Behav Ecol Sociobiol (1985) 17:297–302

Behavioral Ecology and Sociobiology

Sex differences in the energy allocation strategies of house mice

Glenn Perrigo and F. H. Bronson
Institute of Reproductive Biology, Department of Zoology, University of Texas, Austin, Texas 78712, USA

Received November 22, 1984 / Accepted March 18, 1985

Summary. Sex differences in energy allocation were studied in wild stock house mice (*Mus domesticus*). Peripubertal animals of both sexes, either intact or gonadectomized, were subjected for 8 weeks to one of two feeding requirements by using a caging system in which a pellet dispenser was controlled by activity on a running wheel. Recently weaned animals were required to run 200 vs 300 or more wheel revolutions to obtain a pellet of food. The 200 revolution requirement allowed normal body growth and reproductive development; the 300+ requirement was adjusted weekly to maintain food intake at a level that allowed survival but did not permit normal body growth. Reproductive development was completely inhibited in intact females at 300+ revolutions whereas intact males at 300+ revolutions, despite stunted growth, all experienced normal sexual development. At both feeding requirements, however, females exhibited more total locomotor activity and consumed more food than males, regardless of gonadectomy. Furthermore, at the 200 revolution requirement we often observed extensive running activity beyond that needed to generate the amount of food actually eaten, especially among females. This "extra" locomotor activity was gonad-dependent in males, but not so in females. These results suggest that male and female house mice employ different strategies when relating their behavior and reproductive development to existing foraging conditions. Females appear more resource-dependent than males.

Introduction

All mammals share a fundamental energy-related concern: once the initial locomotor and thermoregulatory costs of obtaining food have been met, surplus energy must be allocated parsimoniously among a variety of competing behavioral and somatic demands, particularly those associated with reproduction (e.g. Calow and Townsend 1981). All such needs can be met when feeding conditions are ideal; but when food is scarce a mammal is faced with complex options for partitioning its limited supply of energy. Foraging effort may be increased while some or most other behaviors are curtailed, or energy simply may be shunted differentially to some physiological needs at the expense of others.

In response to obvious geographic and seasonal factors, mammals have evolved diverse strategies for countering energy-related challenges. One also expects such strategies to vary with the age, reproductive state and sex of the individual (e.g. Fisher 1930; Williams 1966; Schoener 1971; Pyke et al. 1977), but these expectations remain only modestly documented (e.g. Clark 1980, Clutton-Brock et al. 1982; Hoffman 1983). The energy-related strategies of small mammals, however, have proven difficult to study. Their cryptic life style hinders a direct examination in the field, while the complex energetic challenges posed by natural habitats are difficult to duplicate in the laboratory. Small mammals often must travel great distances while foraging; thus in the present research we employed a special caging system in which young house mice were challenged to obtain food by working on a running wheel.

The purpose of this experiment was to compare several dimensions of energy allocation between male and female house mice during peripubertal development. We also gonadectomized both sexes to assess the impact of the gonads in relation to energy allocation. Two feeding conditions, defined by the relationship between locomotor effort and food availability, were chosen for study: one which allowed sufficient food for normal post-weaning body growth while the other did not. We report several striking differences in the way the two sexes of house mice reacted to these energetic challenges. Some of the differences were gonad-dependent and others were not.

Methods

Animals. All house mice (*M. domesticus*, see Berry 1981) were from our laboratory breeding colony whose ancestors were trapped in granaries near Calgary, Alberta in 1979. A synchronized mating produced large numbers of 20 day old weanlings culled to the following body weights: 12.6±1.0 g (range) for females and 13.2±1.5 g for males. Ten animals of each sex were anesthetized with Nembutal and gonadectomized on the day of weaning. Another ten animals of each sex underwent sham operations. After surgery, animals were isolated for seven days in 28 × 18 × 12 cm polypropylene cages with pine shaving bedding and ad lib food and water.

Experimental design and procedures. The caging system is illustrated in Fig. 1. An animal must emerge from its nest burrow and run a pre-set number of revolutions on a running wheel to obtain a 45 mg food pellet. Two feeding regimens were used: a requirement of 200 revolutions of the running wheel for each food pellet vs a requirement of 300+ revolutions for each food pellet. Since an objective of the latter treatment was to inhibit body growth, it was necessary to adjust the revolution requirement slightly upwards several times during the experiment. Peripubertal house mice of both sexes, either intact or gonadectomized, were subjected to one of these two feeding regimes in a single replicate 2 × 2 × 2 factorial design with five animals per cell. The experiment began one week after weaning (27 days of age) and ended 8 weeks later (84 days of age).

One week after surgery all 40 animals were placed in running wheel cages with the sexes distributed equally among several rooms (L:D 14:10; 20±0.5° C). The mechanical discharge noise of the pellet dispenser was an adequate conditioning stimulus; animals quickly learned to associate running activity with obtaining food. The initial first day requirement of 100 wheel revolutions per pellet was increased over the next several days in increments of 50 revolutions per day to either 200 or 300 revolutions per pellet. Body weights were recorded at weekly intervals; thus whenever the four groups maintained at the 300+ requirement began gaining weight we raised the running requirement by 20 revolutions/pellet. It should be stressed that this "best guess" adjustment was applied uniformly among all four groups to maintain treatment consistency. By the end of the experiment the 300+ groups actually were feeding at 400 revolutions/pellet.

Behavioral and reproductive measurements. Several ongoing behavioral measurements were obtained during this experiment. First, the number of revolutions run (and food pellets received) was noted daily. Second, the amount of food consumed by each animal was tallied weekly. Any surplus food remaining in the cage or food cup was removed daily; thus, food intake was corrected for uneaten food. Third, a weekly assessment of each animal's "extra" running activity was made. "Extra" was defined as all running activity on the wheel beyond that required to generate the amount of food that was actually consumed by an animal. Since we removed uneaten food from cages daily, extra activity was measured simply by multiplying the number of uneaten food pellets by the number of revolutions required for a pellet. Finally, at the end of the experiment, intact animals were autopsied. Gonads and secondary sex organs were removed and weighed; sperm in the vas deferens and testes were counted (Kirton et al. 1967), and ovaries and oviducts were examined for evidence of ovulation (see Perrigo and Bronson 1983).

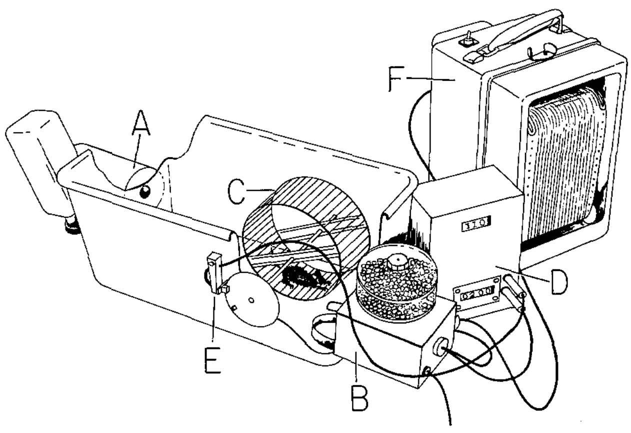

Fig. 1. This cage measures 48 × 27 × 20 cm. The bottom is 1/4-inch (6.5 mm) wire mesh and the cage is supported by 3-inch (75 mm) bolts to allow waste to drop below the cage. A coffee can (A) filled with raw cotton serves as a nest burrow. An automatic pellet dispenser (B, Ralph Gerbrands Co., Arlington, Mass.) is positioned over a feeding cup and delivers 45 mg food pellets (P. J. Noyes, Co., Lancaster, NH; Formula A: 24% protein, 6% fat, 53% carbohydrates, 4.5 Kcal/gram) when animals run on an 8 cm wide and 17 cm diameter running wheel (C). The axle of the wheel is supported by teflon bearings imbedded in both sides of the cage; a lock nut adjustment on the axle allows tension standardization. The number of revolutions required for a pellet is programmed by an electronic interface (D); wheel revolutions are detected by an IR photocell (E). An Esterline-Angus chart recorder (F) provides a temporal record of running activity and pellet delivery

Statistical assessment. In the case of body weight and the behavioral measurements, probability levels were determined by a repeated measures three-way factorial ANOVA for assessing both general treatment effects and weekly time course differences (BMDP computer program P4V; see Davison and Toporek 1983). All autopsy data were analyzed by one-way ANOVAS within each sex.

Results

Body growth, food consumption, and total locomotor activity

As shown in Fig. 2, we effectively inhibited body growth in all four groups maintained at 300+ revolutions, while the four groups maintained at 200 revolutions continued to gain weight throughout the experiment [$F_{1,32} = 32.7$, $P < 0.001$]. The growth curves of the intact animals maintained at 200 revolutions are typical of ad lib fed animals of this stock maintained one per cage in the absence of a running wheel (see Bronson 1984a). As predetermined by our imposed treatments, animals

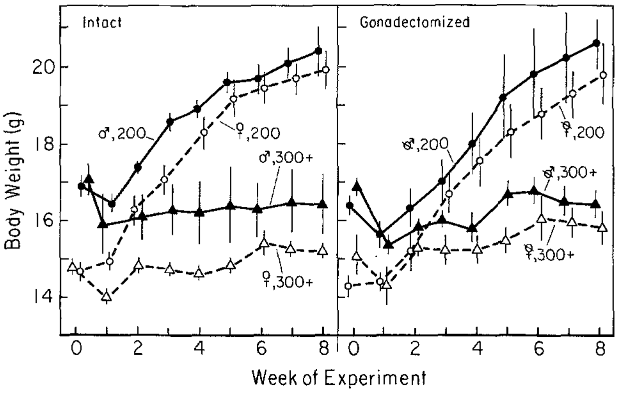

Fig. 2. Weekly body weights $(x \pm \mathrm{SE})$ of intact and gonadectomized animals mainained at either 200 or 300+ revolutions per pellet

at the 300+ regimen also ran more revolutions each day $[F_{1,32}=4.53,\ P<0.05]$, consumed less food $[F_{1,32}=8.68,\ P<0.01]$ and, as a consequence, could not gain weight (Fig. 3).

Several sex-related differences are obvious in Fig. 3 as well. Females – regardless of gonadectomy at both feeding regimens – all experienced greater percentage weight gains, ate more food, and ran more revolutions than males $[F_{1,32}=7.6,\ P<0.01;\ F_{1,32}=4.1,\ P<0.05;\ F_{1,32}=9.0,\ P<0.01$, respectively]. Although gonadectomy had no significant main effects nor interactions associated with these particular measurements, removal of the gonads did alter dramatically the time course of weekly running activity in both sexes at the 200 revolution regimen (Fig. 4). Specifically, gonadectomy resulted in a nearly identical reduction of total revolutions run in both sexes beginning during the third week of the experiment [Week by Gonad × Feeding Regimen, $F_{7,224}=2.07,\ P<0.05$].

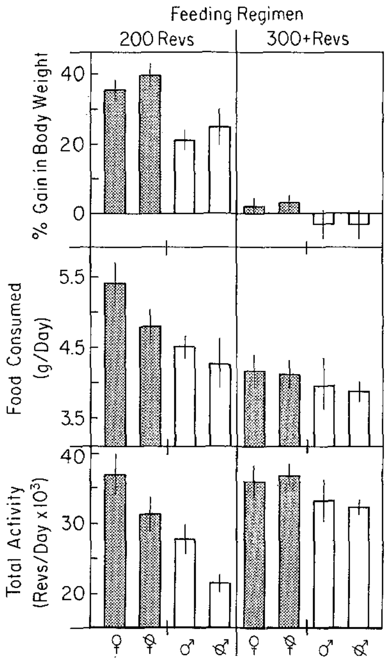

Fig. 3. Percent body weight changes and behavioral assessment $(x \pm \mathrm{SE})$ for all groups studied in this experiment $(n=5$ per group). The data for food consumption and total activity represent a daily average for the entire 8 week experiment

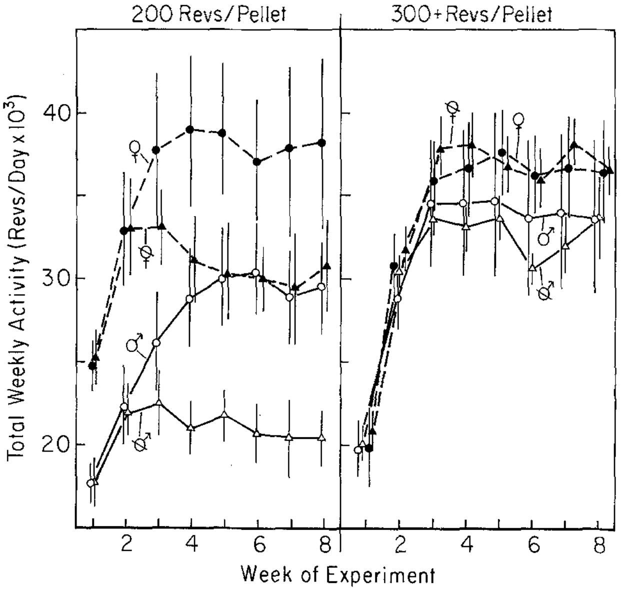

Fig. 4. Daily revolutions $(x \pm \mathrm{SE})$ averaged at weekly intervals for all groups

"Extra" running activity

The fact that females consumed more food than males explains only partially their overall higher levels of running activity. As noted earlier, extra activity was defined as excess wheel running above that needed to obtain the amount of food consumed. As shown in Fig. 5, females engaged in more extra running activity than males $[F_{1,32}=12.8,\ P<0.005]$, especially at the 200 revolution regimen [Sex × Feeding Regimen, $F_{1,32}=7.81,\ P<0.01$]. Also evident in Fig. 5 is the fact that gonadectomized animals reacted through time differently from intact animals (Week by Gonad, $F_{7,224}=6.3,\ P<0.001$), and importantly, that the role of the gonads in supporting this extra "nonfeeding" behavior differed between the sexes as well. In general, at the 200 revolution requirement the extra running activity exhibited by intact and ovariectomized females remained high throughout the experiment, while it increased progressively in intact males as they matured sexually but disappeared almost completely with time in castrated males.

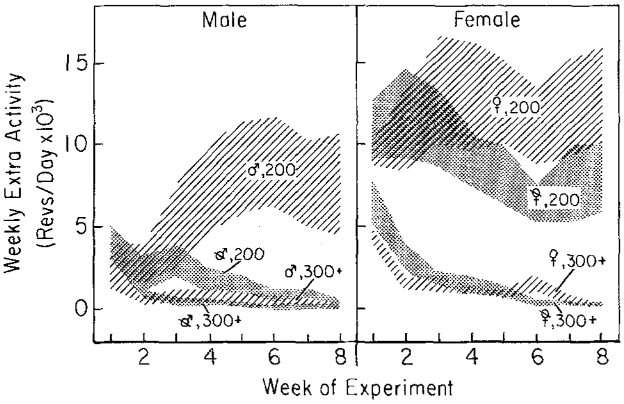

Fig. 5. Weekly changes in "Extra" revolutions during this experiment. Each lined or stippled area represents the mean ± one SE

Table 1. Reproductive development in intact males and females at the beginning of the experiment (4 weeks old) and at the end of the experiment (12 weeks old). All measurements except for ovulation are expressed as mean ± SE

	Start of experiment[a]	End of experiment	
		200 revolutions	300+ revolutions
Males			
Testes wt. (mg)	110 ±2	190 ±10	165 ±10
Seminal ves. wt. (mg)	8 ±1	50 ±5	32 ±5
Sperm in testes (×10^6)	None	1.4±0.1	1.1±0.1
Sperm in vas (×10^6)	None	1.9±0.4	1.1±0.3
Females			
Ovaries wt. (mg)	3.6±0.4	6.5±0.5	3.9±0.2[b]
Uterus wt. (mg)	10 ±1	59 ±11	12 ±2[b]
Number ovulated/total	0/5	4/5	0/5

[a] Based on 5 sham-operated animals of each sex autopsied at the start of the experiment

[b] Probability of difference between the two experimental conditions at the end of the experiment <0.01

Reproductive development

When maintained at the 200 revolution requirement both sexes showed patterns of reproductive development typical of animals housed in small cages with excess food (Bronson 1984a). Females maintained at 300+ revolutions experienced a total inhibition of reproductive development. At autopsy all of these females were reproductively juvenile (Bronson and Desjardins 1974); none had obtained their pubertal ovulation and their uteri were indistinguishable from those of control animals killed at the beginning of the experiment (Table 1). In contrast, all of the males maintained at the 300+ requirement underwent considerable reproductive development during this experiment. At autopsy these males showed only a non-significant suppression of the absolute weights of their reproductive organs and, indeed, despite their total lack of body growth, all of them had developed and stored large numbers of sperm in their vas deferens.

Discussion

For a variety of reasons, the *spontaneous* use of a running wheel has been studied extensively in laboratory rodents, often in relation to the sexual, gonadal, and developmental factors of experimental concern here, and sometimes in relation to food intake as well (e.g. Kennedy and Mitra 1963; Wade 1976; Mather 1981; Blizard 1983). Likewise, the effect of food restriction on reproduction and reproductively-related behavior also has been explored extensively in rodents (e.g. Sachs 1965; Wilen and Naftolin 1978; Glass and Swerdloff 1980). But for obvious energetic reasons a mammal's locomotor effort and its drive to obtain food must be coupled relatively tightly in natural habitats, particularly if the mammal is of small size (Hart 1971). Self-feeding experiments in rodents generally have focused on learning phenomena; the objective of this experiment, however, was to make food intake contingent upon locomotor activity for the specific purpose of studying energy allocation.

Our results clearly suggest that the two sexes of house mice reacted in markedly different ways to the energetic demands imposed by our experiment. Females, but not males, experienced a total suppression of reproductive development when challenged to work extensively for their food. Females also ran more total wheel revolutions, gained a greater percentage of body weight, and thus consumed more food than their male counterparts, regardless of gonadectomy at both feeding regimens. In this regard it should be stressed that in contrast to the typical effects of gonadectomy on body weight in rats and mice maintained in standard cages (e.g. Wright and Turner 1973; Wade and Gray 1979), our gonadectomized animals when forced to work for their food all exhibited growth curves similar to their intact counterparts. Obviously, generalization of our results to natural situations must be done with extreme caution. We suggest, however, that the general pattern of these results parallels what one might predict if the two sexes were compared in natural environments.

It is generally accepted in mammals that the energetic burdens associated with the female's role in reproduction – particularly the enormous energy load incurred by lactation – should result in much of her behavior being oriented towards resource needs (e.g. Clutton-Brock et al. 1982). Male reproductive demands are markedly different: the male's energetic challenges are typically behavioral and focused more on sexual and other social concerns (reviewed by Trivers 1972). These behavioral expectations appear to be reflected in the way both sexes of house mice responded to food-related challenges, especially when the differential partitioning of their running activity at 200 revolutions is viewed in relation to gonadectomy.

Although there is considerable debate as to what motivational determinants correlate with the spontaneous use of a running wheel by small rodents (Mather 1981), there is no doubt that much of our animals' running behavior related directly to obtaining food. Nevertheless, when permitted by feeding conditions that allowed body growth (200 revolutions) both sexes still engaged in considerable "extra" running activity beyond that needed to obtain sufficient food (Fig. 5). In males, this extra activity increased substantially as they matured sexually but it was abolished almost totally by castration (Archer 1975; Daan et al. 1975; Beatty 1979). This strongly suggests that the motivational basis of this behavior in males involves mainly social factors and possibly relates to activities such as mate searching and territorial defense (Christian and Davis 1964).

In sharp contrast, the "extra" activity of females remained high throughout the experiment. This activity was little influenced by reproductive development in intact females, and it was reduced only partially by ovariectomy. This suggests that the motivational basis of this behavior in the female concerns *largely* nonsocial factors. This extensive locomotory activity may reflect the female's greater need to monitor the resources in her environment. Given the long-term energetic impact of reproduction, and her fluctuating hormonal milieu throughout adult reproductive phases, it is not surprising that her locomotor tendencies are organized early in development (Beatty 1979; Blizard 1983) and, as demonstrated in this experiment, remain little affected by post-weaning gonadal influences.

The relatively higher importance of resource dependence in shaping the energy allocation strategies of female house mice is even more obvious when one examines the relationship between feeding conditions and reproductive development. Sexual maturation was totally inhibited in our females when the energetic costs of obtaining food did not allow body growth (see Perrigo and Bronson 1983, 1985). This was not an unexpected finding since even mild food restriction can delay puberty dramatically in both sexes of rats (reviewed by Glass and Swerdloff 1980). But this was not the case in our male house mice maintained at 300+ revolutions; despite their stunted body weights, all of these males attained reproductive maturity.

The house mouse is an opportunist par excellence that now exists globally in a variety of habitats (Bronson 1979, 1984b). It must be emphasized, however, that puberty is a much more labile event in female house mice than it is in males. Given the right circumstances, namely the pheromonal and tactile stimulation of an adult male, a young female can mature from a reproductively juvenile state to achieve her pubertal ovulation within only a few days (Bronson and Macmillan 1983; Vandenbergh 1983), *provided* she has obtained enough food for adequate growth (Perrigo and Bronson 1985). In contrast, the spermatogenic cycle of the male house mouse is initiated shortly after birth and requires a rigidly programmed five week period (Rugh 1968). This difference in potential time required for reproductive development, particularly when set against a short life span (Berry 1970), may be one of the primary reasons sexual maturation in male house mice occurs independently of energetic restrictions on body growth.

Acknowledgements. We thank S. Beckwith, J. Blank, D. Crews, K. Hoskins, F. Marsteller and R. Waddell for advice and assistance. This research was supported by NSF grant PCM8208389.

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