EVALUATION OF MELENGESTROL ACETATE AND GNRH AGONIST IMPLANTS IN CONTROLLING AGGRESSION IN CAPTIVE UNGULATES

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ABSTRACT

In many species, such as the Scimitar-horned oryx (Oryx dammah), high levels of inter-male aggression plague attempts to maintain bachelor herds in captivity. At Fossil Rim Wildlife Center, two groups of 5 male oryx were treated with hormonal implants in an attempt to reduce aggression, with one receiving melengestrol acetate (MGA) and the other a GnRH agonist. At 1-yr post-implantation, the following aspects were examined: (1) the effectiveness of the implants in controlling aggression, (2) the relationship among plasma testosterone, dominance, and aggression, and (3) influences such as the presence of female-typical hormones (progestins) in males, shortened horns in the MGA-implanted group, and possible depressant effects of MGA on inter-group differences in aggression. At 1-yr post-implantation, three types of behavioral data were collected: (1) frequency of social actions using an all-occurrences recording technique, (2) activity state using scan sampling with instantaneous recording at 15-min intervals, and (3) association in terms of subgroup size at 15-min intervals. Within all categories of agonistic behavior, the mean number of acts was significantly lower in the MGA-implanted group than in the GnRH agonist-implanted group ($p=0.0001$). Between groups, there was no significant difference in plasma testosterone concentrations at 1-yr post-implantation ($p=0.1172$). Over all individuals, there was no significant correlation between

plasma testosterone and frequency of ritualized threats ($p=0.93$) or non-ritualized aggression ($p=0.86$). The MGA-implanted group displayed significantly lower levels of all social behaviors ($p=0.0001$), a significantly lower index of association ($p=0.0001$), and a significantly higher index of resting ($p=0.0001$). At 1-yr post-implantation, the MGA implants were more effective in controlling aggression, but the lower levels of aggression could not be attributed solely to depressed plasma testosterone, a "feminizing" effect of MGA, or shortened horns in the MGA-implanted group. The MGA appeared to reduce the frequency of all social behavior, including aggression, and general activity.

INTRODUCTION

Problem of aggression in all-male groups in captivity

In the face of accelerated extinction rates caused by human activities, captive propagation may play a vital role in maintaining biodiversity. Many species, including the Black-footed ferret (Mustela nigripes) [Maguire et al., 1988; Clark and Harvey, 1991] and Scimitar-horned oryx (Oryx dammah) [Lieberman, 1990], still exist only because zoos and other wildlife centers supported viable populations at the time of extinction in the wild. However, to be effective and successful, breeding facilities must balance several inherent opposing factors such as limited resources, small populations, genetic diversity, and biological constraints of the captive species [Conway, 1989].

Limited space, money, time, and provisions severely attenuate the number of animals in captive populations. Small populations may be detrimental to preserving genetic diversity, yet understanding and protecting genetic diversity is vital in the quest to preserve species [Vrijenhoek, 1989]. Through the use of computer modeling systems and regulation of family sizes and sex ratios, captive breeding programs attempt to maximize the effective size of the population and minimize the loss of genetic variability [Foose and Ballou, 1988].

To maximize effective population size in a captive situation, species are typically maintained in single-male/ multi-female groups with adolescent males removed before male-male aggression develops [Blumer et al., 1992]. However, a large number of unpaired males, usually retained for future breeding, accumulates over time. Zoological institutions with larger holding facilities have attempted to establish all-male herds, but high levels of male-male aggression often result in injuries [E. Blumer, personal communication].

Hormonal implants to control aggression

Theoretically, hormonal implants could be used to reduce aggression, based on the presumed association between testosterone and aggression in males [Blumer et al., 1992]. Hormonal implants of Melengestrol Acetate (MGA) or Gonadotropin Releasing Hormone (GnRH) agonists would be predicted to reduce testosterone. If the connection between testosterone and aggression is valid, such implants would therefore be anticipated to reduce aggression in males. Thus, hormonal implants may help alleviate the problem of male-male aggressiveness in maintaining bachelor herds of some species.

In general, testosterone is thought to be positively correlated with aggressiveness in mammals. However, few

studies have demonstrated a direct relationship between testosterone and aggressiveness [Packard et al., 1985; Albert et al., 1986]. Under a colony intruder experimental design, previously dominant male laboratory rats (Rattus norvegicus) showed greatly reduced aggressive behavior after castration and subsequently lost their colonies to the intruders who became the dominant males [Albert et al., 1986]. When castrated animals were treated with testosterone, they continued to exhibit high levels of aggression and maintain their dominant status. Packard et al. [1985] demonstrated a significantly positive correlation between testosterone response to a Luteinizing Hormone Releasing Hormone (LHRH) challenge and aggression in male wolves (Canis lupus). However, other factors including context (colony intruder versus a neutral situation) [Blanchard et al., 1977; Caldwell et al., 1984], previous experience [Ginsburg and Allee, 1942; Scott and Fredericson, 1951; Monaghan and Glickman, 1992], and length of attack latency [Van Oortmerssen et al., 1985] strongly influence the relationship between plasma testosterone levels and aggressiveness.

In contrast to the paucity of studies showing a direct relationship between testosterone and aggression, several studies have examined the hormonal linkages that would result in lower testosterone as a result of chronic exposure to GnRH, LHRH, and their agonists. As GnRH, LHRH, GnRH

agonists, and LHRH agonists are used interchangeably, all will be referred to as GnRH agonists throughout the remainder of this paper.

A reduction in testosterone in males associated with chronic exposure to GnRH agonists may be mediated at several different physiological levels, depending on the species. Chronic exposure to GnRH agonists in males has resulted in reduced testicular LH receptors in rats [Labrie et al., 1978; Bambino et al., 1980], decreased pituitary LH levels in castrated rats [Sandow et al., 1978; Arimura et al., 1979] and bulls (Bos taurus) [Melson et al., 1986], and diminished plasma LH levels in rats [Sandow et al., 1978; Arimura et al., 1979] and humans (Homo sapiens) [Bergquist et al., 1979]. Chronic exposure to GnRH agonist resulted in decreased plasma testosterone levels in rats [Labrie et al., 1978; Bambino et al., 1980], humans [Happ et al., 1978; Bergquist et al., 1979; Smith et al., 1979; Doelle et al., 1981; Faure et al., 1982], dogs (Canis familiaris) [Sandow et al., 1980], Rhesus macaques (Macaca mulatta) [Akhtar et al., 1983], and baboons (Papio sp) [Vickery and McRae, 1980]. In contrast to reduced plasma levels of LH or testosterone, Fraser and Lincoln [1980] reported a reduced LH response to chronic injections of LHRH and reduced testosterone response after chronic injections of GnRH agonist in rams (Ovis sp), as did Sundaram et al. [1982] in Rhesus macaques.

Furthermore, chronic exposure in bulls decreased pituitary LHRH receptor numbers [Melson et al., 1986]. Reduction in serum testosterone after repeated GnRH agonist treatment may be related to Leydig cell desensitization because of elevated serum testosterone [Hseuh et al., 1976, 1977; Dufau et al., 1979; Belanger et al., 1980], depressed LH secretion caused by pituitary desensitization [Belchetz et al., 1978; Sandow et al., 1978], or direct inhibition of testosterone synthesis via testicular LHRH receptors [Clayton et al., 1980].

Unlike the numerous studies demonstrating the connection between chronic administration of GnRH agonists on hormone levels, few studies have illustrated the behavioral implications of exogenous progestins and GnRH agonists. In male humans, chronic administration of GnRH agonists to treat prostate cancer [Faure et al., 1982] resulted in decreased sexual performance and drive [Doelle et al., 1981; Rousseau et al., 1988]. Presumably due to the "antiandrogenic" effects [Money and Walker, 1977], synthetic progestins used in men have resulted in the reduction of sexual motivation [Bancroft et al., 1974; Lehne, 1988]. In addition, synthetic progestins are widely prescribed by veterinarians to control inappropriate sexual behavior in domestic dogs and cats [Hart, 1979; Blumer, personal communication].

Regarding the influence of synthetic progestins and GnRH agonists on aggressive behavior, only a few clinical studies

have been conducted. In male Reeve's muntjacs (Muntiacus reevesi), extended treatment with MGA resulted in a subjective decrease in aggression [Stover et al., 1985]. In addition, progestin treatment in men depressed sexually-deviant, aggressive activities [Lehne, 1988]. Likewise, in male Scimitar-horned oryx, chronic treatment of males with MGA and GnRH implants resulted in a decrease of aggression in bachelor herds, as evaluated subjectively in a trial study [Blumer et al., 1992]. Prior to implantation, male-male aggression was commonly observed. After implantation, the group implanted with MGA continued to exhibit minor aggressive displays, but no serious fighting occurred; whereas, the group implanted with a GnRH agonist performed no aggressive or dominance-related behaviors. However, at 8-mo post-implantation the aggressive behavior returned in the oryx implanted with GnRH agonist, and two males of a closely-related species (Addax nasomaculatus) were severely gored.

Scimitar-horned oryx

The Scimitar-horned oryx represents one of those species mentioned previously, which is typically maintained in single-male/multi-female groups in captivity [Blumer, personal communication]. This endangered species is possibly extinct in the wild due to overhunting, habitat loss as a result of human encroachment and competition with domestic

livestock, and desertification of its habitat [Newby, 1988]. The Scimitar-horned oryx originally ranged from Rio de Oro and Sengal to the Nile and from the southern edge of the Atlas Mountains to Sudan [Walther, 1990]. The natural social organization consists of multi-male/multi-female herds in which one adult male dominates several subordinate males within the large group of adult females and calves [Walther, 1990].

The purposes of this behavioral study were to 1) evaluate the hypothesis that GnRH agonist and MGA implants are equally effective in controlling aggression in two captive male groups of Scimitar-horned oryx at approximately 1-yr post-implantation; 2) examine the relationships among plasma testosterone levels, intergroup, and intragroup differences in aggressiveness; and 3) explore alternative hypotheses for intergroup differences in aggression regarding spatial relations within each group, the effects of female-typical hormones on male behavior in the MGA group, and the possible depressant effects of progesterone.

METHODS

Study site and study subjects

The Scimitar-horned oryx involved in this study were part of an endangered species captive propagation program at Fossil

Rim Wildlife Center in Somervell County, Texas. Located at the transition zone between the Western Cross Timbers subregion (Oak Woods and Prairies Natural Region) and the Grand Prairie subregion (Blackland Prairies Natural Region), the climate and habitat at Fossil Rim are similar to those of the native range of the oryx.

Two male groups of oryx (Group M and Group G), each effectively containing 5 individuals, were observed from 10 June - 27 July 1992. Group M contained 6 individuals, but one animal remained separated in dense vegetation and was not included in this behavioral study. Both groups occupied approximately 160-ha pastures in which they were free-roaming. All individuals in both groups were sexually-mature adults. However, individuals differed in age both within and between groups, and the exact age of all individuals was not known (Table 1). In addition to free grazing access to native grasses, both groups were provided with a supplemental pelleted feed as part of a daily animal care routine.

In Group M, the animals' horns had been removed to about 15 cm from the base prior to the beginning of the study (at the time of implantation) to eliminate the possibility of severe injury during aggressive interactions. In addition, Group M was not accessible to the public as part of the normal tour route available to visitors of Fossil Rim Wildlife Center. Two male Grevy's zebras (Equus grevyi) and

an immature male Common eland (Taurotragus oryx) were present in the pasture with Group M.

Group G was on public display in a pasture located within a section of the normal tour route and retained their full-length horns of approximately 1 m. In the pasture with Group G was a variety of species including Blackbuck (Antilope cervicapra), Sable antelope (Hippotragus niger), Black rhinoceros (Diceros bicornis), Black wildebeest (Connochaetes gnou), ostriches (Struthio sp), Blesbok (Damaliscus dorcas phillipsi), Llamas (Lama glama), Thompson's gazelles (Gazella thomsoni), and White-tailed deer (Odocoileus virginianus).

Hormonal implantation

Hormonal implants were placed in all subjects approximately 1 yr prior to the beginning of this behavioral study. The methods of implantation for each group are described in detail by Blumer et al. [1992] and summarized below.

On 17-18 April 1991, all Group M animals were immobilized and transported to the Fossil Rim Veterinary Clinic for the surgical implantation procedure. Prior to implantation, blood was collected from each animal for hormonal assays. Homogeneous silastic implants containing 12.6 - 13.8 g of melengestrol acetate (MGA, Upjohn Corp.,

Kalamazoo, Michigan 49001, U.S.A.) were implanted intramuscularly in the left lateral aspect of the neck. The MGA implants were 2 cm diameter X 7 cm length. Individuals were isolated until 22 April 1991 to allow blood levels of MGA to become established before being placed in a group situation.

On 26 June 1991, all Group G animals were immobilized and transported to the Fossil Rim Veterinary Clinic for the surgical implantation procedure. Prior to implantation, blood was collected from each animal for hormonal assays. Homogeneous silastic implants containing 0.12 - 0.16 g of the GnRH agonist $_{D}Trp^{6}Pro^{9}NHEt$ GnRH-HOAc (provided to E. Plotka by investigators at N.I.H.) were implanted in the dorsal aspect of the left pinna. The small size of the implant (1 cm diam X 0.3 cm thick) dictated the selection of the implant site because of the need for reliable palpitation and removal at later stages of the study. Before being placed in a group situation, individuals were isolated until 26 July 1991 to allow establishment of blood levels of $_{D}Trp^{6}Pro^{9}NHEt$ GnRH-HOAc and regression of the transient rise in serum testosterone that occurs following the use of GnRH agonists. Immediately prior to releasing them into their pasture, serum was collected from each animals for testosterone assays. The hormonal assays for both groups were conducted in the laboratories of E. Plotka and T. Gross using double antibody

radioimmunoassay techniques.

Behavioral data collection

Since all animals at Fossil Rim were habituated to automobiles, observations were conducted from a vehicle that served as a moving blind. High power binoculars (15 x 60) were used to facilitate individual identification and detailed observations of behavior. The oryx were observed 9 h per day from 7:00 - 12:00 and 16:00 - 20:00 such that one group was observed per day (i.e., a day of observation was not divided between groups). Observations were refined during a 3-d pilot period during which Group G was observed. Subsequently, Group G then Group M was observed for 19 d each.

Three types of behavioral data were collected: 1) frequency of social actions, 2) activity state at 15-min intervals, and 3) subgroup size at 15-min intervals. Frequency of social behaviors and activity states were recorded separately for each individual (i.e., the frequency of social behaviors was recorded as an individual measure). In contrast, the measure of subgroup size was a group measure such that the data were recorded for the group as a whole.

Frequency of social behaviors was sampled using focal group observation procedures with continuous all-occurrences recording techniques [Martin and Bateson, 1986]. The

sampling interval was continuous for the extent of observation on each day such that the observation period from 7:00 to 12:00 comprised a 5-h continuous all-occurrences recording interval and the observation period from 16:00 to 20:00 comprised a 4-h recording interval. All occurrences of social behavior were recorded by hand into field notes or spoken into a micro-tape recorder and later transcribed into field notes. The social action patterns were divided into categories of slight threat, ritualized threat, non-ritualized aggression, defensive, affiliative, sexual, and scent-related behaviors (Table 2). Each observed occurrence of a social action pattern was tallied on a check-sheet with columns for each individual. A separate check-sheet was kept for each day of observation.

Activity state measurements consisted of scan sampling paired with instantaneous recording [Martin and Bateson, 1986]. This method was used to record the activity state of each individual in the group at 15-min intervals as designated by the tone of a stop-watch. At the tone, I recorded the state of each animal in terms of resting, feeding, maintenance, locomotion, socializing, or other activity (Table 3).

Proximity of individuals within each group was measured in terms of subgroup size. A subgroup was defined as the number of animals within 3 body lengths of each other.

Measurement of subgroup size consisted of scan sampling with instantaneous recording at the same 15-min intervals used in the measurement of activity states. At the tone, I recorded the size of each subgroup within the group. For example, if 3 of the 5 individuals in the group were within 3 body lengths of each other and the other 2 animals were greater than 3 body lengths from any other animal, subgroup sizes were recorded as 3, 1, 1.

Animals in each group were assigned a subjective dominance rank based on ability to supplant and/or evoke a submissive/defensive response from another animal. The most dominant animal was assigned the highest rank (eg., 5), and the least dominant animal was assigned the lowest rank (eg., 1). Animals that tied in their subjective dominance position received the same rank.

Physiological data collection at 1-yr post-implantation

On 28 and 29 July 1992, subjects of both groups (except one individual who was captured on 30 July 1992) were immobilized and transported to the Fossil Rim Veterinary Clinic under the supervision of E. Blumer. Blood was collected from all individuals for testosterone assays, and the GnRH agonist implants were removed. Behavioral observations were terminated at this time for two reasons. First, Group G was not returned to its original group nor original pasture.

Second, although Group M was returned to its original pasture with the original group animals, the oryx became elusive and remained unobservable for several weeks after being returned to their pasture.

Data analysis

The data were checked for normality to determine whether to employ parametric or nonparametric statistics. Because of high levels of skewness and kurtosis in the frequency distribution of the number of acts in a category committed by each animal on each day, nonparametric statistics were deemed appropriate in analyzing the all-occurrences data. Within each group, the individuals differed significantly in the frequency of all categories of social behavior (Table 4).

The significant variation between individuals justified maintaining separate totals for each individual per category and summing across the days to obtain the total number of acts in each category performed by each individual (Fig. 1). Within each behavioral category, means of individual values were compared across groups using the Mann-Whitney U test [Abacus Concepts, 1987].

Pairwise comparisons of plasma testosterone concentrations were made across time (pre-, 1-mo post-, and 1-yr post-implantation) within individuals using the Wilcoxon signed-rank test [Abacus Concepts, 1987]. Within two time

periods (pre- and 1-yr post-implantation), testosterone concentrations were compared between groups using the Mann-Whitney U test [Abacus Concepts, 1987]. Correlations between testosterone and concentrations and behavioral variables were made using the non-parametric Kendall's tau (τ) [Abacus Concepts, 1987].

A general linear models procedure [SAS, 1988] was used to examine the variance due to treatment in the dependent variables that were indices of feeding and resting. For example, the model for the feeding index was: FEED = TREATMENT DAY(TREATMENT) ID. The index of activity (feeding or resting) was calculated by summing the number of recorded instances of feeding or resting over all the 15-min intervals for each animal for each day.

The index of association for each group was calculated as the sum of the number of instances over all the 15-min intervals per day when a subgroup size of three or more individuals was recorded. The Student's t-test was used to compare the mean index of association for each group, with the means calculated across days within groups.

RESULTS

Treatment effect on aggression at 1-yr post-implantation

Within each category of aggressive behavior, the mean number

of acts was significantly lower in Group M than Group G (Fig. 2, Mann-Whitney U-test: slight threats- U=3316.5, p=0.0001; ritualized threats- U=2080, p=0.0001; non-ritualized aggression- U=76.5, p=0.0001). In Group M, the social hierarchy was well-defined and no ties in rank were assigned (Y116 > Y111 > R66 > Y0228 > R56). In Group G, two pairs of ties were assigned: the most dominant animal (B58) received a dominance rank of 5, the two intermediate animals (Y0201 and Y117) were ranked 3.5, and the two least dominant animals (Y0226 and G338) were ranked 1.5. Despite the absence of a well-defined hierarchy, one individual (B58) was clearly dominant over all others in Group G.

Treatment effect on plasma testosterone

Group G showed a significant decrease in plasma testosterone concentrations between baseline and 1-mo post-implantation (Fig. 3, Wilcoxon signed rank, Z=-2.023, p=0.0431). The mean testosterone decreased from 4.94 $\pm$ 1.37 ng/ml before implantation with the GnRH agonist to 2.28 $\pm$ 1.33 ng/ml at 1-mo post-implantation. Every animal implanted with GnRH agonist displayed a decrease in plasma testosterone levels 1-mo after implantation (Fig. 4a). However, there was not a significant difference in testosterone between 1-mo post- and 1-yr post-implantation of GnRH agonist (Fig. 3, Wilcoxon signed-rank, Z=-0.674, p=0.5002). The plasma testosterone

levels of every animal except the dominant male (B58) increased between 1-mo post- and 1-yr post-implantation (Fig. 4a). Mean plasma testosterone increased from 2.28 ± 1.33 ng/ml at 1-mo post-implantation to 3.58 ± 0.74 ng/ml at 1-yr post-implantation. Furthermore, there was no significant difference between baseline and 1-yr post-implantation plasma testosterone levels in Group G (Fig. 3, Wilcoxon signed-rank, $Z=-0.405$, $p=0.6858$).

In contrast, Group M displayed a significant decrease between baseline and 1-yr post-implantation plasma testosterone levels (Fig. 3, Wilcoxon signed-rank, $Z=-2.023$, $p=0.0431$). Mean plasma testosterone decreased from 11.56 ± 2.95 ng/ml before implantation to 6.20 ± 1.98 ng/ml at 1-yr post-implantation. The plasma testosterone levels of every individual remained lower 1 yr after MGA implantation (Fig. 4b).

The difference in baseline plasma testosterone between Group M and Group G was not significant (Fig. 3, Mann-Whitney U-test, $U=8$, $p=0.3472$). However, mean plasma testosterone was higher in Group M at baseline (Fig. 3, Group M: 11.56 ± 2.95 ng/ml, Group G: 4.94 ± 1.37 ng/ml) and at 1-yr post-implantation (Fig. 3, Group M: 6.20 ± 1.37 ng/ml, Group G: 3.58 ± 0.74 ng/ml) than in Group G. In addition, the difference in mean plasma testosterone 1-yr post-implantation (i.e., during the behavioral study) between Group M and Group

G was not significant (Fig. 3, Mann-Whitney U-test, U=5, p=0.1172).

Relation between testosterone and observed behaviors

Individuals in both groups demonstrated a significant positive correlation between number of slight threats and dominance (Fig. 5, Kendall's correlation coefficients, τ=0.8, p=0.05). There was a significant positive correlation between dominance rank and 1-yr post-implantation plasma testosterone levels in Group M (Fig. 6c, Kendall's correlation coefficient, τ=0.8, p=0.05). In Group G, there was no significant correlation between dominance rank and plasma testosterone levels at 1-mo post-implantation (Fig. 6a, Kendall's correlation coefficient, τ=0.3, p=0.4624) or 1-yr post-implantation (Fig. 6b, Kendall's correlation coefficient, τ=-0.2, p=0.6242).

Across all individuals, there was no significant correlation between plasma testosterone at 1-yr post-implantation and frequency of ritualized threats (Fig. 7a, Kendall's correlation coefficient, τ=-0.022, p=0.9287), frequency of non-ritualized aggression (Fig. 7b, Kendall's correlation coefficient, τ=0.044, p=0.858), or frequency of defensive behaviors (Fig. 7c, Kendall's correlation coefficient, τ=-0.111, p=0.6547). Although testosterone was significantly positively correlated with overall

aggressiveness (defined as the total number of slight threats, ritualized threats, and non-ritualized aggression) in Group M (Kendall's correlation coefficient, τ=0.8, p=0.05), it was not in Group G (Kendall's correlation coefficient, τ=-0.4, p=0.3272).

Alternative hypotheses

All other categories of social behavior were less frequent in Group M than Group G (Fig. 2, Mann-Whitney U-test: defensive- U=2568.5, p=0.0001; sexual- U= 13, p=0.0001; affiliative- U=1313, p=0.0001; scent-related- U=1089, p=0.0001). Indices of feeding and resting were significantly higher for Group M than Group G (Table 5, Fig. 8). The mean index of association was significantly lower for Group M than Group G (Fig. 9, unpaired t-test one tailed, t=15.939, p=0.0001).

DISCUSSION

My major hypothesis that implants of MGA and GnRH agonist would be equally effective at controlling aggression in male groups of Scimitar-horned oryx at 1-yr post-implantation was rejected. Aggression was higher in the GnRH agonist-implanted group compared to the MGA-implanted group. A corollary hypothesis that differences in aggression would be directly correlated with plasma testosterone concentrations was also rejected. As an alternative explanation, I propose

the working hypothesis that the MGA implant resulted in an overall suppression of all social behaviors, not exclusively aggression, and general activity.

The reasons for proposing this alternative hypothesis are described below. First, I will address the effect of the treatments on aggressive behavior. Second, I will discuss the relationships among plasma testosterone, aggressive behaviors, and dominance. Finally, I will explain why I propose that the effectiveness of the MGA treatment in lowering aggression may have been due to an overall reduction of activity.

Effectiveness of hormonal implants

At 1-yr post-implantation, the progestin (MGA) implants were more effective in reducing aggression than GnRH agonist implants. All categories of agonistic behavior, including slight threats, ritualized threats, non-ritualized aggression, and defensive behaviors, were significantly lower in the group implanted with MGA. However, the MGA implants did not induce a total cessation of all aggressive behaviors as reported by Blumer et al. [1992] in the first 8 mo after the implantation of the GnRH agonist.

Relation between plasma testosterone and aggressive behaviors

Previous studies have supported a positive correlation

between testosterone and aggression in male mammals [Packard et al., 1985; Albert et al., 1986]. If differences in aggressiveness are purely the result of lower plasma testosterone in male mammals, the MGA-implanted group that displayed a significantly lower frequency of all aggressive behaviors would be predicted to possess lower plasma testosterone. However, there was no significant difference in the plasma testosterone levels between the two groups, and mean plasma testosterone levels in the MGA-implanted group were actually (though not significantly) higher than in the GnRH-implanted group. The lack of significance may be due to small sample size. If no other factors influence the relationship between testosterone and aggression in Scimitar-horned oryx males, a direct positive correlation between testosterone and ritualized threats and non-ritualized aggression would be predicted for all animals regardless of their experience with each other and which animals were housed together. The fact that there was no significant correlation between plasma testosterone levels and ritualized threats and non-ritualized aggression when all animals were considered together supports the conclusion that there is not a direct correlation between plasma testosterone levels and aggressiveness in Scimitar-horned oryx males.

Lower frequency of aggression in the MGA-implanted group than in the GnRH-implanted group cannot be accounted for

solely by depressed plasma testosterone levels in the MGA-implanted group. The high individual variation within each group with regard to both plasma testosterone levels and aggression suggests that the large difference in aggression between groups cannot be attributed simply to an influence of plasma testosterone levels. As discussed below, the residual influences of learned dominance relations within each group appear to distort a direct relationship between testosterone and aggression.

A factor that appears to complicate the relationship between testosterone and aggressiveness is the role of dominance. There was a significant correlation between subjective dominance rank and plasma testosterone levels at 1-yr post-implantation in the MGA-implanted group. In the GnRH-implanted group, plasma testosterone levels at neither 1-mo post- nor at 1-yr-post implantation were significantly correlated with dominance rank. However, at 1-mo post-implantation when the GnRH-implanted animals were placed into a group, the individual (B58) with the highest testosterone became the dominant individual in the group. As noted in Fig. 4a, the plasma testosterone level of the animal that became dominant was at least sixfold higher than any other animal in the group at the time the group was formed. At 1-yr post-implantation, the dominant individual (B58) no longer possessed the highest testosterone level. It was interesting

to note that the previously dominant individual (B58) lost his dominance status when the group was reassembled after this study. Four of the individuals (B58, G338, and Y0226, and Y0201) formerly implanted with GnRH agonist were placed into a different pasture with two sexually immature males. One of the previously implanted animals (G338) transferred into the new group had the highest testosterone level of the GnRH-implanted group at 1-yr post-implantation and subsequently became the dominant animal in the new social group. Moreover, the new dominant male (G338) was dominant over the previously dominant male (B58). This anecdote suggests that in male Scimitar-horned oryx, the establishment of the alpha male may be related to plasma testosterone levels at the time a group is assembled; however, after dominance has been established, the dominant male may maintain his dominance without possessing the highest plasma testosterone level.

The effect of testosterone levels on the rank attained by animals after group formation appears to vary between species. Rose et al. [1971] found no correlation between testosterone prior to formation of a group and the dominance rank achieved after group establishment in Rhesus macaques. In all experiments, the testosterone of the male that became dominant rose rapidly after having established his dominance, and in several cases, the alpha male attained the highest

testosterone level. However, in long-existent stable groups, Rose et al. [1971] found no correlation between dominance rank and testosterone levels.

Dominance within both groups was significantly positively correlated with slight threats, with the dominant male performing the most slight threats in both groups. Slight threats were mainly approaches (see Table 2) in which the dominant individual supplanted other individuals or disrupted a social interaction between other animals. In the GnRH agonist-implanted group, the dominant individual showed the lowest frequency of non-ritualized aggression. In the MGA-implanted group the dominant male performed the highest frequency of non-ritualized aggression mainly in the form of a pursuit run after approaching another male.

In summary, it appears that dominance in the oryx may be asserted mainly through the use of slight threats and that high levels of non-ritualized aggression may not be "necessary" if the dominant individual has already established his dominance over others in his group. Within the GnRH agonist-implanted group, plasma testosterone levels were not positively correlated with aggressiveness (a combined total of slight threats, ritualized threats, and non-ritualized aggression). However, within the MGA-implanted group, plasma levels of testosterone were significantly correlated with aggressiveness. Therefore, the

relationship that will develop between animals with regard to dominance or aggression within a social group cannot be determined based on a knowledge of plasma testosterone levels alone.

In the first months after implantation, Blumer et al. [1992] reported a subjectively detectable decrease in aggression in both the GnRH-implanted group and the MGA-implanted group corresponding to the significant post-implantation reduction of plasma testosterone levels. Therefore, a relative reduction in plasma testosterone levels may contribute to the observed decrease in aggression between animals interacting within the same group but cannot be used to explain differences in aggression between two groups that do not interact. This result supports previous studies that demonstrate the importance of other factors, such as experience [Scott and Fredericson, 1951], in the relation between testosterone and aggression.

The presence of a threshold amount of testosterone may be necessary for the expression of aggression, but beyond this threshold, testosterone levels may not be adequate predictors of an individual's aggressiveness. Similar results were obtained by Barkley and Goldman [1977] in their study on the development of aggression in intact male mice. They reported an increase in prepuberal testosterone that coincided with the initiation of aggressive behavior.

However, plasma testosterone levels were not correlated with aggression in adult males. Packard et al. [1985] found that breeding and non-breeding males in a wolf pack showed testosterone levels supportive of spermatogenesis. Although baseline testosterone was not correlated with aggressive behavior, testosterone responsiveness to LHRH injection was correlated with aggression.

Alternative hypotheses

Alternative hypotheses should be considered in discussion of the treatment effect and the possible mechanisms involved. In the following discussion, I will address (a) the possible "feminizing influence of progestins, (b) confounding effects of horn removal, and (c) general reduction in activity.

In female rats, lower blood progesterone levels are associated with higher aggression [Hood, 1984]. All-female groups of oryx are less aggressive than the all-male groups (Blumer, personal communication). If the MGA were producing a "feminizing effect," other alterations in male-typical behavior in addition to reduced aggression such as a higher frequency of affiliative behavior and closer proximity as observed in all-female groups would also be predicted in the MGA-implanted group. This "feminizing effect" hypothesis was rejected because the MGA-implanted group displayed a lower frequency of affiliative behavior and a lower index of

association.

Closer proximity as manifested in a higher index of association would be predicted in the MGA-implanted group due to the presence of shorter horns. However, as mentioned above, Group M displayed lower proximity (i.e., they maintained a higher inter-individual distance) than in the GnRH agonist-implanted group that retained their full horns. Therefore, the altered behavior in the MGA-implanted group, including the reduced aggression, cannot be attributed solely to the shorter horns of those animals.

The general reduction in social interactions and increased proportion of time spent resting as compared to the GnRH agonist-implanted group suggest that the progestin (MGA) acted as a general depressant in the male oryx. As all categories of social behavior were less frequent in the MGA-implanted group, the effects of the MGA implant were not restricted to a reduction in aggressive behaviors alone. The suppression of general activity did not extend to feeding behavior as the MGA-implanted group also spent more time feeding. An increase in feeding is compatible with the observed side-effect of increase in appetite in domestic cats and dogs administered synthetic progestins to control sociosexual behavior [Hart, 1979].

Previous studies also demonstrate a depressant effect of progesterone. In rats, progesterone suppresses the movement-

correlated increase in cerebellar Purkinje cell firing [Smith et al., 1989]. Schumacher [1990] demonstrated a high affinity of GABAa (an inhibitory neurotransmitter) receptors for progesterone and its metabolites in rats. Therefore, I recommend that future studies examine the working hypothesis that MGA implants reduce aggressiveness in male ungulates via mechanisms of a general depressant effect. However, when predicting the relationship between hormones and behavior, it is important to consider species differences [Crews, 1992].

CONCLUSION

1. At 1 year post-implantation, the MGA-implanted group was less aggressive than the GnRH agonist-implanted group.
2. The difference in aggression between the groups could not be explained solely on the basis of depressed plasma testosterone levels in the MGA-implanted group.
3. Plasma testosterone levels were not directly correlated with aggression in Scimitar-horned oryx males. Other factors such as learned dominance relations within groups influenced the relationship between testosterone and aggression.
4. Alternative hypotheses to explain the lowered aggression in the MGA-implanted group that could be rejected included a "feminizing effect" of progestins in the males and shortened horns.
5. Progestins appeared to reduce the frequency of all social

behaviors and the general activity level in the MGA-implanted group. Therefore, the effect was not specific to aggressiveness.

6. A working hypothesis arising from this study needs to be examined further in future studies: MGA implants reduce aggressiveness in bachelor groups of ungulates via a general depressant effect on social activity.

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Table 1. Birth dates and ages of oryx individuals

GROUP	ID NUMBER	BIRTHDATE	AGE IN MONTHS
MGA	Y116	Unknown	Adult
MGA	Y111	Unknown	Adult
MGA	R66	14 Jun 1984	96
MGA	Y0228	20 Feb 1987	64
MGA	R56	Unknown	Adult
GnRH agonist	B58	?? ??? 1988	48
GnRH agonist	Y0201	17 May 1990	25
GnRH agonist	Y117	28 Nov 1989	31
GnRH agonist	G338	10 Apr 1990	26
GnRH agonist	Y0226	21 Aug 1990	21

Table 2. Categories and descriptions of social action patterns

CATEGORY	ACTION PATTERN	DESCRIPTION	REFERENCES
SLIGHT THREATS	lateral body present	standing at a right angle in front of or behind another with head and neck erect	Walther 1984--lateral T-position Estes 1991--lateral presentation
	approach	walking toward another resulting in a social interaction	Walther 1984--approach
	angle horn toward	tilting the head such that the horn tips point or angle toward another	Walther 1984--sideward angling of horns Estes 1991--angle horn
	pursuit walk	walking toward another who is attempting to move away	Walther 1984--pursuit
RITUALIZED THREATS	nodding	a quick, forward downward movement of the horns toward another but with no contact	Walther 1984--nod threat Estes 1991--nodding (symbolic butting)
	horn sweep	quick movement of nose to flank causing the horns to move in a wide arc	Walther 1984--swing-out movements Estes 1991--horn-sweeping

Table 2. continued

CATEGORY	ACTION PATTERN	DESCRIPTION	REFERENCES
	high horn present	neck is erect with chin tucked and horns tilted slightly toward another	Walther 1984--high presentation of horns Estes 1991--high-horn presentation
	medial horn present	neck is horizontal with chin tucked and horns tilted slightly toward another	Walther 1984--medial presentation of horns Estes 1991--medial-horn presentation
	low horn present	head is close to or on the ground with horns pointing toward another	Walther 1984--low presentation of horns Estes 1991--low-horn presentation
	stiff legged pacing pursuit	walking pursuit with legs held stiffly and fore and rear leg on same side moving simultaneously	
	rushing	running abruptly toward a stationary animal	Walther 1984--rush attack
	kneeling	dropping to carpals such that the body tilts down from rear to shoulders	Walther 1984--kneeling Estes 1991--kneeling

Table 2. continued

CATEGORY	ACTION PATTERN	DESCRIPTION	REFERENCES
NON-RITUALIZED AGGRESSION	butting	delivering forward, downward blows of the forehead and base of horns to another	Walther 1984--butting
	horn stab	hitting tips of horns to body of another; includes over-the-shoulder-stabbing	Walther 1984--stab-over-the-shoulder Estes 1991--stabbing
	horn clash	delivery of forward, downward blows by two animals such that the body of the horns clash	Estes 1991--clash fighting
	pursuit run	running toward an animal who is moving away	Walther 1984--chasing Estes 1991--chasing
	horn wrestle	two animals lock horns and grapple, twisting head and horns	Estes 1991--front-pressing, horn pressing
DEFENSIVE	head low posture	neck and head held below horizontal with nose close to the ground	Estes 1991--head-low posture
	head throwing	repeated lifting of the nose such that the horns are tossed back; head may be above or below the horizontal	Walther 1984--head throwing Estes 1991--chin-lifting, head-throwing

Table 2. continued

CATEGORY	ACTION PATTERN	DESCRIPTION	REFERENCES
	quick step away	quick movement of one to a few steps away from another animal or object	
	leave-walk	walking away from another	
	leave-run	running away from another	
SEXUAL	circling	standing in reverse-parallel position, two animals follow each others' rumps	Walther 1984--agonistic circling, mating whirl-around Estes 1991--circling
	foreleg kick	lifting the foreleg from the ground directed at another and often making contact	Walther 1984--foreleg kick, *Laufschlag* Estes 1991--foreleg lifting
	chin rest	placing the chin on another	Estes 1991--chin-resting
	mount	resting the forequarters on another	Walther 1984--mounting
	erection	erect penis extending from the sheath	
	tail raise	tail held at or above the horizontal with no defecation	

Table 2. continued

CATEGORY	ACTION PATTERN	DESCRIPTION	REFERENCES
AFFILIATIVE	lick	tongue of one individual contacts body of another	
	nudge	pushing on another with bridge of nose	Estes 1991--nudging
	nose touch	touching tip of nose to another	
SCENT-RELATED	sniff urine	placing nose in urine stream of another	Estes 1991--urine testing
	flehman	lifting the nose and curling the upper lip back	Walther 1984--Flehman
	sniff anus	sniffing anus of another	
	sniff urogenital	sniffing the urogenital region of another	

Table 3. Descriptions of behavioral states

STATE	DESCRIPTION
resting	inactivity while lying or standing; not involved in feeding, locomotion, socialization, or maintenance
feeding	any activity involved with ingestion including grazing, eating supplemental feed, and masticating and swallowing newly-consumed material; does not include cud-chewing
locomotion	displacement of the body from one point to another by the power of the animal
socializing	any interaction between two animals in which signals are directed from one animal to another with the possibility of response from the recipient (see Table 2 for social action patterns and categories)
maintenance	actions that permit animals to meet the requirements of living, provide protection from normal environmental conditions and adversities, and keep the body operational (Grier and Burk, 1992); includes urination, defecation, grooming, scratching; excludes those behaviors that are present at all times such as respiration and internal, unobservable processes; excludes feeding

Table 4. Summary of results from Friedman's analysis of variance conducted to examine individual variation in actions within each behavioral category

BEHAVIORAL CATEGORY	CHI-SQUARED VALUE[a]	P=
slight threat	137.7	0.0001
ritualized threat	128.0	0.0001
non-ritualized aggression	149.2	0.0001
defensive	150.5	0.0001
sexual	165.1	0.0001
affiliative	106.8	0.0001
scent-related	121.0	0.0001

[a]For the Friedman's analysis, ranks were assigned across individuals within days. Analysis was conducted using the Statview program; the Friedman's statistic is reported as Chi-Squared [Abacus Concepts, 1987].

Table 5. Results of General Linear Models analysis of effects of MGA and GnRH agonist implants for resting and feeding indices

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE	F VALUE	PR>F
DEPENDENT VARIABLE: REST					
Model	45	3009.5	66.9	15.0	0.0001
Error	144	640.7	4.4		
Corrected Total	189	3650.2			
TREATMENT[a]	1	968.6	968.6	217.7	0.0001
DAY(TREATMENT)[a]	36	1828.7	50.8	11.4	0.0001
ID[a]	8	212.4	26.5	6.0	0.0001
DEPENDENT VARIABLE: FEED					
Model	45	1985.1	44.1	9.0	0.0001
Error	144	707.6	4.9		
Corrected Total	189	2692.7			
TREATMENT[a]	1	104.6	104.6	21.3	0.0001
DAY(TREATMENT)[a]	36	1776.8	49.4	10.0	0.0001
ID[a]	8	103.6	13.0	2.6	0.0100

[a]Type I SS

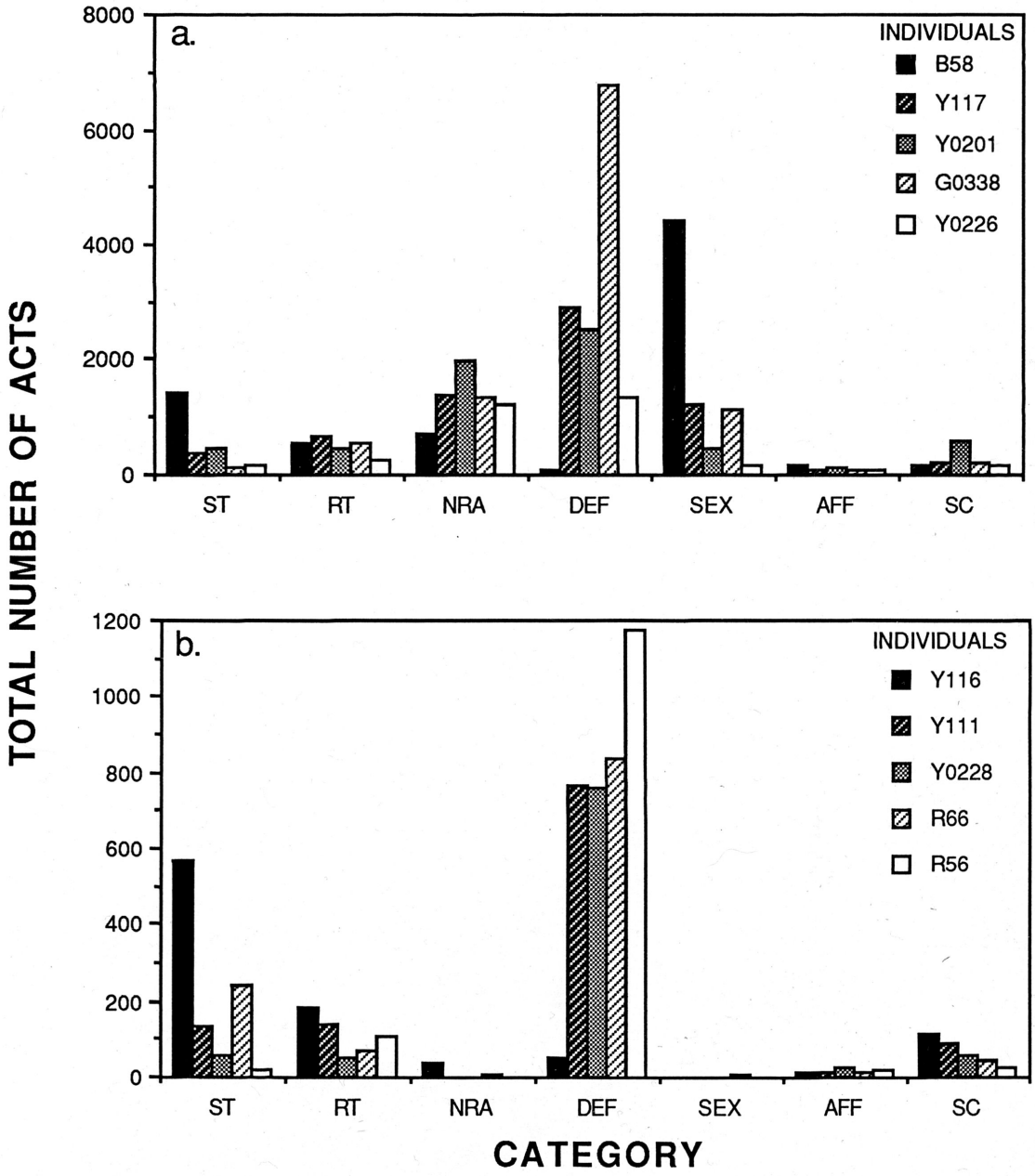
a.
INDIVIDUALS
B58
Y117
Y0201
G0338
Y0226
8000
6000
4000
2000
0
ST
RT
NRA
DEF
SEX
AFF
SC
b.
INDIVIDUALS
Y116
Y111
Y0228
R66
R56
1200
1000
800
600
400
200
0
ST
RT
NRA
DEF
SEX
AFF
SC
TOTAL NUMBER OF ACTS
CATEGORY

Figure 1.

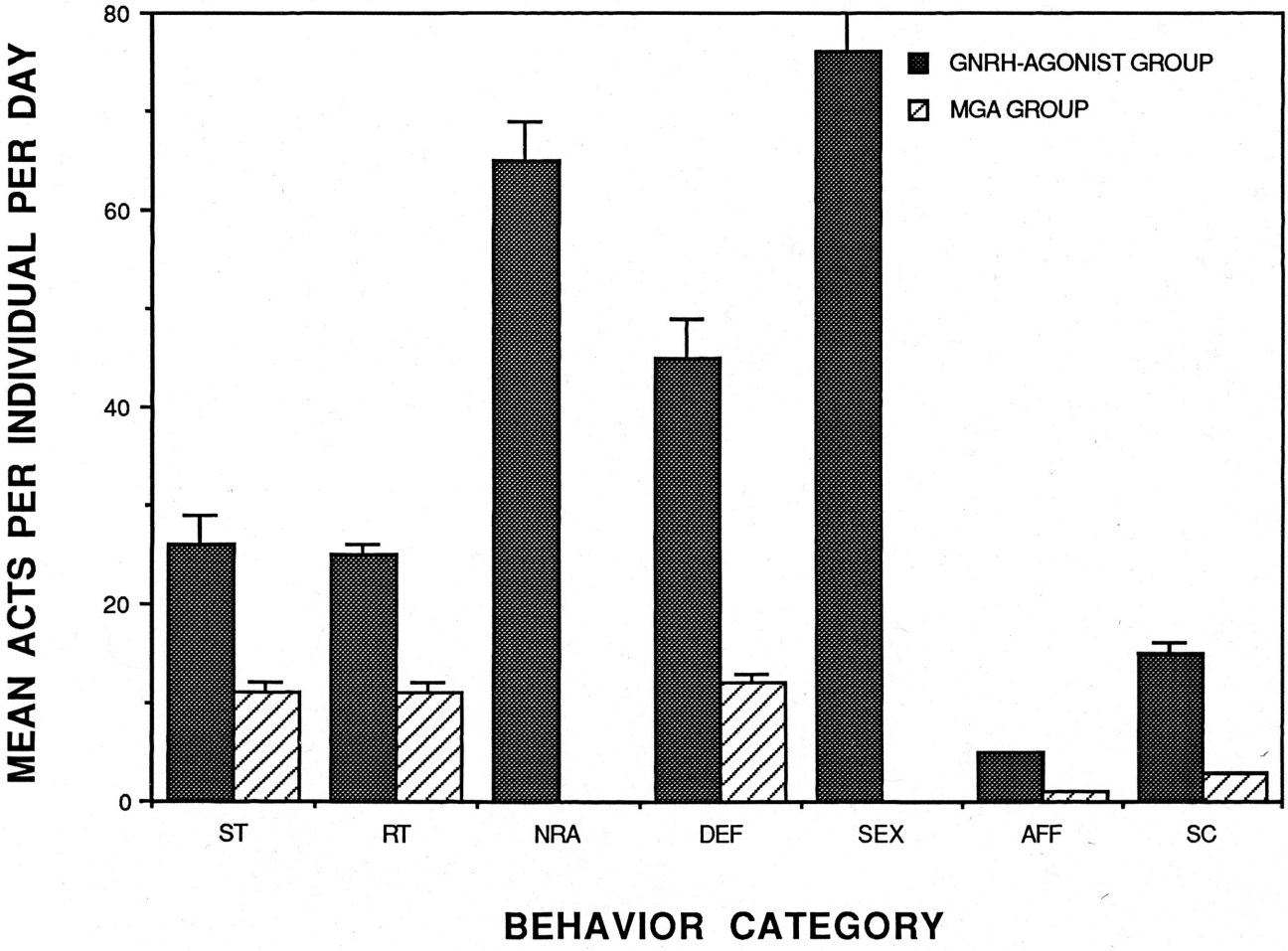
MEAN ACTS PER INDIVIDUAL PER DAY
80
60
40
20
0
GNRH-AGONIST GROUP
MGA GROUP
ST
RT
NRA
DEF
SEX
AFF
SC
BEHAVIOR CATEGORY

Figure 2.

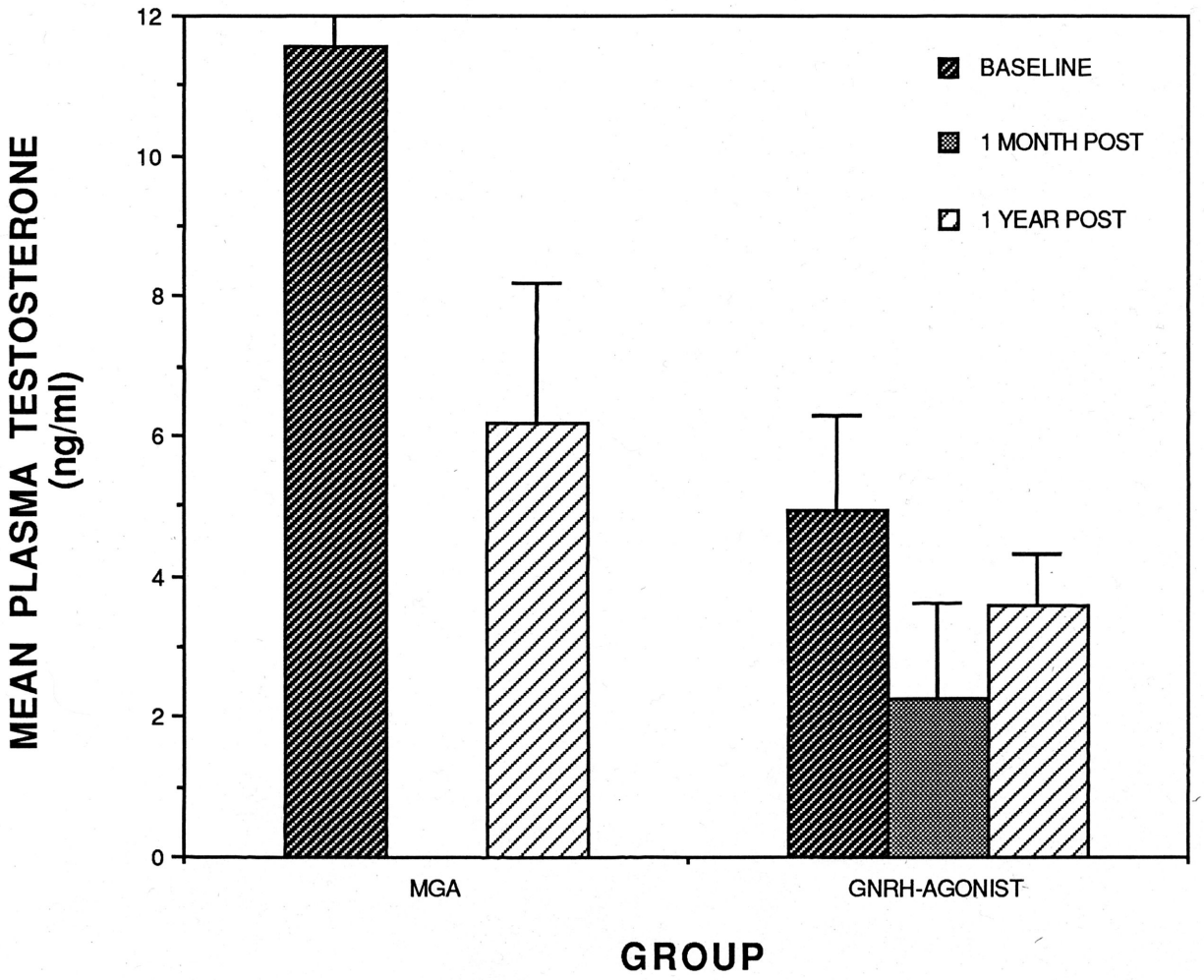
MEAN PLASMA TESTOSTERONE
(ng/ml)
12
10
8
6
4
2
0
BASELINE
1 MONTH POST
1 YEAR POST
MGA
GNRH-AGONIST
GROUP

Figure 3.

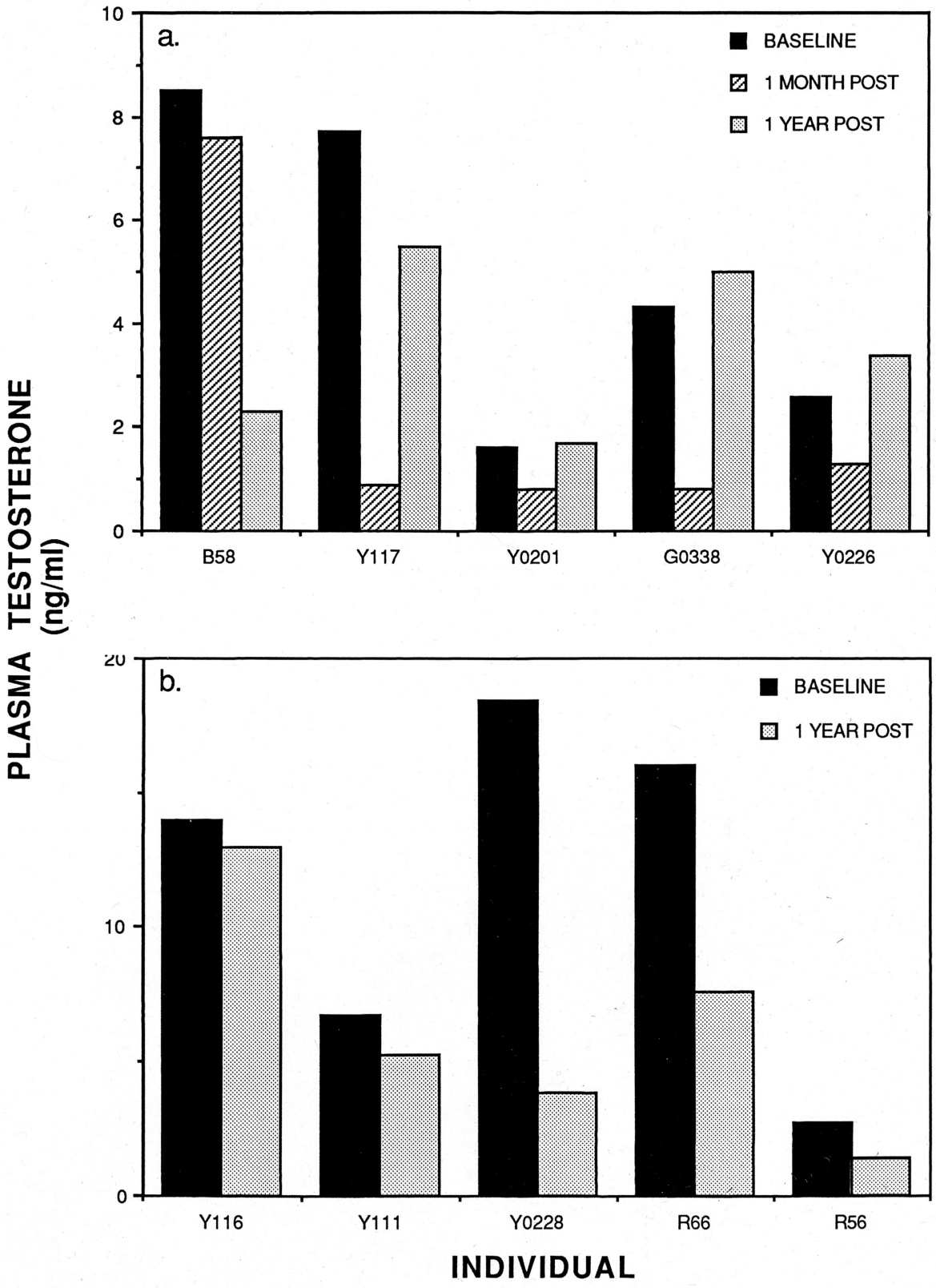
a.
BASELINE
1 MONTH POST
1 YEAR POST
10
8
6
4
2
0
B58
Y117
Y0201
G0338
Y0226
b.
BASELINE
1 YEAR POST
20
10
0
Y116
Y111
Y0228
R66
R56
PLASMA TESTOSTERONE (ng/ml)
INDIVIDUAL

Figure 4.

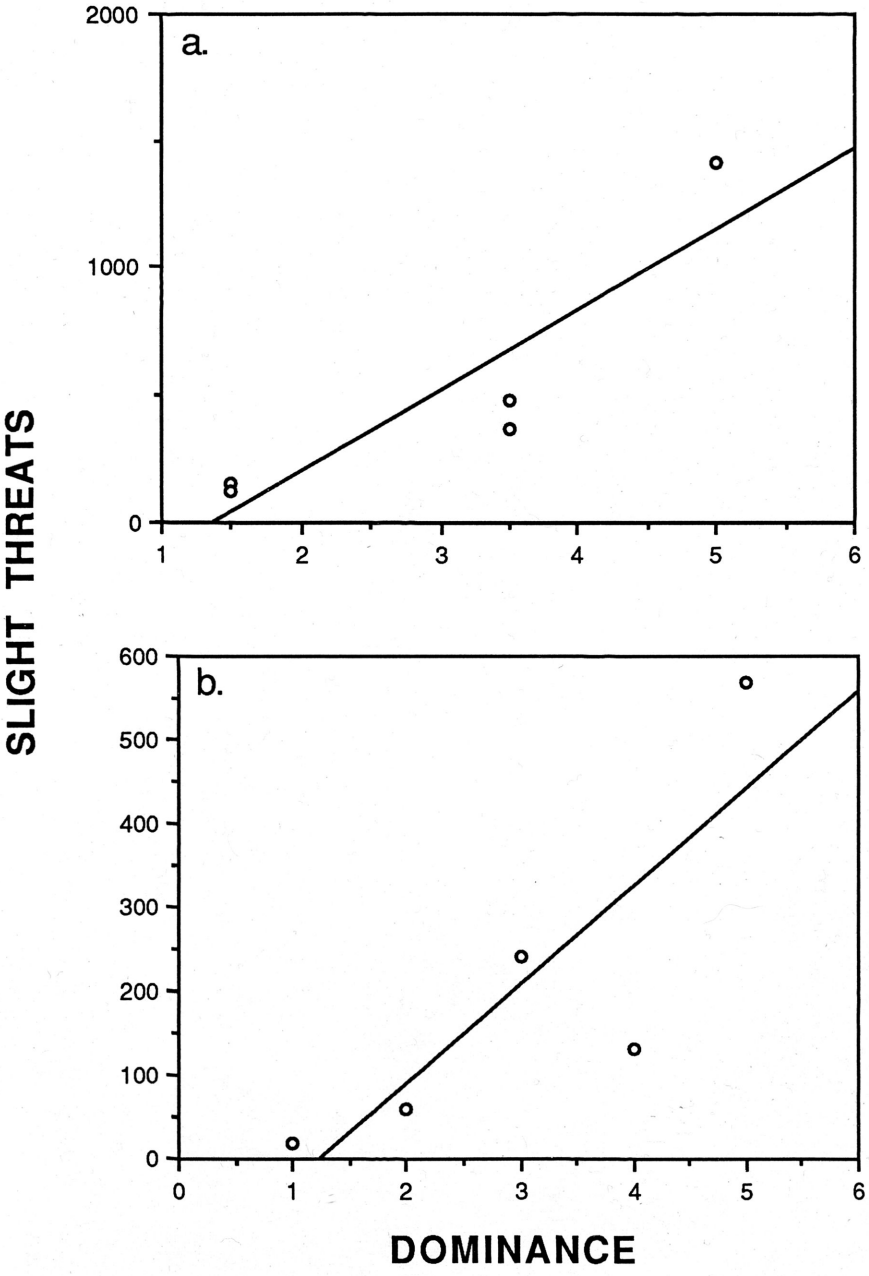
a.
2000
1000
0
1
2
3
4
5
6
b.
600
500
400
300
200
100
0
0
1
2
3
4
5
6
SLIGHT THREATS
DOMINANCE

Figure 5.

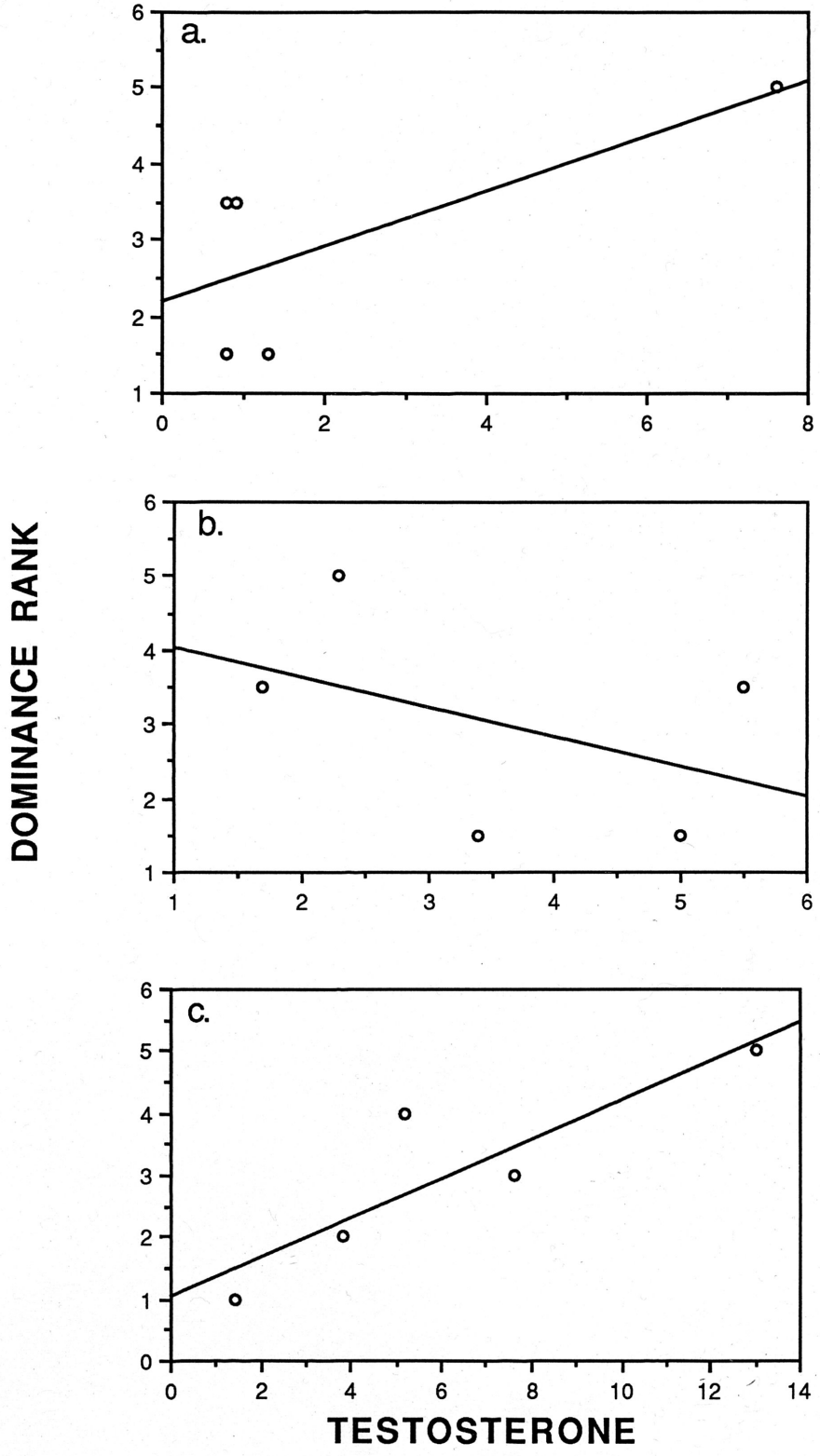

Figure 6.

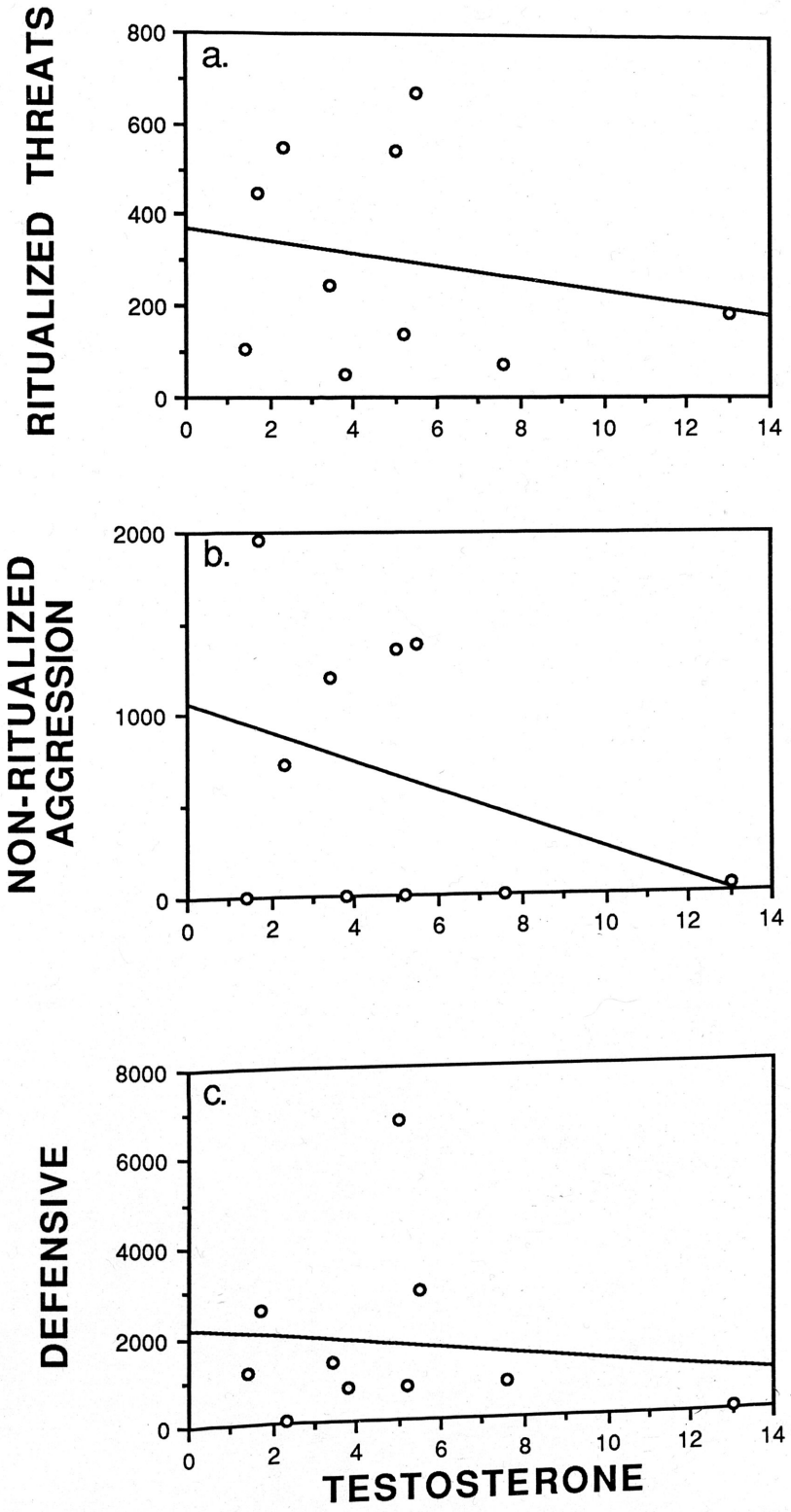
RITUALIZED THREATS
a.
800
600
400
200
0
0
2
4
6
8
10
12
14
NON-RITUALIZED AGGRESSION
b.
2000
1000
0
DEFENSIVE
c.
8000
6000
4000
2000
0
TESTOSTERONE

Figure 7.

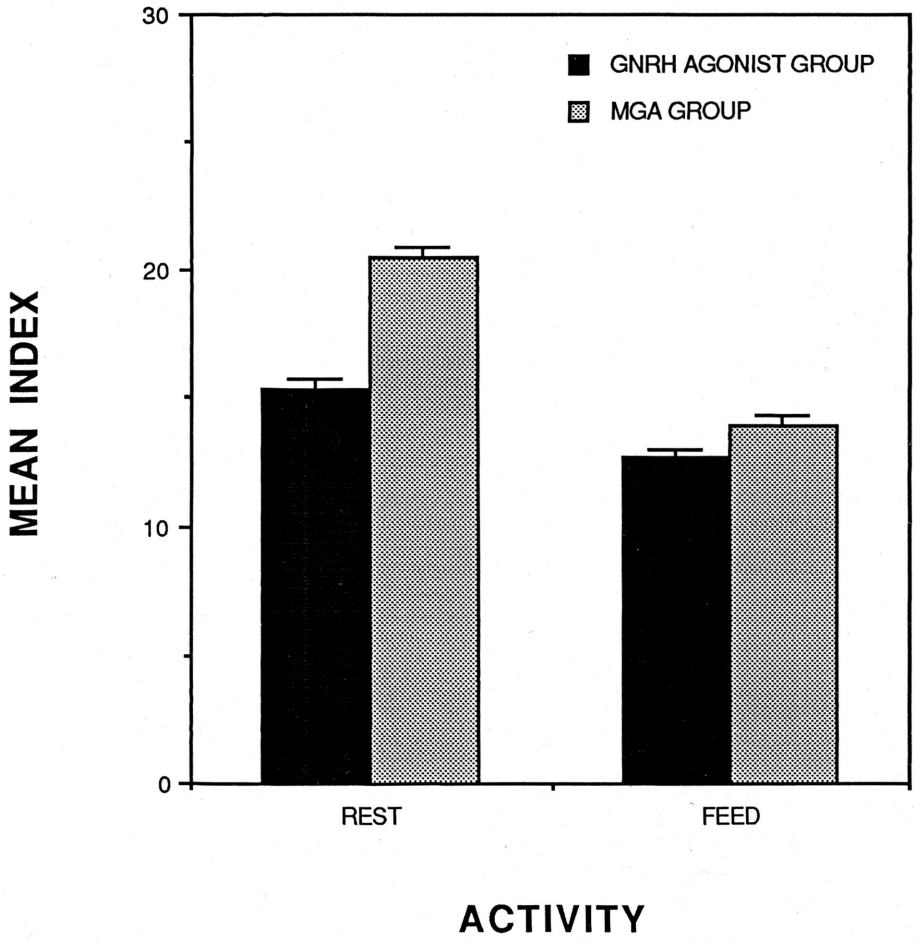
30
20
10
0
MEAN INDEX
GNRH AGONIST GROUP
MGA GROUP
REST
FEED
ACTIVITY

Figure 8.

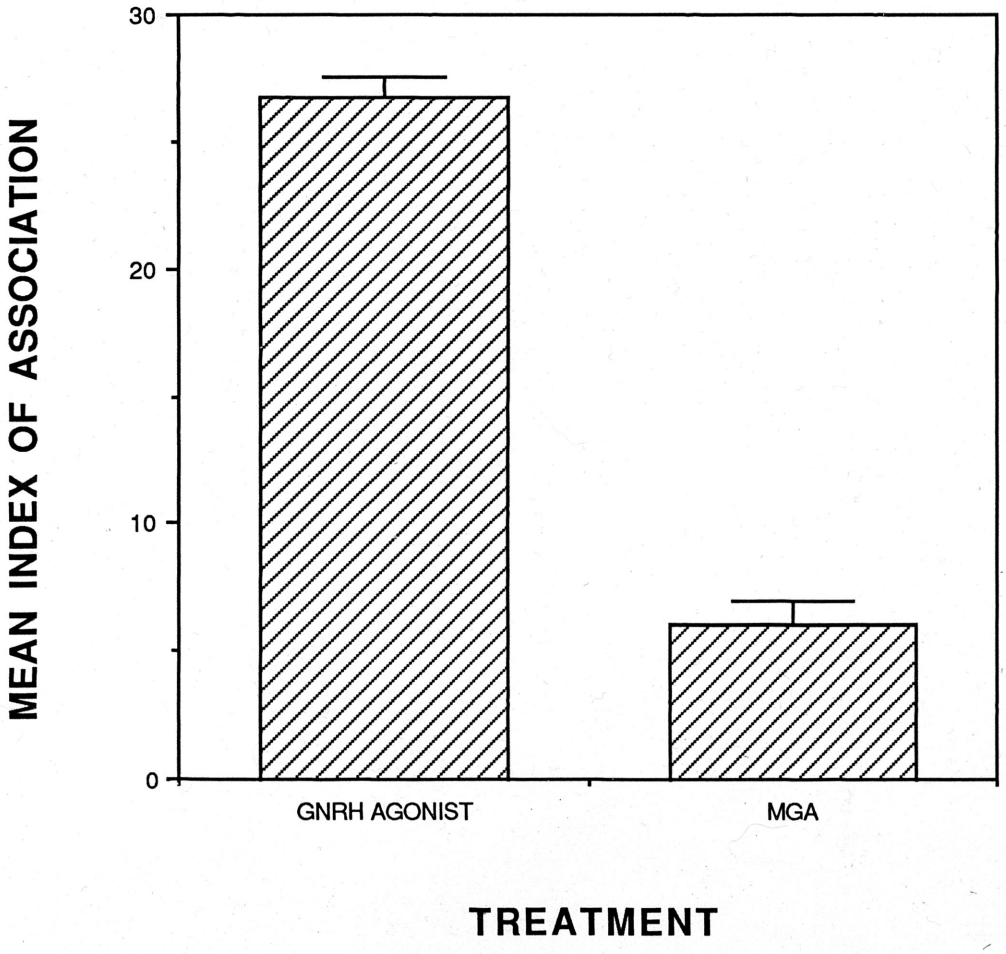
MEAN INDEX OF ASSOCIATION
30
20
10
0
GNRH AGONIST
MGA
TREATMENT

Figure 9.

LIST OF FIGURE LEGENDS

Figure 1. Individual behavioral variation in groups implanted with (a) GnRH agonist and (b) MGA. The behavioral categories were slight threats (ST), ritualized threats (RT), non-ritualized aggression (NRA), defensive (DEF), sexual (SEX), affiliative (AFF), and scent-related (SC).

Figure 2. At 1-yr post-implantation, the mean acts per individual differed significantly between groups within each behavioral category. The behavioral categories were slight threats (ST), ritualized threats (RT), non-ritualized aggression (NRA), defensive (DEF), sexual (SEX), affiliative (AFF), and scent-related (SC).

Figure 3. Comparison of mean plasma testosterone concentration by treatment group and time period (baseline, 1-mo post-implantation, and 1-yr post-implantation).

Figure 4. Individual variation and changes in plasma testosterone concentration in groups implanted with (a) GnRH agonist and (b) MGA by time period relative to implantation.

Figure 5. The correlation between slight threats and dominance rank was significant for the groups implanted with (a) GnRH agonist and (b) MGA.

Figure 6. The correlation between dominance rank and plasma testosterone was not significant for individuals implanted with GnRH agonist and sampled at (a) 1-mo post-implantation and (b) 1-yr post-implantation, although it was significant for individuals (c) implanted with MGA at 1-yr post-treatment.

Figure 7. Plasma testosterone was not significantly correlated with frequency of (a) ritualized threats, (b) non-ritualized aggressive acts, or (c) defensive acts across all individuals.

Figure 8. Mean indices of resting and feeding were significantly higher in the group implanted with MGA than the group implanted with GnRH agonist.

Figure 9. The mean index of association was significantly greater in the group implanted with GnRH agonist than MGA.