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Effects of gonadal hormones on food intake and body weight in adult Mongolian gerbils.

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EFFECTS OF GONADAL HORMONES ON FOOD INTAKE AND BODY WEIGHT IN ADULT MONGOLIAN GERBILS

A Thesis Presented

by

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Introduction

Over the past decade, evidence has accumulated from a variety of species demonstrating that body weight and food consumption measures vary predictably with fluctuations in gonadal steroid titers (see Wade, 1976, for a review). In particular, extensive research with rats has shown that both sex and hormonal status exert considerable effects on eating and body weight (Kakolewski, Cox & Valenstein, 1968; Leshner & Collier, 1973; Gentry & Wade, 1976). The intent of the present research is to assess the nature of the relations between levels of gonadal steroids and these variables in Mongolian gerbils, *Meriones unguiculatus*.

The effects of changes in androgen titers on eating and body weight have been amply demonstrated in male rats. Male castration (orchiectomy) produces delayed but permanent reductions in both food intake and body weight (Kakolewski *et al.*, 1968; Leshner & Collier, 1973; Gentry & Wade, 1976). Androgen replacement by exogenous administration of *either* low to moderate doses of testosterone proprionate (TP), *or* of a range of doses of dihydrotestosterone proprionate (DHTP, the 5α-reduced metabolite) reverses the effects of orchiectomy, although DHTP is somewhat less effective than TP (Gentry & Wade, 1976).

In female rats, the relations between gonadal hormones and eating and body weight are more complex, and the effects of sex steroid secretion on these measures are more pronounced than in males. Presumably, the fact that ovarian hormone titers vary considerably, albeit systematically, over different reproductive conditions contributes to this rather dramatic sex difference in gonadal hormone effects on eating and body weight. Specifically, at proestrus (when estrogen titers peak), intact cycling rats decrease their food intake (Slonaker, 1924a) and so lose weight (Brobeck, Wheatland, & Strominger, 1947). At diestrus, when progesterone titers are high, the reverse pattern is observed: food intake increases (Slonaker, 1924b) and a weight gain occurs (Brobeck *et al.*, 1947). Intact female rats, then, tend to balance energy intake and expenditure over a single estrous cycle (Kennedy & Mitra, 1963a). Further, during pregnancy and pseudopregnancy (when progesterone titers are also high), eating and body weight increase as in diestrus, although these effects are more pronounced (Slonaker, 1924b). Finally, exogenous administration of progesterone to intact female rats increases body weight (both lean and fat tissue) and eating (Hervey & Hervey, 1964, 1965c; Hervey & Hervey, 1966). By contrast, additional estradiol has little or no effect on these measures when administered alone to intacts (Hervey & Hervey, 1965c). However, exogenous estradiol treatment does block the body weight and food intake increases produced by progesterone administration to intacts (Hervey & Hervey, 1965c).

Removal of endogenous ovarian hormones by ovariectomy produces substantial increases in both eating and body weight in cycling female rats. The time course as well as the direction of these changes are quite different from those observed following orchiectomy. Ovariectomy produces an initial rapid rise in both food intake and body weight; subsequently, body weight is maintained at an elevated level, while food intake returns to levels of intact females (Kakolewski *et al.*, 1968; Tarttelin & Gorski, 1971; Mook, Roberts, Nussbaum & Rodier, 1972; Gentry & Wade, 1976). Apparently, the effects of ovariectomy are highly similar to those obtained following exogenous progesterone administration to intact female rats. However, the effects of these two treatments are not additive: neither progesterone-treated females that were subsequently ovariectomized, nor previously ovariectomized females later given exogenous progesterone treatment showed a significant additional weight gain (Hervey & Hervey, 1966).

Although replacement with exogenous progesterone *alone* has no effect on eating and body weight in ovariectomized rats, exogenous estrogen administration reverses the effects of gonadectomy on these measures. Specifically, when previously ovariectomized females receive injections of estradiol benzoate (EB), both body weight and food intake initially decrease (Tarttelin & Gorski, 1971; Mook *et al.*, 1972; Redick, Nussbaum & Mook, 1973; Wade, 1975). Recent evidence indicates that the reductions in these measures in response to estradiol are approximately dose dependent (Wade, 1975). Once body weight returns to levels of intact females, food intake is adjusted to support normal weight gain, despite continued EB injections (Tarttelin & Gorski, 1971; Mook *et al.*, 1972; Redick *et al.*, 1973; Wade, 1975). Additionally, if exogenous estradiol is given immediately following ovariectomy, the body weight gain usually observed is prevented (Wade, 1975). Thus, exogenous estrogen administration to ovariectomized rats produces approximately the same effects on eating and body weight as are observed in intact cycling females when estrogen titers are high. These effects of estrogen replacement seem to be specific to estradiol. Although treatment with exogenous estrone, the principal metabolite of estradiol, has also been demonstrated to reverse the effects of ovariectomy, large doses were necessary to obtain significant reductions in eating and body weight, and the effects were smaller than those observed with much lower doses of EB (Wade, 1975). Finally, decreases in body weight and food intake are also observed in ovariectomized rats receiving hypothalamic estradiol implants. Specifically, when crystalline EB is unilaterally implanted in the ventromedial hypothalamus (VMH), or in the VMH-arcuate area of ovariectomized rats, both eating and body weight are reduced. Neither estradiol implants in other brain areas, nor implants of progesterone or cholesterol in the VMH or VMH-arcuate produce these effects (Jankowiak & Stern, 1974; Wade & Tucker, 1970c).

The studies assessing the relations between changes in circulating levels of ovarian hormones in intact female rats and changes in food intake and body weight, when combined with results of studies examining the effects of ovariectomy and ovarian hormone replacement on these same measures, suggest that estradiol and progesterone have very different roles in body weight regulation in the female rat. Apparently, the primary action of estrogens is to reduce body weight, while the observed transient reduction in food intake that accompanies high estrogen titers is a secondary effect. The fact that exogenous estrogen administration does not affect rats maintained at lean body weights lends further support to this notion

(Zucker, 1972; Redick *et al.*, 1973). Although identification of the precise role of progesterone in the maintenance of energy balance initially proved troublesome (e.g., Tarttelin & Gorski, 1973), recent evidence suggests that the primary action of this hormone is to attenuate the effects of estrogens on body weight (e.g., Ross & Zucker, 1974; Wade, 1975). In particular, Wade (1975) has demonstrated dose-dependent increases in body weight and food intake when progesterone was administered concurrently with EB to ovariectomized rats.

The above discussion suggests that the effects of gonadal steroids on eating and body weight in the rat have been amply empirically established. To summarize, androgens stimulate body weight gain and eating in males. By contrast, estrogens tend to suppress these measures in females, while progesterone acts to inhibit estrogenic effects. The extent of inter-species generalization of these relations is also an important research question. With respect to males of other species, empirical evidence of the actions of testicular androgens on body weight regulation is rather scarce. Among male rodents examined, inhibition of body weight gain has been observed following orchiectomy of both mice and guinea pigs (Wright & Turner, 1973; Slob, Goy & Van der Werff ten Bosch, 1973). By contrast, the male golden hamster does *not* exhibit rat-like androgenic stimulation of body weight gain. Rather, in hamsters, removal of endogenous androgens by orchiectomy produces *increases* in total body weight, while exogenous androgen replacement with TP depresses both body weight and food intake (Zucker, Wade & Ziegler, 1972). Notably, unlike rats, adult male hamsters eat and weigh less than adult females. This species difference may somehow account for the discrepant findings obtained from the male hamster. Data demonstrating androgenic action on energy balance in male primates are rarer than those pertaining to rodents. Available evidence, however, indicates that male primates behave like rats, in response to androgens. For example, Zuckerman and Parkes (1939) reported a decrease in the total body weight of a baboon following castration, and an increase in body weight following exogenous androgen replacement to a castrated Rhesus monkey.

Comparative studies among non-rat species to date have also provided a somewhat incomplete profile with respect to ovarian hormone-body weight and food intake relations. Again, among the rodent species studied, female mice and guinea pigs, like female rats, exhibit an increase in total body weight following ovariectomy (Wright & Turner, 1973; Slob et al., 1973). In addition, Czaja and Goy (1975) have reported that ovariectomized guinea pigs given exogenous EB injections show rapid, transient decreases in food intake, as well as pronounced reductions in body weight. By contrast, exogenous progesterone administration had no effect on these measures. Czaja and Goy also noted that both eating and body weight of intact cycling guinea pigs were significantly lower during cycle days of peak estrogen titers, as compared to other cycle days.

The earliest available reports indicated that female golden hamsters, like their male counterparts, provide an exception to, rather than support for rat generalizations of gonadal steroid on eating and body weight. For example, Zucker et al. (1972) found no effect of ovariectomy on these measures in the hamster over an 86-day post-operative period. In addition, a relatively high dose of EB (10 μg/day) failed to demonstrate rat-like estrogenic suppression of body weight and food intake (Zucker et al., 1972). Recently, however, Morin and Fleming (unpublished) have reported cyclic variation in eating and body weight, comparable to that observed in rats, in intact female hamsters. Specifically, food intake and body weight were higher during diestrus, when estrogen titers are low. Although these data do not provide evidence of direct estrogenic effects on these measures, they are indicative of the occurrence of rat-like fluctuations in eating and body weight with fluctuations in estrogen titers in female hamsters. Morin and Fleming also suggest that the failure of previous studies to find the usual post-operative weight gain in females of this species may merely reflect that ovariectomy-induced changes in energy balance have a considerably longer latency in hamsters than in rats.

Although ovarian hormone effects on eating and body weight in primates have been less thoroughly examined than in rodents, the available data indicate that these relations are similar to those observed in rats. For instance, in an initial study, Czaja (1975) reported an increase in the incidence of food rejection among cycling Rhesus monkeys during the periovulatory period, when levels of circulating estrogens are high. Recently, Czaja and Goy (1975) replicated these results using food intake as the dependent measure, and also demonstrated that exogenous EB (but not progesterone) treatment administered to ovariectomized Rhesus monkeys decreases eating.

The brevity of the above summary of the available comparative literature suggests that, although our understanding of the relations between changes in gonadal steroid output and changes in behaviors related to energy balance is quite extensive with respect to the rat, the range of species over which we can comfortably generalize these relations is disturbingly restricted. The present studies propose to evaluate the possibility of extending the rat generalizations of gonadal hormone action on eating and body weight to the Mongolian gerbil. Specifically, two studies assess first, the effects of androgen removal by orchiectomy, and second, exogenous androgen replacement of either testosterone proprionate (TP) or dihydrotestosterone proprionate (DHTP), on food intake and body weight in adult male gerbils. A third study then examines the effects of exogenous administration of estradiol benzoate (EB), progesterone, or EB plus progesterone on eating and body weight in previously ovariectomized adult female gerbils. Since our females did not exhibit normal cycling behavior, the effects of ovariectomy on energy balance are not assessed in this series of studies.

GENERAL METHODS

Subjects

Male and female Mongolian gerbils, approximately 14 weeks old, were obtained from Tumblebrook Farms, West Brookfield, Massachusetts, for use as subjects. All animals were individually housed in standard laboratory cages with wire mesh bottoms. Purina Laboratory

Chow and tap water were available *ad libitum*. A 12:12 light-dark cycle (lights on at 8:00 a.m.) was maintained throughout the experiments. Subjects were permitted to acclimate to housing, food, water and light cycle conditions for 3 weeks before baseline measurements were obtained.

Procedures

Measurements of body weight and of food consumption, including spillage, to the nearest 0.1 g. were obtained every 3 days between 12 noon and 1 p.m. throughout the experiments. During periods when exogenous hormone treatments were administered, animals received injections between 1 and 2 p.m. daily.

EXPERIMENT 1

The first experiment assessed the effects of orchiectomy on food intake and body weight in gerbils.

Method

Subjects were approximately 120 days of age at the beginning of the study. Initially, baseline measurements of food intake and body weight were obtained (as described above) for 9 days. Two groups of males were then matched on these measures. Fifteen animals were castrated and 10 received sham operations on day 10, under Metofane anesthesia. Measurements of food intake and body weight were obtained for 48 days postoperatively, until all animals had stabilized.

Results

Three of the orchiectomized gerbils and 1 sham operated animal died during or as a result of surgical manipulations, leaving N's of

12 and 9 in the two groups, respectively. Analyses were performed on individuals' body weight gains between day 6 of baseline and day 48 of the post-operative period. The results demonstrate that orchiectomy significantly increased body weight gains in gerbils, $\underline{t}$ (19) - 2.21, $p < .05$ (Figure 1). By contrast, mean daily food intake was not systematically affected by this manipulation (Figure 2).

EXPERIMENT 2

The findings of the first experiment revealed that removal of endogenous androgens produces substantial increases in body weight gains in gerbils. A second experiment assessed the effects of exogenous androgen treatment, and its subsequent withdrawal, on these measures in previously orchiectomized gerbils.

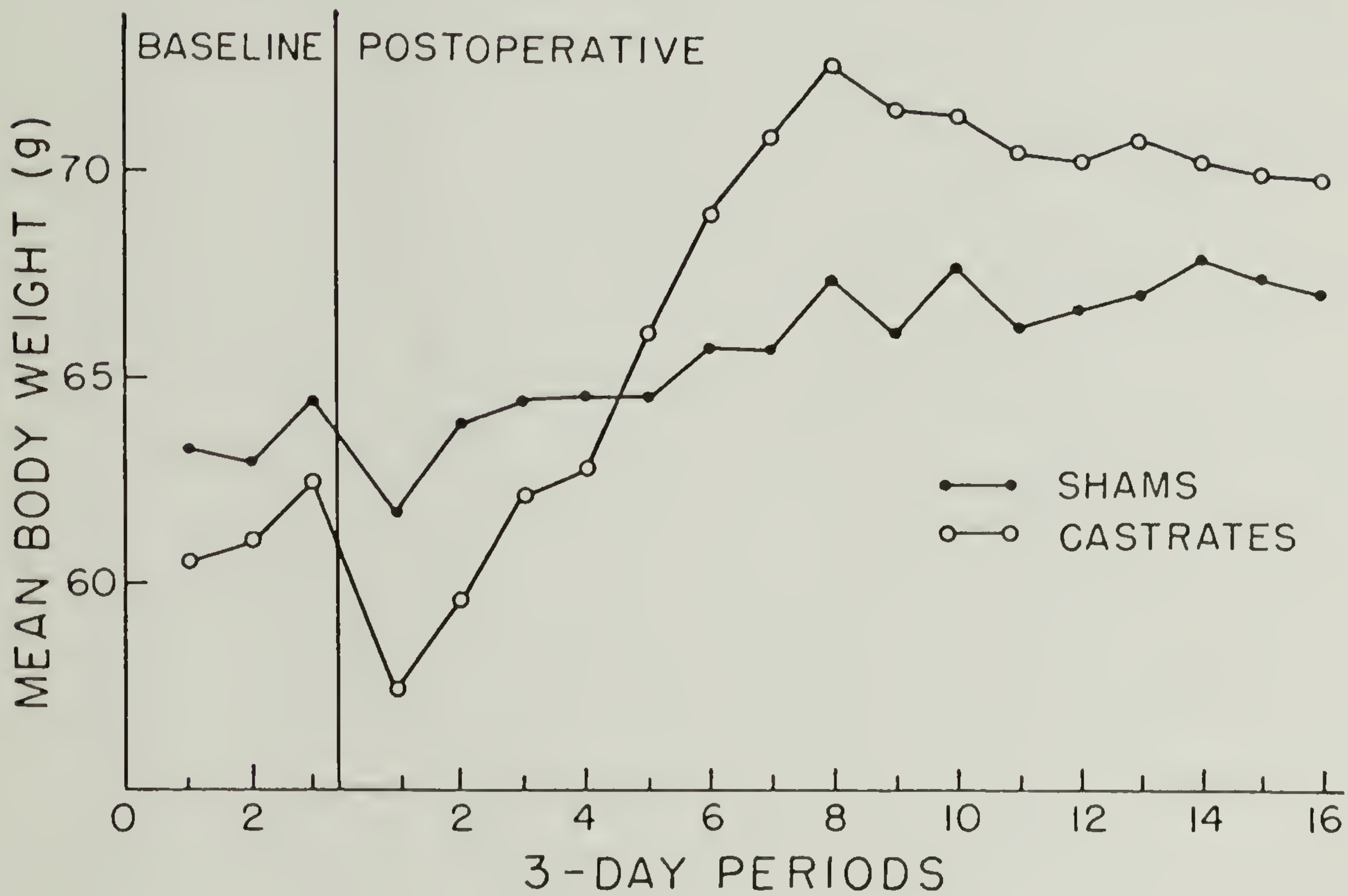
Method

Eighteen male gerbils, castrated at 130 days of age, were permitted to recover under constant conditions for 8 weeks. (Twelve of these 18 were used in Experiment 1). Baseline measurements of food intake and body weight were then obtained as before for 9 days, and subjects were assigned to 1 of 3 groups matched on these measures. The next 30 days constituted a hormone replacement phase, and animals received daily 0.1 cc. subcutaneous injections of either 100μg. of testosterone proprionate (TP), 100μg. of dihydrotestosterone proprionate (DHTP), or sesame oil. Both TP and DHTP were suspended in the oil vehicle. Food intake and body weight measurements were obtained throughout the hormone treatment period. Hormone administration was then discontinued, and the effects of withdrawal of the exogenous androgen treatment on eating and body weight was

FACE PAGE FOR FIGURE 1

Figure 1. The effects of orchiectomy on mean body weight.

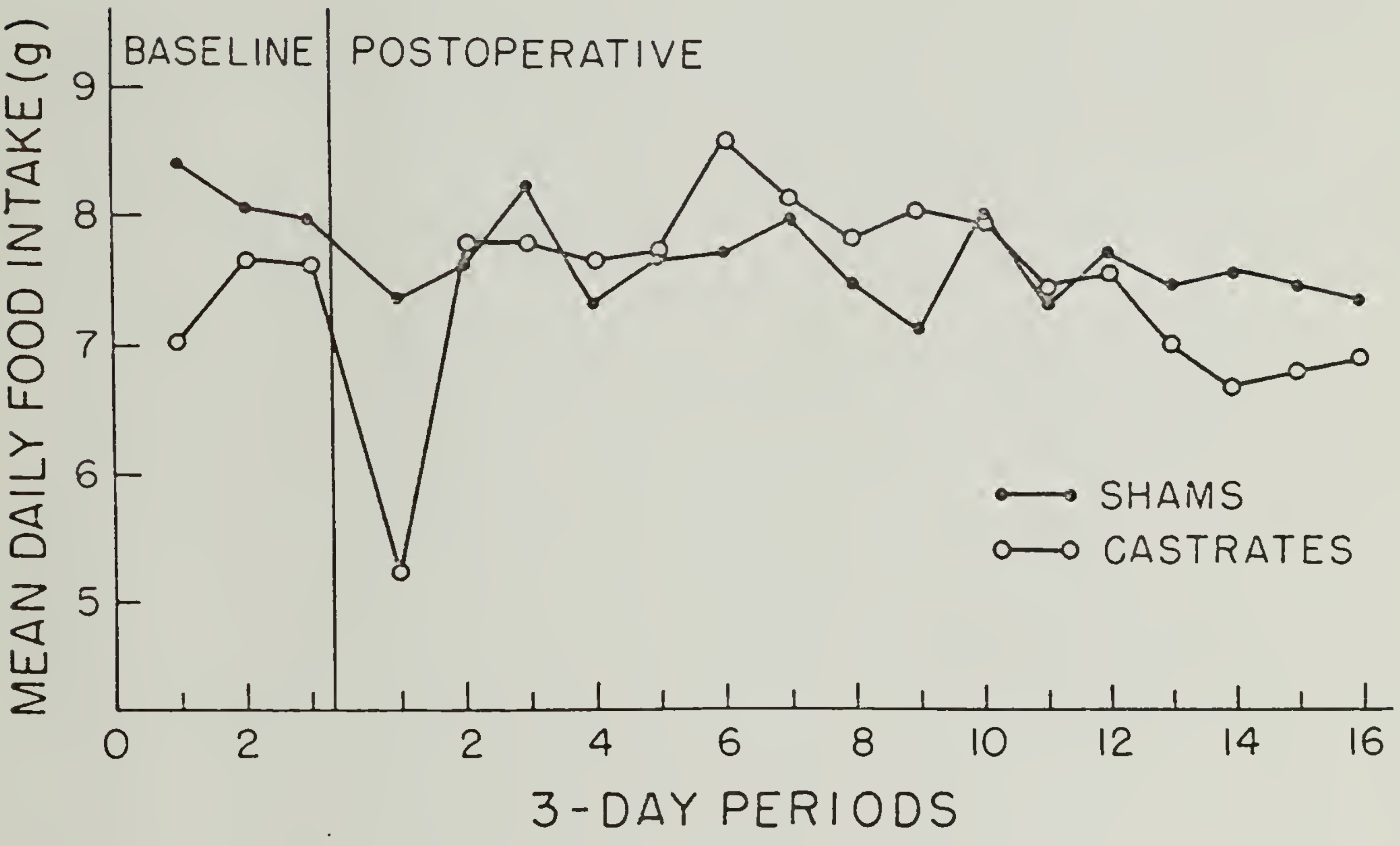
EFFECT OF ORCHIECTOMY ON BODY WEIGHT



FACE PAGE FOR FIGURE 2

Figure 2. The effects of orchiectomy on mean daily food intake.

EFFECT OF ORCHIECTOMY ON FOOD INTAKE



assessed for an additional 48 days, until all animals had stabilized.

Results

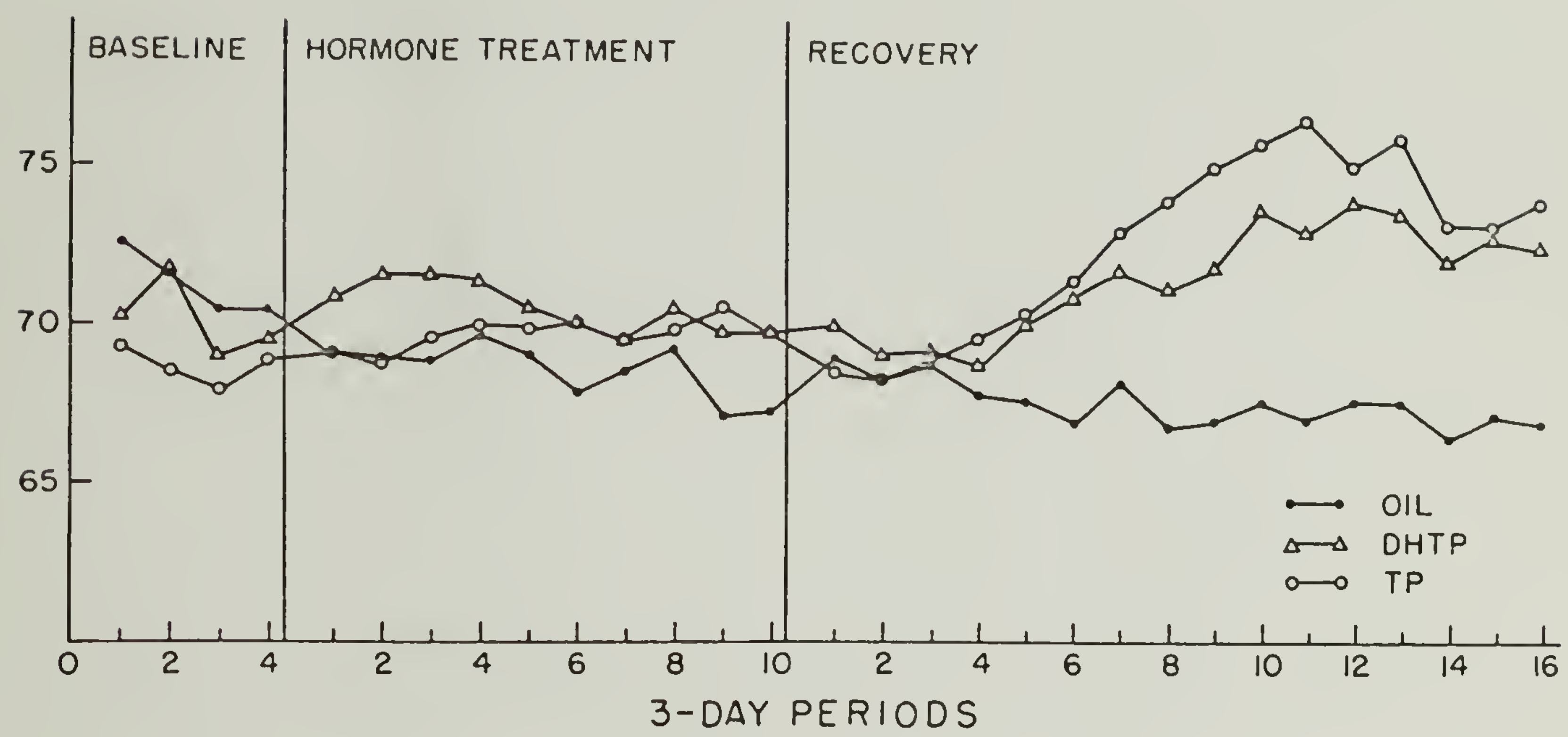
Mean body weight of previously orchiectomized gerbils was not affected by exogenous administration of either TP or DHTP (Figure 3, center panel). However, following withdrawal of exogenous androgens, increases in body weight were observed in both hormone treated groups. By day 48 of the recovery phase (Figure 3, last panel), TP treated animals weighed significantly more than oil injected controls, t (10) = 2.36, $p < .05$. Although DHTP treated animals also exhibited elevated body weights on day 48, they did not differ significantly from controls on this measure, t (10) = 1.75, $p > 0.2$. A second analysis was performed on individuals' body weight gains between day 6 and day 48 of the recovery phase. These findings indicate that withdrawal of either exogenous TP or of exogenous DHTP produced significantly greater body weight gains over the recovery period than did withdrawal of the oil vehicle, t (10) = 4.77, $p < .001$ and t (10) = 3.93, $p < .01$. There was no evidence that withdrawal of exogenous TP had a significantly greater effect on body weight gain than did withdrawal of exogenous DHTP.

Exogenous administration of either TP or DHTP to orchiectomized gerbils also failed to affect mean daily food intake over the injection period (Figure 4, center panel). Further, there were no statistically significant increases in this measure following withdrawal of exogenous TP or DHTP over recovery days 12-33, when body weight measures were increasing in the hormone treated groups (see the last panels of Figures 3 & 4, for comparison).

FACE PAGE FOR FIGURE 3

Figure 3. The effects of exogenous androgen treatment, and its subsequent withdrawal, on mean body weight.

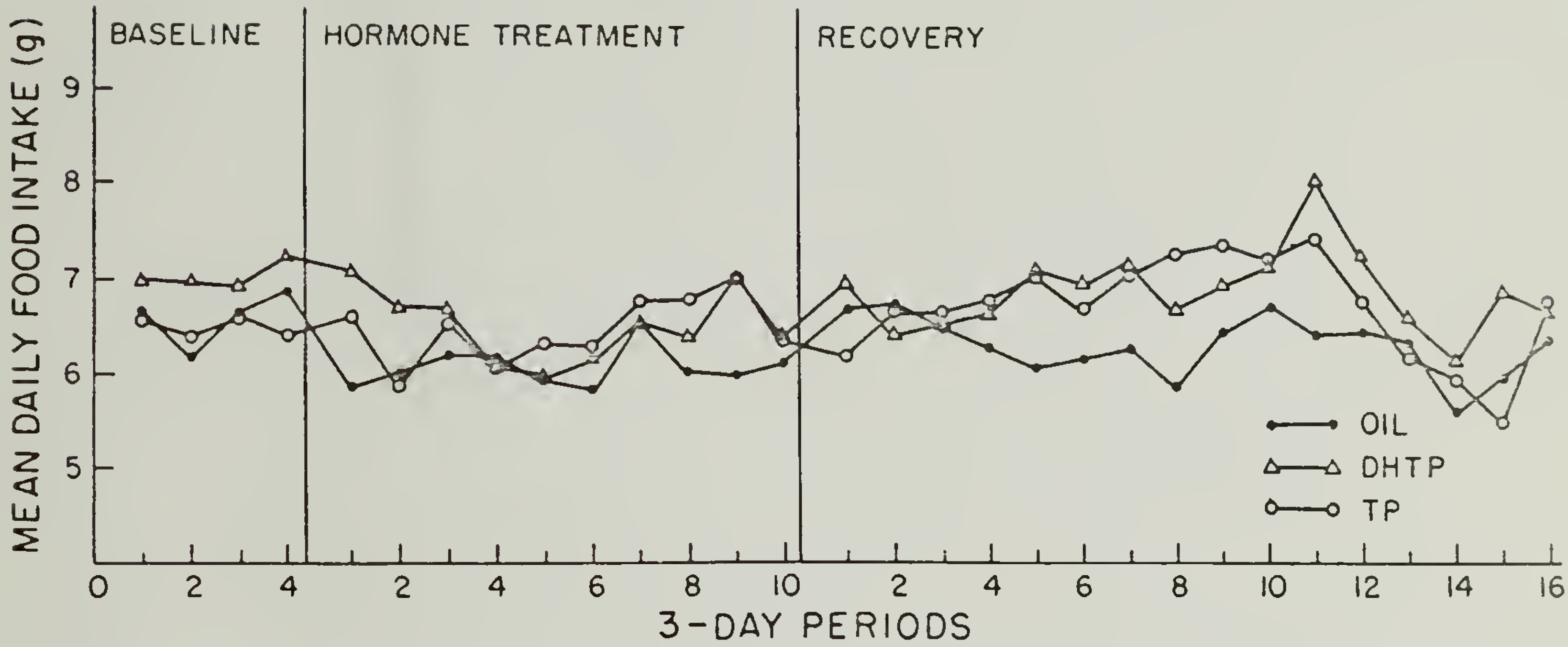
EFFECT OF ANDROGEN TREATMENT ON BODY WEIGHT



FACE PAGE FOR FIGURE 4

Figure 4. The effects of exogenous androgen treatment, and its subsequent withdrawal, on mean daily food intake.

EFFECT OF ANDROGEN TREATMENT ON FOOD INTAKE



To summarize, the effects of withdrawal of exogenous androgen treatment administered to previously orchiectomized gerbils were highly similar to those observed following orchiectomy of intacts: body weight measures exhibited substantial gains, while food intake measures were not systematically affected.

EXPERIMENT 3

A final experiment examined the effects of exogenous ovarian hormone treatment, and its subsequent withdrawal, on food intake and body weight in previously ovariectomized gerbils.

Method

Twenty-four female gerbils were ovariectomized under Metofane anesthesia at 130 days of age and maintained under constant conditions for 8 weeks, until their body weights and daily food consumption had stabilized. Baseline measurements were then obtained as described above for 9 days. At the end of this period, animals were assigned to 1 of 4 hormone treatment groups matched for mean body weight and mean daily food intake. For the next 30 days, animals received daily 0.1 cc. subcutaneous injections of either 2 μg. of estradiol benzoate (EB), 1 mg. of progesterone (P), 2 μg. of EB plus 1 mg. of P, or sesame oil. The hormones were again suspended in the oil vehicle. Measurements of food intake and body weight were obtained throughout the hormone replacement phase. At the end of this 30 day period, the effects of withdrawal of the exogenous ovarian hormone treatment on eating and body weight was assessed for an additional 24 days, until all animals had stabilized.

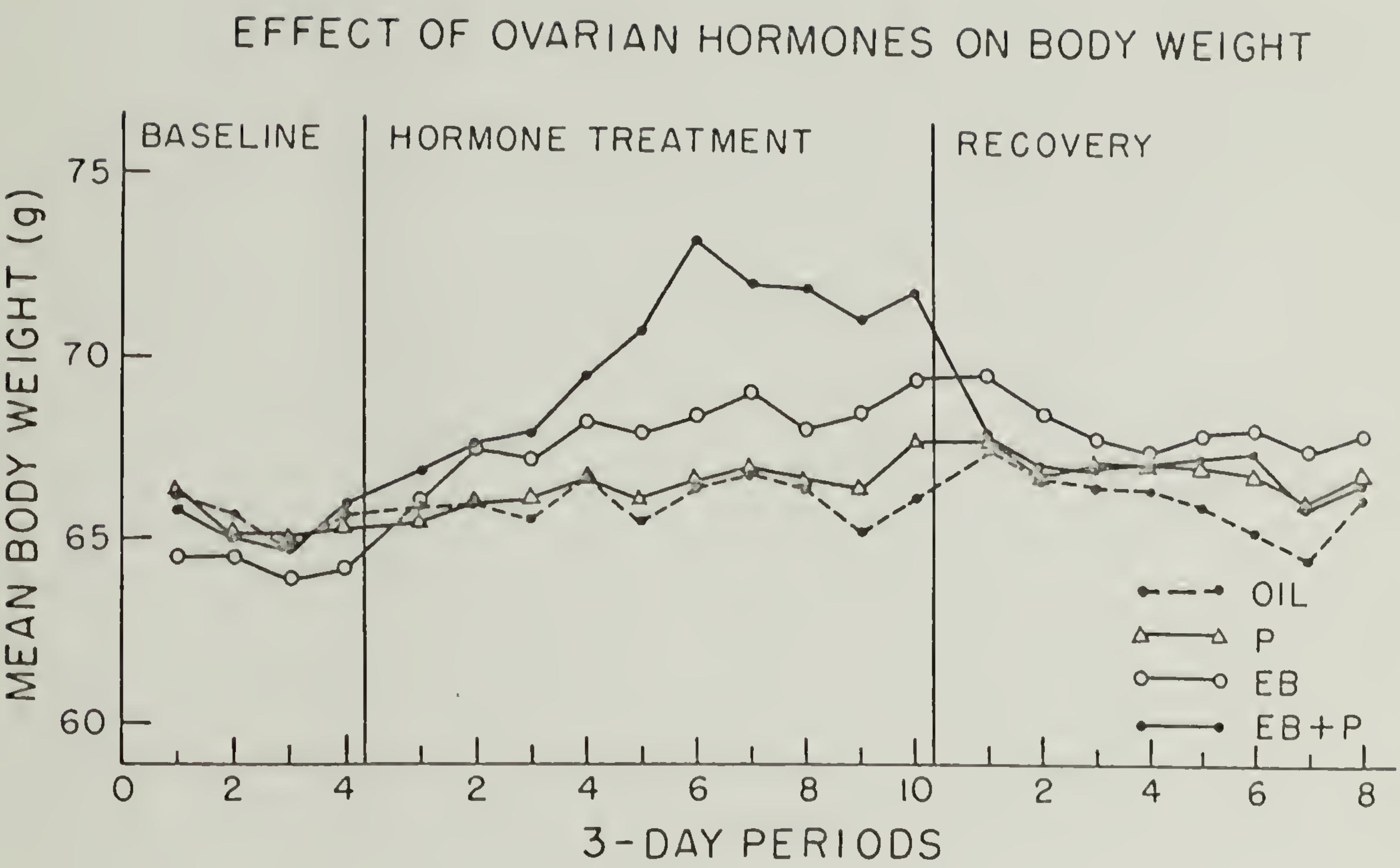
Results

Analyses were performed on individuals' body weight gains over the 30 days of exogenous ovarian hormone treatment. Each of the hormone treated groups was compared to the oil injected controls. The results indicate that ovariectomized gerbils receiving exogenous EB and those receiving exogenous EB plus P gained significantly more weight over the hormone treatment phase than did animals receiving only oil injections, $\underline{t}$ (10) = 2.29, $p < .05$ and $\underline{t}$ (10) = 3.63, $p < .01$ (Figure 5, center panel). Injections of P alone had no effect on body weight. Further, there was no evidence that P antagonized EB in the EB plus P treatment group. In fact, EB plus P treated gerbils gained slightly more weight over the hormone treatment phase than did gerbils receiving EB alone. A comparison of EB and EB plus P injected groups did not yield statistical significance, however. Once treatment with the exogenous ovarian hormones was discontinued, individuals' body weights returned to approximately control levels within 3½ weeks (Figure 5, last panel).

Analyses were also performed on the change in individuals' daily food intake from baseline days 6-12 to days 18-27 (Figure 6) of hormone treatment (the period of peak weight gain in Figure 5). Each hormone treated group was again compared with the oil injected controls. The results demonstrate that both exogenous EB alone and exogenous EB plus P produced greater increases in mean daily food intake during the latter half of the hormone treatment phase than did oil injections, $\underline{t}$ (10) = 4.66, $p < .001$ and $\underline{t}$ (10) = 7.35, $p < .001$. Treatment with exogenous P alone did not affect food intake measures. Further, there was no evidence that P antagonized the EB effects, since a comparison of the EB and EB plus P injected groups shows

FACE PAGE FOR FIGURE 5

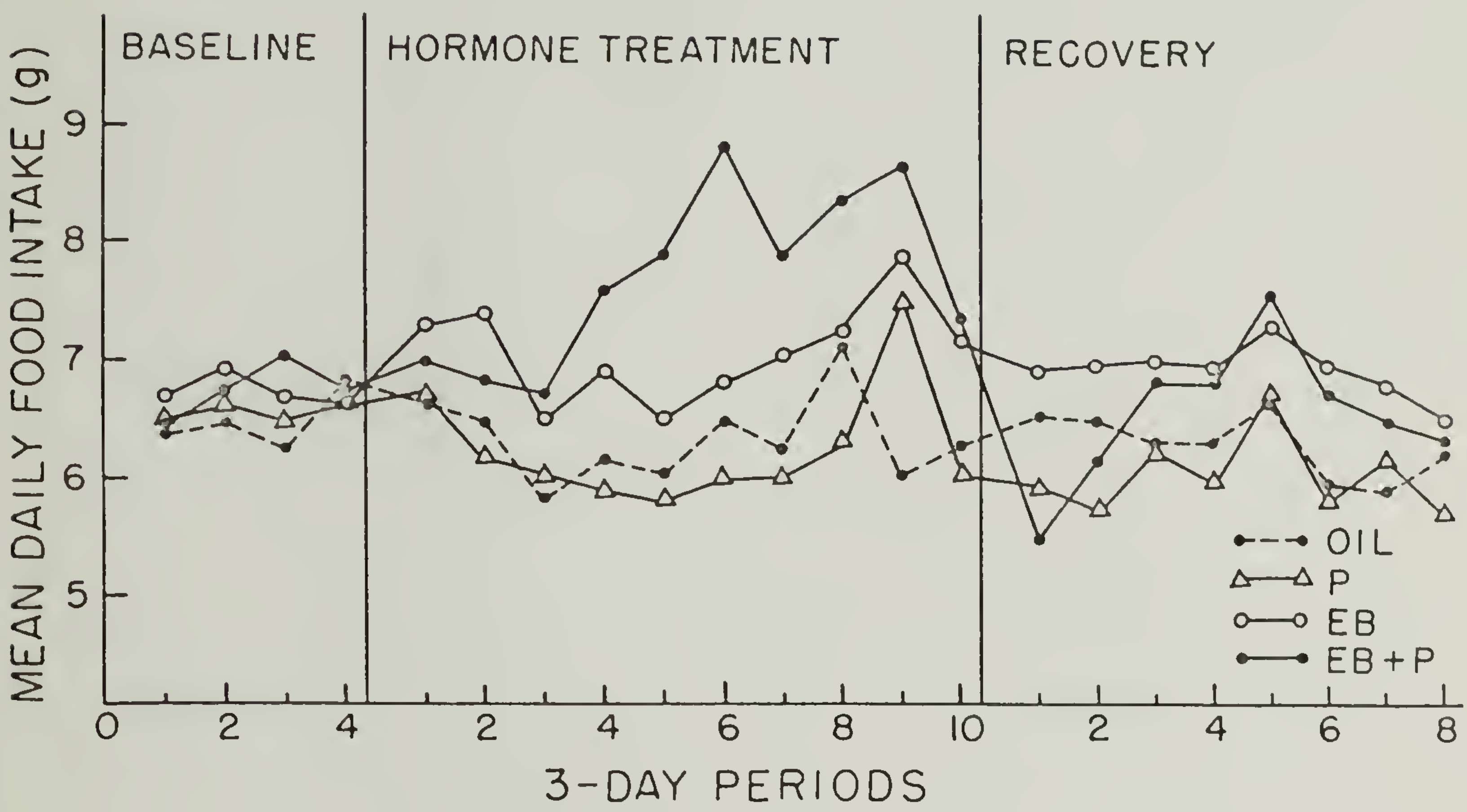
Figure 5. The effects of exogenous ovarian treatment on mean body weight.


EFFECT OF OVARIAN HORMONES ON BODY WEIGHT
BASELINE
HORMONE TREATMENT
RECOVERY
MEAN BODY WEIGHT (g)
75
70
65
60
0
2
4
2
4
6
8
10
2
4
6
8
3-DAY PERIODS
OIL
P
EB
EB+P

FACE PAGE FOR FIGURE 6

Figure 6. The effects of exogenous ovarian treatment on mean daily food intake.

EFFECT OF OVARIAN HORMONES ON FOOD INTAKE



that the latter treatment was more effective than the former in increasing daily food intake, t (10) = 3.86, $p < .01$.

DISCUSSION

The combined results of the first two experiments demonstrate that the relations between levels of circulating androgens and eating and body weight that have been described for male rats cannot be accurately generalized to male gerbils. In rats, orchiectomy produces permanent reductions in both food intake and body weight measures, while exogenous replacement of TP or DHTP (in appropriate doses) reverses these effects (Kakolewski *et al.*, 1968; Leshner & Collier, 1973; Gentry & Wade, 1976). By contrast, removal of androgens in gerbils, either by orchiectomy or by withdrawal of exogenous TP or DHTP treatment to gonadectomized animals, produces substantial body weight gains and no systematic changes in food intake. Further, the already elevated body weights of orchiectomized gerbils are not reduced by exogenous androgen replacement, but rather exhibit additional gains when hormone administration is withdrawn. It is noteworthy that although androgenic effects on body weight in the two species are in opposite directions, their onset is delayed in both cases. Additionally, in both rats and gerbils variations in TP levels seem to consistently produce greater fluctuations in body weight than do comparable fluctuations in DHTP levels.

Certainly the results reported here do not provide evidence of the nature of the mechanism by which androgen removal increases body weight in gerbils. Leshner and Collier (1973) used carcass analysis techniques to demonstrate that gonadectomy of male rats produced decreases in lean body mass, but did not affect the percentage of fat content in the total body mass. Similar studies of carcass composition comparing intact and orchiectomized gerbils could provide a more detailed account of the changes that accompany androgen removal in this species.

The findings of the third experiment indicate that observed relations between ovarian hormone titers and body weight and food intake measures cannot be generalized from rats to gerbils either. Exogenous administration of EB alone to ovariectomized rats reduces body weight and produces transient decreases in food intake (Tarttelin & Gorski, 1971; Mook *et al.*, 1972; Redick, Nussbaum & Mook, 1973; Wade, 1975). In ovariectomized gerbils, the observed effect of exogenous EB is just the reverse: both body weight and food intake increase considerably during the period of hormone injections. Exogenous P alone has no effect on body weight or eating in ovariectomized rats (e.g., Hervey, E. & Hervey, G. R., 1966; Wade, 1975) or gerbils. However, P has been shown to antagonize, or at least attenuate the effects of EB when the two hormones are administered together to ovariectomized rats (Wade, 1975). By contrast, the present findings demonstrate at least a mild facilitation of estrogenic effects on food intake and body weight when EB and P are administered together to ovariectomized gerbils.

There is recent evidence to support the species differences in ovarian hormone effects on eating and body weight reported here. Roy, Maass, and Wade (1976) have shown that MER-25 (an anti-estrogen that is estrogenic with respect to its effects on body weight and food intake in rats) increases both of these measures in ovariectomized gerbils. Additionally, Roy *et al.* found *no* evidence of antagonism of EB by P in ovariectomized gerbils receiving either MER-25 plus EB plus P (MEP), or EB plus P. At present studies are being conducted to demonstrate the relation between changes in estrogen and progesterone titers, and fluctuations in eating and body weight in intact, cycling gerbils, and to assess the effects of ovariectomy on these measures in reliably cycling animals. The molecular details of the estrogen-progesterone interaction in gerbils are also being investigated. Studies comparing the carcass composition of intact and ovariectomized gerbils should also be undertaken to further explicate the results presented here.

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