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### The Energetic Costs of Rough and Tumble Play in the Juvenile Rat

#### Abstract

The metabolic costs of rough-and-tumble play behavior were studied in juvenile rats. Using indirect calorimetry, it was determined that energy expenditure during play is increased by 66-104% over the resting metabolic rate, indicating that play accounts for between 2% and 3% of the total daily energy budget of the rat. In a subsequent experiment, food intake and body weight were monitored for three weeks in rats allowed to play for one hour per day and in rats not allowed to play. While the body weights of the two groups did not differ significantly from each other, those rats allowed to play ate 7% more over the three week period that did those rats not given an opportunity to play. These data are consistent with previous reports describing the energetic costs of mammalian play with play accounting for less than 10% of the daily energy budget in three species tested so far. These data are also consistent with viewing play as a type of exercise and may lead to a better understanding of putative benefits of this behavior.

#### Keywords

calorimetry, metabolism, play studies

#### Disciplines

Behavioral Neurobiology | Psychology

# The Energetic Costs of Roughand-Tumble Play in the Juvenile Rat

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The metabolic costs of rough-and-tumble play behavior were studied in juvenile rats. Using indirect calorimetry, it was determined that energy expenditure during play is increased by 66–104% over the resting metabolic rate, indicating that play accounts for between 2% and 3% of the total daily energy budget of the rat. In a subsequent experiment, food intake and body weight were monitored for 3 weeks in rats allowed to play for 1 hr/day and in rats not allowed to play. While the body weights of the two groups did not differ significantly from each other, those rats allowed to play ate 7% more over the 3-week period than did those rats not given an opportunity to play. These data are consistent with previous reports describing the energetic costs of mammalian play, with play accounting for less than 10% of the daily energy budget in three species tested so far. These data are also consistent with viewing play as a type of exercise and may lead to a better understanding of putative benefits of this behavior.

The juveniles of most mammals engage in play behavior (Fagen, 1981). Given the widespread prevalence of play, this complex social behavior is generally thought to have an important function in development, although what this function might be remains elusive. While there is an abundance of speculation concerning putative functions of play behavior, there are very few empirical studies looking at this issue (but see Martin & Caro, 1985; Potegal & Einon, 1989; Taylor, 1980; Vincent & Beckoff, 1978). Likewise, there are even fewer studies which have

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#### 138 SIVIY AND ATRENS

looked at putative costs associated with play behavior. As pointed out by Martin and Caro (1985), this is an especially important issue, for if play is a very costly behavior then one can assume that it has significant benefits. On the other hand, if play is not very costly it may have minimal benefits. Therefore, an empirical assessment of costs associated with play is an important prerequisite for fully understanding any benefits associated with this behavior.

Play will often only occur once-primary needs have first been met, with ambient energy levels affecting the probability of play occurring. Food deprivation reduces play in a variety of species (Muller-Schwarze, Stagge, & Muller-Schwarze, 1982; Siviy & Panksepp, 1985), including humans (Rutischauser & Whitehead, 1972). Play is also reduced if obtaining food becomes more difficult (Baldwin & Baldwin, 1976). While energy levels clearly affect play behavior, little is known about the effects of play behavior on energy balance. Martin (1984) measured energy expenditure in junvenile cats during rough-and-tumble play bouts and found that energy expenditure during play was increased by 60% over the resting metabolic rate. Extrapolating from these data, it was concluded that the energetic cost of play in this species accounts for somewhere between 4% and 9% of the total daily energy expenditure budget. More recently, Miller and Byers (1991) estimated the energetic costs of locomotor play in pronghorn fawns and reported that play in this species accounts for about 3% of the total daily energy expenditure budget, excluding growth.

Play can take different forms in various species, suggesting that any function of play may vary from species to species. However, since many species who play engage to some extent in rough-and-tumble wrestling (Fagen, 1981), considerable insight into functional aspects of this behavior might be gained by studying the play of common laboratory animals such as the rat. In the rat, rough-and-tumble play begins to appear in the animal's behavioral repertoire shortly after independent locomotion has been attained and wanes at about puberty (Meany & Stewart, 1981; Panksepp, 1981). Play bouts normally involve dyadic encounters during which the rats rapidly chase each other and engage in bouts of wrestling, eventually resulting in one animal being "pinned" by the other rat (Meany & Stewart, 1981; Poole & Fish, 1975, 1976). At its maximum, play in the rat accounts for approximately 3% of the total daily time budget (Thiels, Alberts, & Cramer, 1990). To place this into some perspective, juvenile rats spend approximately 50% of the day sleeping, 10% eating and drinking, and 6% grooming (Thiels et al., 1990). In the present study, the energetic costs of rough-and-tumble play in the rat were estimated by both indirect calorimetry and, in a separate experiment, by monitoring food intake and body weight of rats allowed to play and comparing these data to rats not allowed to play.

#### Experiment 1

Play shares many characteristics with other motivated behaviors (Panksepp, Siviy, & Normansell, 1984). For example, depriving rats of the opportunity to play increases the probability of play occurring when given the opportunity (Panksepp & Beatty, 1980). This paradigm has been useful in that the amount of play occurring over a relatively short observation period (e.g., 5–30 min) can be amplified by housing juvenile rats individually. This could be especially useful in estimating the

energetic costs associated with play, as energy expenditure can be measured when play is maximal. Accordingly, a "play deprivation" paradigm was used in the present experiment and energy expenditure monitored by indirect calorimetry during a 30-min opportunity to play.

#### Methods

Eighteen male Wistar rats, bred and born at the University of Sydney Psychology Department Animal Facilities, were used. At 2 days of age, the litters were culled to 8 or 10 pups. Rats were weaned at 21 days of age and housed individually in solid-bottom cages throughout the experiment. Food and water were available ad lib. The colony room was maintained at 22°C, with a 15:9 hr light/dark cycle. All testing was conducted during the light phase of the light/dark cycle.

Beginning on postnatal Day 23, the rat pups were weighed daily and acclimated to playing in a cylindrical acrylic testing chamber (19 cm high, 20 cm in diameter). The volume of the chamber was 6.28 liters. Compressed atmospheric air was drawn through the chamber at a flow rate of 1600 ml/min. A sample was drawn from air exiting the chamber, directed through a Permapure (model PD-750-12PP) permeation drier and passed through an Ametek S-3A oxygen (O<sub>2</sub>) analyzer and an Ametek CD-3A carbon dioxide (CO<sub>2</sub>) analyzer at a flow rate of 110 ml/min. The analyzers were calibrated daily with primary gravimetric standards (Commonwealth Industrial Gases, Sydney). Activity was monitored throughout by placing the metabolic chamber on a Mettler PE-2000 electronic balance, with the unintegrated signal from the balance providing an index of activity. Control and monitoring of the apparatus were accomplished through a Z-80 based, S-100 bus microcomputer system. Data concerning O2 consumption, CO2 production, and activity counts were recorded every min. Energy expenditure (in joules/ gram body weight) was calculated from O2 consumption and CO2 production according to the formula provided by Kleiber (1975). For the nonfasted animal, energy expenditure (kilojoules) = moles  $O_2$  (364 + 113 RQ), where RQ is the respiratory quotient (vol. CO2 produced/vol. O2 consumed). To account for difference in body weight, energy expenditure was expressed in joules/gram body weight.

After 5 days of acclimation to the apparatus, measurements began. Pairs of rats, separated by a wire mesh grid, were initially placed in the metabolic chamber for 1 hr. The grid was then removed for half of the pairs, allowing them the opportunity to play, and energy expenditure was monitored for 30 min. The amount of time engaged in rough-and-tumble play was also recorded. Rough-and-tumble activity was defined as occurring when the animals were engaged in chasing or wrestling. The grid was then placed back in the chamber, separating the rats, and energy expenditure was monitored for 1 additional hr. For the other half, the grid remained in place during the 30-min test period and 60-min posttest period. One week later, those animals that were allowed to play during the test period were monitored with the grid in place. Conversely, those animals that were not allowed to play in the previous trial were given an opportunity to play during this period. On days in between, rats were given daily opportunities to play in a chamber identical to the test chamber.

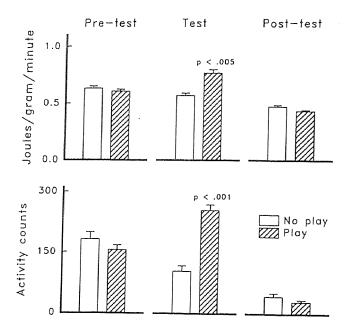


Fig. 1. Mean (+*SEM*) energy expenditure (top) and activity counts (bottom) for rats allowed to play and rats not allowed to play before, during and after the test period. Values for the pretest and posttest energy expenditure were averaged from 60 one-min samples. Values for the test energy expenditure were averaged from 30 one-min samples.

#### Results

Resting metabolic rate (RMR) was estimated from values obtained during the 30-min test period when the rats did not have an opportunity to play. Values for activity and average energy expenditure were fitted to a regression equation and the y intercept (i.e., energy expenditure when activity is 0) was determined. According to this method, RMR was calculated to be 0.46 joules/gram/min. For comparison, resting metabolic rate was also estimated according to formulae provided by Kleiber (1975) and used by Martin (1984) in estimating the RMR of kittens in that study [RMR = 1.5 times basal metabolic rate (BMR), where BMR = 70 body weight (kg)<sup>0.75</sup>]. Applying these formulae to the rats used in the present study, which had a mean ( $\pm SEM$ ) body weight on the testing day of 121.3  $\pm$  10.2 grams, resulting in a value of 0.52 joules/gram/min for RMR. Therefore, the value obtained for RMR using metabolic data from the present experiment was in close agreement with that obtained from an established method for estimating this value.

When averaged over the 30-min test period and compared to energy expenditure during the same period when not allowed to play, energy expenditure during play was increased by 34.6% (Fig. 1). This increase was statistically significant, t(8) = 4.52, p < .005. When compared to the resting metabolic rate of 0.46 joules/gram/min, energy expenditure during play was increased by 66%. This is comparable to the value reported by Martin (1984) for the cat. Energy expenditure between the no-play and play conditions did not differ during either the 60-min pretest or posttest.

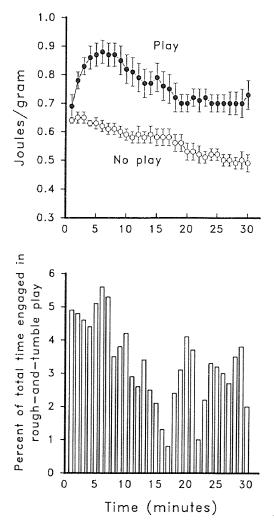


Fig. 2. Top: Mean ( $\pm SEM$ ) energy expenditure during each min of the 30-min test period for rats given an opportunity to play and rats not given an opportunity to play. Bottom: Frequency histogram showing percent of total play time for each min of the 30-min test period (mean total time spent in rough-and-tumble play = 506.2 s).

Even though a play deprivation paradigm was used, amount of play was not constant throughout the 30-min test period, with rats spending (mean  $\pm$  SEM) 28.1  $\pm$  5.6% of the test session in rough-and-tumble activity. As a result, the value obtained by averaging over the 30-min test period is probably not an accurate reflection of energy expenditure during active play. Figure 2 depicts the amount of energy expended for each min of the test period (top) and the relative distribution of play across the test period (bottom). Maximum energy expenditure, which coincided approximately with the period of maximal play, was 65% greater than the average amount of energy expended during the no-play condition and 104% greater than the calculated value of RMR.

When monitoring both  $O_2$  consumption and  $CO_2$  production, an indirect measure of substrate utilization can be obtained through the respiratory quotient

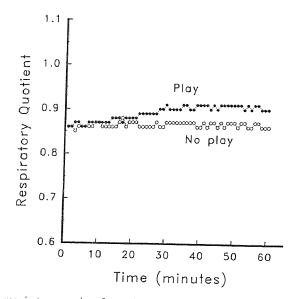


Fig. 3. Mean respiratory quotient for each min during the 1-hr posttest period for rats given an opportunity to play during the 30 min preceding these measurements and for rats not given an opportunity to play.

 $(RQ = volume CO_2 produced/volume O_2 consumed)$ . For example, when carbohydrates are the primary source of energy being oxidized, the expiration of  $CO_2$  is at approximate equilibrium with the consumption of  $O_2$ . This results in an RQ which approaches 1.0. As utilization of lipids increases,  $O_2$  consumed exceeds  $CO_2$  expired and as a result, RQ tends to decrease. The RQ for pure fat is 0.7 (Kleiber, 1975). During the pretest period and 30-min test period, there was no difference in RQ between those rats allowed to play and those not allowed to play. As shown in Figure 3, there was a steady and significant increase in RQ in those rats allowed to play during the hr immediately following the play period, F(59,472) = 2.26, p < .001 for the group by time interaction. This would suggest an increase in RQ has also been reported following exercise (Petley & Bayley, 1988).

#### **Experiment 2**

The data from the previous experiment show that play in the rat increases energy expenditure by somewhere between 66% and 104% over the resting metabolic rate. Assuming that a rat spends approximately 3% of the day playing (Thiels et al., 1990), it can be estimated that play accounts for approximately 2–3% of the total energy budget in this species. Another approach to estimating the energetic costs associated with play would be to monitor food intake and body weight for rats allowed to play and compare these values to rats of the same age not allowed to play. The incremental energetic cost associated with play should be reflected in either an increase in food intake and/or a decrease in body weight. This was assessed in the present experiment.

#### Method

Twenty male Sprague-Dawley derived rats (Harlan Sprague-Dawley, Frederick, MD) were obtained at 21 days of age and housed individually in solid-bottom cages. Food and water were available ad lib. The colony room was maintained at  $22 \pm 2^{\circ}$ C, with a 12:12 hr light/dark cycle.

Ten rats were given a 30-min daily opportunity to play (in pairs) in a neutral solid-bottom cage ( $48 \times 27 \times 20$  cm) beginning on postnatal Day 22 and continuing for the next 21 days. Although play was not quantified, the rats were casually observed to make sure that all were playing. The other 10 rats received no opportunity for social interaction. Daily food intake (to the nearest 0.1 gram) and body weight (to the nearest 1.0 gram) were recorded for all of the rats.

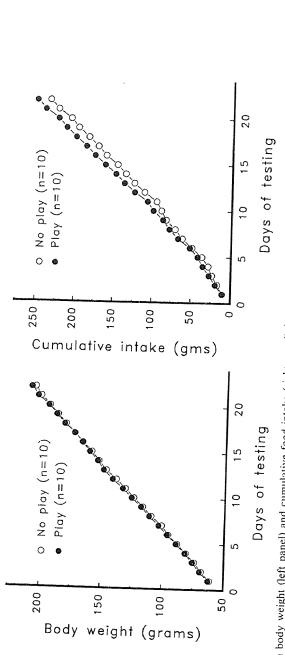
#### Results

The data, presented in Figure 4, indicated that the body weight gain of those rats that were given a 30-min daily opportunity to play was 1.4% greater than that of rats not given an opportunity to play. This difference was not significant, F(1, 18) < 1.0, p > .05 for the main effect of group. However, those rats allowed to play ate 7% more over the 3-week period than did those rats not given an opportunity to play. This difference was statistically significant, F(1,18) = 5.50, p < .05 for the main effect group. These data demonstrate that rough-and-tumble play results in a net decrease in energy efficiency of 5.6% (i.e., food intake exceeds body weight gain in rats allowed to play).

#### **General Discussion**

Rough-and-tumble play clearly requires energy, although until recently this had not been quantified. Knowing the energetic requirements of play behavior is especially important in discussing putative functions of play since, as pointed out by Martin and Caro (1985), one can assume that play has significant benefits if it takes up a significant portion of the energy budget. On the other hand, if play is not a costly activity, then any benefits derived from play may be minimal. In the present study, two methods were used to estimate the energetic costs of play in the juvenile rat. Using values obtained from indirect calorimetry, play was found to increase energy expenditure by 65–104% over the resting metabolic rate. Assuming that a juvenile rat spends 3% of the day playing (Thiels et al., 1990), play would account for approximately 2–3% of the total energy budget in this species.

In Experiment 2, it was found that rats allowed to play for 30 min a day ate 7% more than rats not allowed to play, while only gaining 1.4% more body weight. This suggests a net increase in energy expenditure of 5.6% for rats given a 30-min opportunity to play each day. While this is greater than the value obtained using indirect calorimetry, design differences between the experiments may account for this apparent discrepancy. For example, the area available for play was much greater in Experiment 2 than for Experiment 1. Since energy expenditure is directly elated to horizontal running velocity (Wunder, 1975), rats having a larger area in which to chase each other would be expected to expend more energy than those n a more restricted area. It is also possible that this discrepancy reflects a true





144

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difference. In this case, the acute increase in energy expenditure during a bout of play would be augmented by a persistent increase lasting well beyond the actual play bouts. This would be similar to what is observed following exercise training in adults (Gleeson, Brown, Waring, & Stock, 1982; Hill, Davis, Tagliaferro, & Stewart, 1984; Itey, Rivest, & Richard, 1991; Petley & Bayley, 1988), an effect which is proposed to be due to an enhanced thermic effect of food (Balon & Welk, 1991; Young, Treadway, Balon, Gavras & Ruderman, 1986). Further work using long-term metabolic measurements will be needed in order to more fully assess the extent to which play might enhance basal metabolism.

The data from the present study are comparable to those obtained in two previous studies looking at the energetic costs of play. For example, Martin (1984) used indirect calorimetry to monitor energy expenditure during play behavior in the cat and reported that play accounts for approximately 4–9% of the total daily energy expenditure budget in this species. Miller and Byers (1991) used a time-budget analysis to determine the energetic costs of locomotor play in pronghorn fawn and estimated that play in this species accounts for approximately 3% of total daily energy expenditure. Therefore, play has been estimated to account for less than 10% of the total daily energy budget in three different species.

It has been argued that play is not an energetically costly activity and, thus, may not have any major benefits (Martin, 1984; Martin & Caro, 1985). It is difficult to judge the extent to which the amount of energy expended during play represents a "significant" cost in either the life of the individual animal or the natural history of a species. While an increase in energy expenditure of 5% seems relatively small, approximately 80% of the total energy budget of the rat is spent on involuntary costs, such as those associated with internal homeostasis (Corbett & Keesev, 1982). This involuntary portion of the energy budget would be even greater in juveniles given the energetic costs associated with growth. When viewed as part of the 20% or less devoted to voluntary activity, the relative proportion of voluntary energy expenditure spent on play appears more significant. In addition, there may be energetic and metabolic costs associated with play that go beyond those which accrue during the actual play bout. For example, there was a steady increase in RQ during the hour immediately following a play bout. This indicates an increase in carbohydrate utilization and a reduction in fat catabolism, similar to that observed ollowing exercise (Petley & Bayley, 1988). With carbohydrates being utilized at 1 faster rate, these animals will experience a more rapid drop in blood glucose evels than rats that do not play. Since a drop in blood glucose occurs prior to the nset of a meal (Campfield & Smith, 1986; Louis-Sylvestre & LeMagnen, 1980), mimals which play might require more meals than those which do not play, hus increasing the amount of energy expended for foraging activities and also ncreasing the risks associated with predation. Any activity which decreases blood lucose may be especially relevant for the juvenile, as plasma glucose and insulin lecreases more rapidly after a meal in juveniles than in adults (Cameron, Koerker, & Steiner, 1985).

There may also be other costs associated with play that are much harder to juantify than those relating to energy balance, such as risks associated with ustaining physical injury during play and increased risk of predation (Fagen, 981). These types of costs also need to be more closely examined. For example, Caro (1987) has reported that the play of cheetah cubs decreases the hunting success of their mother, thus reducing the amount of food available to the cubs.

Play has been proposed as a mechanism for promoting physical fitness (e.g., Bekoff, 1988). Play would then be expected to have metabolic similarities with exercise. The present data are consistent with this putative function of play. According to this conceptualization, play may have evolved partly as a means to ensure that the young of a species engage in some form of exercise. While exercise can be energetically costly, there may also be certain advantages. For example, mammals deal with changing ambient temperatures through a number of mechanisms, both behavioral and physiological (Bligh, 1973; Kleiber, 1975; Nicholls & Locke, 1983). An animal can respond to a declining ambient temperature by seeking out warmer surroundings or by increasing its internal temperature through an increase in energy expenditure. Prior to weaning, adequate body temperature can often be maintained by the heat associated with huddling in the nest (e.g., Leon, 1986). This is especially important for animals born with little insulating material, such as the rat. The weaning animal, however, must assume more of the burden associated with thermoregulation. This can be accomplished primarily through nonshivering thermogenesis (Leon, 1986). In adults, exercise training increases the thermogenic effect of cold exposure (Hirata, 1982; Hirata & Nagasaka, 1981). Therefore, an animal that exercises is better equipped to deal with falling temperatures. Rough-and-tumble play may also enhance the ability of an animal to deal effectively with daily and seasonal fluctuations of ambient temperature. In this regard, it is perhaps of more than passing interest that play is one of several "signature" behaviors that are thought to separate mammals from reptiles (MacLean, 1989). Unlike mammals, reptiles do not have a comparable arsenal of thermoregulatory mechanisms at their disposal and must attain thermoneutrality primarily through behavioral means (e.g., Bowker, 1984; MacLean, 1989; Peterson, 1987). In fact, the presence or absence of play in a species has been suggested to be at least partly dependent upon metabolic and thermoregulatory considerations (e.g., Burghardt, 1988). Whether play has a role in the development of thermoregulation and other forms of thermogenesis remains to be determined.

In conclusion, these data are consistent with previous reports (Martin, 1984; Miller & Byers, 1991) detailing the energetic costs of play behavior. In the three species looked at so far, play accounts for less than 10% of the total daily energy budget. Whether this represents a significant cost is probably a question that may never be completely resolved, for it depends largely upon one's own definition of what constitutes a "significant" cost. However, these data provide an excellent starting point from where other issues relating to the metabolic consequences of mammalian playfulness can be more vigorously pursued.

#### References

Baldwin, J. D., & Baldwin, J. I. (1976). Effects of food ecology on social play: A laboratory simulation. Zeitschrift fur Tierpsychologie, 40, 1–14.

Balon, T. W., & Welk, G. J. (1991). Effects of prior exercise on the thermic effect of glucose and fructose. Journal of Applied Physiology, 70, 1463-1468.

Bekoff, M. (1988). Motor training and physical fitness: Possible short- and long-term influences on the development of individual differences in behavior. *Developmental Psychobiology*, 26, 601-612.

- Bligh, J. (1973). Temperature regulation in mammals and other vertebrates. Amsterdam: North-Holland.
- Bowker, R. G. (1984). Precision of thermoregulation of some African lizards. *Physiological Zoology*, 57, 401-412.
- Burghardt, G. M. (1988). Precocity, play, and the ectotherm-endotherm transition. In E. M. Blass (Ed.), Handbook of behavioral neurobiology: Vol. 9. Developmental psychobiology and behavioral ecology. New York: Plenum Press, pp. 107-148.
- Cameron, J. L., Koerker, D. J., & Steiner, R. A. (1985). Metabolic changes during maturation of male monkeys: Possible signals for onset of puberty. American Journal of Physiology, 249, E385–E391.
- Campfield, L. A., & Smith, F. J. (1986). Functional coupling between transient declines in blood glucose and feeding behavior: Temporal relationships. *Brain Research Bulletin*, 17, 427–433.
- Caro, T. M. (1987). Indirect costs of play: Cheetah cubs reduce maternal hunting success. Animal Behaviour, 35, 295-297.
- Corbett, S. W., & Keesey, R. E. (1982). Energy balance of rats with lateral hypothalamic lesions. American Journal of Physiology, 242, E273-E279.
- Fagen, R. (1981). Animal play behavior. New York: Oxford University Press.
- Gleeson, M., Brown, J. F., Waring, J. J., & Stock, M. J. (1982). The effects of physical exercise on metabolic rate and dietary-induced thermogenesis. *British Journal of Nutrition*, 47, 173–181.
- Hill, J. O., Davis, J. R., Tagliaferro, A. R., & Stewart, J. (1984). Dietary obesity and exercise in young rats. *Physiology & Behavior*, 33, 321-328.
- Hirata, K. (1982). Blood flow to brown adipose tissue and norepinephrine-induced calorigenesis in physically trained rats. *Japanese Journal of Physiology*, 32, 279–291.
- Hirata, K., & Nagasaka, T. (1981). Enhancement of calorigenic response to cold and to norepinephrine in physically trained rats. *Japanese Journal of Physiology*, 31, 657–665.
- Hey, P., Rivest, S., & Richard, D. (1991). Effects of exercise on energy balance in meal-fed mice. *Physiology & Behavior*, 49, 271–276.
- Kleiber, M. (1975). The fire of life. Huntington, NY: Robert E. Krieger Publishing Company.
- Leon, M. (1986). Development of thermoregulation. In E. M. Blass (Ed.), Handbook of behavioral neurobiology: Vol. 8. Developmental psychobiology and developmental neurobiology. New York: Plenum Press, pp. 297–322.
- Louis-Sylvestre, J., & LeMagnen, J. (1980). A fall in blood glucose level precedes meal onset in freefeeding rats. *Neuroscience and biobehavioral reviews*, 4(Suppl. 1), 13-15.
- MacLean, P. D. (1989). The triune brain in evolution: Role in paleocerebral functions. New York: Plenum Press.
- Martin, P. (1984). The time and energy costs of play behaviour in the cat. Zeitschrift fur Tierpsychologie, 64, 298-312.
- Martin, P., & Caro, T. M. (1985). On the functions of play and its role in behavioral development. Advances in the Study of Behavior, 15, 59–103.
- Meany, M. J., & Stewart, J. (1981). A descriptive study of social development in the rat (*Rattus norvegicus*). Animal Behaviour, 29, 34–45.
- Miller, M. N., & Byers, J. A. (1991). Energetic cost of locomotor play in pronghorn fawns. Animal Behaviour, 41, 1007-1013.
- Muller-Schwarze, D., Stagge, B., & Muller-Schwarze, C. (1982). Play behavior: Persistence, decrease, and energetic compensation during food shortage in deer fawn. *Science*, 215, 85–87.
- Nicholls, D., & Locke, R. (1983). Cellular mechanisms of heat dissipation. In L. Girardier and M. J. Stock (Eds.), *Mammalian thermogenesis*. London: Chapman and Hall.
- Panksepp, J. (1981). The ontogeny of play in rats. Developmental Psychobiology, 14, 327-332.
- Panksepp, J., & Beatty, W. W. (1980). Social deprivation and play in rats. Behavioral and Neural Biology, 30, 197-206.
- Panksepp, J., Siviy, S., & Normansell, L. (1984). The psychobiology of play: Theoretical and methodological perspectives. *Neuroscience and Biobehavioral Reviews*, 8, 465-492.
- Peterson, C. R. (1987). Daily variation in the body temperatures of free-ranging garter snakes. *Ecology*, 68, 160-169.
- Petley, M. P., & Bayley, H. S. (1988). Exercise and postexercise energy expenditure in growing pigs. Canadian Journal of Physiology and Pharmacology, 66, 721–730.
- Poole, T. B., & Fish, J. (1975). An investigation of playful behaviour in *Rattus norvegicus* and *Mus musculus* (Mammalia). *Journal of Zoology*, 175, 61-71.

#### 148 SIVIY AND ATRENS

Poole, T. B., & Fish, J. (1976). An investigation of individual, age, and sexual differences in the play of *Rattus norvegicus* (Mammalia: Rodentia). *Journal of Zoology*, 179, 249–260.

- Potegal, M., & Einon, D. (1989). Aggressive behaviors in adult rats deprived of playfighting experience as juveniles. *Developmental Psychobiology*, 22, 159–172.
- Rutischauser, I. H. E., & Whitehead, R. G. (1972). Energy intake and expenditure in 1- to 3-year-old Ugandan children living in a rural environment. *British Journal of Nutrition, 28*, 145–152.
- Siviy, S. M., & Panksepp, J. (1984). Energy balance and play in juvenile rats. *Physiology & Behavior*, 35, 435-441.

Taylor, G. T. (1980). Fighting in juvenile rats and the ontogeny of agonistic behavior. Journal of Comparative and Physiological Psychology, 94, 953-961.

Thiels, E., Alberts, J. R., & Cramer, C. P. (1990). Weaning in rats: II. Pup behavior patterns. Developmental Psychobiology, 23, 495-510.

Vincent, L. E., & Bekoff, M. (1978). Quantitative analyses of the ontogeny of predatory behaviour in coyotes, Canis latrans. Animal Behaviour, 26, 225-231.

Wunder, B. A. (1975). A model for estimating metabolic rate of active or resting mammals. Journal of Theoretical Biology, 49, 345-354.

Young, J. C., Treadway, J. L., Balon, T. W., Gavras, H. P., & Ruderman, N. B. (1986). Prior exercise potentiates the thermic effect of a carbohydrate load. *Metabolism*, 35, 1048-1053.