a small, but insignificant, effect on the home range size used by both juvenile males and females. Experimental males and females showed a minor tendency to inhabit larger home ranges (Table 4).

There was no difference in space use between experimental and control males or females ($\chi^2 = 14.91$, $p = 0.25$ (Table 5). However, eight

Table 2. The mean time ($\pm SE$) in seconds that females and males of the two treatments, control and testosterone propionate injected (Experimental), (sample size in parenthesis) spent performing each of ten activities (differences between control and experimental tested using Mann-Whitney *U* statistic, *Z* value shown).

Behaviours	Females		Males	
	Control (10)	Experimental (14)	Control (7)	Experimental (13)
Huddle	325.6 \pm 32.9 <i>Z</i> = -1.76 <i>P</i> = 0.08	234.0 \pm 36.2	127.3 \pm 35.8 <i>Z</i> = -0.28 <i>P</i> = 0.78	145.0 \pm 28.8
Stationary	46.0 \pm 16.7 <i>Z</i> = -0.94 <i>P</i> = 0.35	25.2 \pm 7.1	125.32.2 \pm 15.81 <i>Z</i> = -2.89 <i>P</i> = 0.004	29.3 \pm 4.6
Walk, edge	59.4 \pm 12.9 <i>Z</i> = -1.46 <i>P</i> = 0.14	97.9 \pm 15.9	98.7 \pm 10.2 <i>Z</i> = -0.60 <i>P</i> = 0.55	103.3 \pm 6.5
Walk, centre	11.0 \pm 3.6 <i>Z</i> = -2.11 <i>P</i> = 0.03	21.9 \pm 3.6	19.8 \pm 6.2 <i>Z</i> = -0.63 <i>P</i> = 0.53	28.1 \pm 6.2
Reach	37.8 \pm 6.6 <i>Z</i> = -2.28 <i>P</i> = 0.02	74.1 \pm 10.8	74.7 \pm 6.5 <i>Z</i> = -0.95 <i>P</i> = 0.34	90.9 \pm 9.8
Groom	110.0 \pm 17.5 <i>Z</i> = -0.62 <i>P</i> = 0.54	124.8 \pm 13.8	212.1 \pm 25.1 <i>Z</i> = -1.47 <i>P</i> = 0.14	158.7 \pm 13.0
Standing	4.8 \pm 16.7 <i>Z</i> = -0.68 <i>P</i> = 0.50	10.7 \pm 3.8	26.4 \pm 6.6 <i>Z</i> = -0.40 <i>P</i> = 0.96	24.5 \pm 7.1
Running	0.8 \pm 0.6 <i>Z</i> = -2.00 <i>P</i> = 0.05	4.7 \pm 1.7	0.0 \pm 0.0 <i>Z</i> = -2.05 <i>P</i> = 0.04	12.7 \pm 8.4
Dig	3.9 \pm 3.2 <i>Z</i> = -0.35 <i>P</i> = 0.73	3.4 \pm 2.4	4.1 \pm 4.1 <i>Z</i> = -0.93 <i>P</i> = 0.35	6.2 \pm 2.7
Other	0.8 \pm 0.43 <i>Z</i> = -1.66 <i>P</i> = 0.10	3.4 \pm 1.4	2.0 \pm 1.2 <i>Z</i> = -0.56 <i>P</i> = 0.57	1.2 \pm 0.6
Combined activities:				
Huddle and Stationary	371.6 \pm 25.5 <i>Z</i> = -2.11 <i>P</i> = 0.04	259.1 \pm 34.3	253.1 \pm 20.1 <i>Z</i> = -1.94 <i>P</i> = 0.05	174.4 \pm 28.4
Walk (edge and centre), and Run	71.2 \pm 16.2 <i>Z</i> = -1.87 <i>P</i> = 0.06	124.5 \pm 17.6	118.5 \pm 13.5 <i>Z</i> = -1.15 <i>P</i> = 0.25	114.1 \pm 15.4
Reach, Groom, Rearing, Dig, and Other	156.4 \pm 17.4 <i>Z</i> = -2.25 <i>P</i> = 0.02	212.9 \pm 18.7	226.4 \pm 26.5 <i>Z</i> = -1.62 <i>P</i> = 0.10	280.3 \pm 18.6

Table 4. A comparison of home range size in meters squared (HR)($\pm SD$) for males and females of both treatments using an unpaired *t*-test.

	HR	<i>t</i> -value Probability
Female		
Control <i>n</i> =15	160.0 \pm 46.1	1.28
Experimental <i>n</i> =23	192.4 \pm 90.3	<i>p</i> = 0.21
Male		
Control <i>n</i> =15	135.0 \pm 52.4	1.2
Experimental <i>n</i> =15	158.3 \pm 54.0	<i>p</i> = 0.24

experimental females compared to only 2 control females dispersed across the fence but this was not significant. Only one experimental male established a home range in the release enclosure (space use pattern Type 3) compared to five control males.

Litter size and sex ratio did not influence the space use pattern of individual voles, whether control or experimental.

4. Discussion

Neonatal exposure to testosterone caused an increase in activity later in life particularly of females. These results are consistent with those of

other studies (Beatty 1979). The effect of neonatal exposure to testosterone on home range size and dispersal was not clear. Although 8 of 29 testosterone exposed females entered the adjacent enclosure and only 2 of 25 control females did so this was not significant. These results, therefore, are not consistent with the study done by Holecamp et al. (1984) in which female Belding's ground squirrels exposed to TP exhibited higher dispersal rates.

Currie (1995) studied space use of non-manipulated meadow voles in two 35 by 105 meter enclosures by live trapping. Female voles were captured at weaning age (about 15 to 21 days of age) and released them at the point of capture immediately after recording their activity in the field using much the same method as this study. Females that dispersed (settled on breeding home ranges away from the natal home ranges) were more active than females that were philopatric as breeding adults. This supports the hypothesis that increased activity is correlated with a tendency to disperse.

Wong and Bondrup-Nielsen (1992) studied the long-term effects of malnutrition on activity of meadow voles. Females malnourished as infants showed increased activity and had activity profiles similar to that of males whether malnourished as infants or not (Wong & Bondrup-Nielsen 1992). The activity profiles of infant malnourished meadow voles and testosterone injected meadow voles from this study were very similar. Increased activity on the part of females may relate to stress where the stress can be in the form of high levels of testosterone, malnutrition and maybe even high density. Female meadow voles from a high density island population had activity levels similar to that of females malnourished as infants and injected with TP at birth (Nichols unpublished data).

In a study of growth rates of meadow voles fed different diets there was a significant maternal effect (Bondrup-Nielsen & Folley 1993). In this study all individuals of a litter received the same treatment. Although some litters on average may have been prone to be more active than other litters there was still a significant effect due to treatment. There was no maternal effect on space use. Roughly equal fractions of young from a litter exhibited the three types of space use

patterns.

It appeared that experimental females established slightly larger home ranges than the control females, although the difference was not significant. These results are consistent with Zielinski et al. (1992) who found that 2M females (females which had testosterone exposure in utero) had larger home ranges than 0M females (females with no testosterone exposure). Male experimental voles also showed a slight but not significant increase in home range size. These results suggest that high testosterone exposure of female and male neonates will slightly alter home range sizes used as juveniles. It is possible that the effect of testosterone is dosage dependent. That is, a certain amount of testosterone exposure has to occur before an effect on space use becomes evident, but dispersal tendency may be independent of activity and home range size.

Many studies support the hypothesis that dispersal is density dependent (Stenseth 1983). The higher the density, the higher the amount of competition, and hence the higher dispersal rates. In this study the density was kept relatively constant, so if density promotes dispersal, then each vole had the same probability or chance of dispersing. This shows that difference in juvenile dispersal rates can not be explained by density in this particular study. However, there is the possi-

Table 5. Contingency table for spatial patterns (for a description see Material and methods) by individual control and experimental males and females.

	Males		Females	
	Exp.	Contr.	Exp.	Contr.
Philopatric	5	6	8	9
Philopatric with excursion	5	3	5	5
Dispersal across fence	5	4	8	2
Dispersal on same side of fence	1	5	6	7
Everywhere	7	3	2	2
Total	23	21	29	25

bility of a seasonal effect which could not be controlled for.

Wolff (1992) has shown that in white-footed mice (*Peromyscus leucopus*), natal dispersal by an individual is affected by the presence of the opposite-sexed parent, which supports the hypothesis that dispersal has in part evolved to suppress inbreeding. In this study due to the experimental nature a litter's mother was always present, males density was kept constant throughout the experiment; the biological father of the litters were not necessarily present but reproductive males generally roamed throughout the enclosures. Therefore, nothing can be concluded from the effect of parents on dispersal but conditions throughout the experiment varied as little as possible.

Pusey (1987) proposed that sex biased dispersal in mammals evolved to prevent inbreeding. But literature is contradictory with respect to inbreeding avoidance. Pugh and Tamarin (1988) found that the meadow vole does not avoid inbreeding when mating. The findings of Bollinger et al. (1991), however, do suggest that the meadow vole does avoid inbred matings. Bollinger et al. (1993) found that dispersal tendency in meadow voles is increased when siblings are present. In this study there was no difference in the number of siblings present between control and experimental groups. Sandell et al. (1990) found contradictory results for inbreeding avoidance in *M. agrestis* but suggest that inbreeding avoidance is not an important factor behind dispersal in this species. The literature on inbreeding avoidance in microtines is clearly controversial and more studies are required.

The results of this study suggest that a single high dose of testosterone early in life will not affect natal dispersal behaviours of meadow voles, although dosage level and timing of injection were not experimented with. Ims (1989, 1990) has shown that female grey sided voles that disperse tend to come from male-biased litters. However, it appears that for *M. pennsylvanicus*, sex ratio and testosterone exposure does not affect dispersal tendency of females. It is therefore only the grey-sided vole where female dispersal is affected by sex ratio. Why this difference? First of all, it is essential to determine if female dispersal in other *Clethrionomys* sp. is similarly to

that of the grey-sided vole. If this is the case then we must look for broad differences between *Clethrionomys* spp. and *Microtus* spp. to determine why it is adaptive for *Clethrionomys* spp. to have somewhat inflexible dispersal mechanism. In *Clethrionomys* spp. young females cannot mature on their mothers home range but must find available space where they can set up an exclusive home range (Saitoh 1981, Bondrup-Nielsen 1986). In *Microtus pennsylvanicus* sexual maturation of daughters may occur on the mothers home range and dispersal is not essential for sexual maturation to occur (e.g. Rodd & Boonstra 1988).

Studies of the determinants of dispersal in female *Clethrionomys* spp. other than *C. rufocanus* are sorely needed.

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