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The role of gonadal hormones in the occurrence of objectionable behaviours in dogs and cats [1]

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Abstract

The most common way of controlling or altering the behaviour of companion animals is through gonadectomy. Information about the behavioural effects of gonadectomy comes from extrapolation of findings from laboratory studies and from surveys of pet owners whose pets were castrated or spayed. The role of the placebo effect in the latter source of information is unknown. With these limitations in mind, both laboratory studies and pet owner surveys have provided information indicating that: (1) it is the sexually dimorphic behavioural patterns that are reduced or eliminated in males by castration; (2) not all males undergo a change in behaviour following castration; (3) experience and age at time of castration does not predict which males will be altered by castration; and (4) there are apparent species-specific differences between dogs and cats with regard to percentage of males showing a behavioural change related to castration. © 1997 Elsevier Science B.V.

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1. Introduction

In the course of human history with domestic animals, one of the oldest means of altering behaviour was by castration of male animals. The first animals castrated were livestock and, for thousands of years, castration of male cattle, sheep, goats and swine has been a routine husbandry practice. The fact that castration was so readily adopted by animal owners in early human societies is a testimony to the perceived, if not actual,

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effectiveness of the procedure in altering behaviour. Clearly, these ancient animal caretakers believed that castration reduced the chance of serious fighting among adult male conspecifics as well as the tendency for male animals to be aggressive towards their human caretakers (of course, a few non-castrated animals were kept for breeding). The castration of companion animals and the practice of ovariectomy has been more recent. The time in history when it became routine for male cats to be castrated is unclear, and male dogs were never routinely castrated.

Given the current widespread practice in Europe and North America of routinely castrating male cats before adulthood to prevent objectionable behaviour and the growing practice of castration of male dogs in an attempt to alter objectionable behaviour in adults, it is important to examine what is known about the effects of castration in altering male behaviour. Issues that have received some attention are: (1) which behaviours are affected; (2) the probability that a specific behaviour in an individual will be affected by castration; (3) the role of experience in the retention of a behavioural pattern after castration; (4) species differences in response to castration; and (5) a comparison of animals castrated before adulthood (i.e. before or during puberty) with those castrated as adults. Ovariectomy or ovariohysterectomy (spaying) usually results in complete and immediate elimination of female sexual behaviour, but there are questions about changes in non-sexual behaviour associated with the operation.

Clinically relevant information about alteration of gonadal hormones comes from both experimental studies of laboratory dogs and cats and surveys of pet owners whose pets were castrated or spayed. Information from surveys of pet owners necessarily involves relying upon the owner's observations. This brings up the issue of the so-called placebo effect if the owner expects gonadectomy to alter the behaviour in some way. In clinical trials in human behavioural pharmacology, it is common to use placebo treatment in double-blind studies to differentiate drug effects from placebo effects. The placebo effect may be quite pronounced resulting sometimes in as many as 30 percent of patients responding to placebo (Benkert and Maier, 1990; Rudorfer, 1993). The degree to which a placebo effect may be involved in the reports of owners of animals about the effects of castration remains to be seen. One could argue that this effect may be less important than that in human behavioural pharmacology because the animal has no expectations of a behavioural change. On the other hand, the placebo effect could be greater because the owner does not see all of the animal's behaviour and may be biased towards expecting a favorable response and/or institutes some behavioural modification procedures without investigator's knowledge (Hart and Cliff, 1996). With regard to castration, it is not feasible to have a placebo group, except perhaps with the ethically questionable procedure of using prosthetic testicles and a sham operation. Once several double-blind placebo-controlled studies are conducted with psychoactive drugs with animals, there will be some indication of the potential for a placebo effect and this could possibly be factored into the results of studies where client reports are used to create the data base. Until that time, the only alternative is to report the results from carefully conducted clinical surveys where an effort is made to acquire unbiased responses from pet owners. A placebo effect, if it does exist, is probably greater with the more subjective evaluations such as changes in aggressive behaviour than with less subjective judgements such as changes in urine deposits in the house.

In the text below, we lay some groundwork for discussion of the effects of gonadectomy on clinically relevant behaviour by covering the concept of sexually dimorphic behavioural patterns and the effects of castration on sexual behaviour as studied in the laboratory. The discussion then turns to the effects of castration on clinically relevant behaviours of adult male cats and dogs, followed by a comparison with males castrated before or at the time of puberty. Finally, there will be some mention of the effects of gonadectomy on aggressive behaviour of female dogs.

2. Concept of sexual dimorphism

A well-established concept in mammalian sociosexual development is that males experience a surge in testosterone secretion late in prenatal life, early in neonatal life, or across both periods. This surge apparently acts on the brain to bring about gender-specific cytoarchitectural changes in the hypothalamus and other areas of the brain that are related to the later display of male sex-typical behaviour (Arnold and Gorski, 1984). Actually, the mediation of the effects of testosterone in male brains is through local aromatization of testosterone to estrogen which brings about early organization of both the sexually dimorphic structures in the brain and behaviour (Hutchison and Beyer, 1994). Hypothalamic areas of the female brain are structurally organized in a feminine direction due to the lack of testosterone (and estrogen). Developmentally, the female phenotype is shaped first and through the action of androgens (aromatized to estrogen), the male phenotype is reshaped from the existing female pattern.

The above concept, developed from work on laboratory rodents and primates, presumably applies to all, or almost all, mammalian species, including dogs and cats. However, the hormonal profiles of dogs and cats during the prenatal period have not been characterized. Measurements of serum testosterone from newborn dogs from birth through 7 weeks postpartum, revealed only slightly higher levels in males than females. The levels in males were too low to represent a neonatal testosterone surge (Hart and Ladewig, 1979). Thus, assuming that a perinatal surge in testosterone occurs in dogs (and cats) as it does in other mammals studied, it would probably be prenatal.

Once the period of perinatal brain development has passed, the tendency towards masculinity in males and femininity in females seems to be permanently built into the brain. It is important to point out that both males and females appear to have the basic neural circuitry for the behavioural patterns typical of both sexes (Hart and Leedy, 1985). The difference in brain organization relates to the probability or frequency with which the masculine or feminine system is activated.

Prior to puberty, and presumably before biologically significant amounts of gonadal hormones are produced, males differ from females behaviourally. This has been documented with regard to play in rodents (Thor and Holloway, 1983; Meaney et al., 1985), primates (Owens, 1975) and ungulates (Crowell-Davis et al., 1987; Gomendio, 1988). Male and female dogs and cats may also differ in play (Deag et al., 1988), but differences have not been profiled to the same degree as rodents or primates. One prominent difference between juvenile male and female dogs is the urination posture; male dogs use a stand-lean urination posture and female dogs a squat posture.

As mentioned previously, sexually dimorphic differences between males and females are of degree or frequency, not absolute. Among sexually dimorphic traits there is also an apparent difference in the degree to which males and females differ. For example, leg lift urination is obviously a highly dimorphic trait in which males almost always differ from females. Territorial guarding, if sexually dimorphic, would appear to differ less frequently between males and females. A systematic survey of canine authorities regarding differences between male and female dogs was conducted as part of a project on behavioural profiles of dog breeds (Hart and Hart, 1985a). This survey revealed a continuum with regard to degrees of sexual dimorphism among 13 behavioural traits. Those that were considered to be most characteristic of males or females by authorities interviewed are shown in Fig. 1. Urine marking in the house and mounting other dogs or people were not included in the original survey but they are already acknowledged as highly dimorphic; these two traits are added to the data of Fig. 1.

As will be discussed below, it is the most sexually dimorphic, male sex-typical behaviour that one would expect to be altered by castration of males. Thus, in reference to Fig. 1, urine marking, mounting, aggression to other dogs and aggressive dominance towards people should be altered more readily than activity level or watchdog barking.

Some females display male sex-typical behaviour more than other females. In exploring the possible role of perinatal hormones in this difference among females, investigators have found that intrauterine position can alter the degree to which females of a number of rodent species display male-like sexual behaviour. There are two mechanisms for such intrauterine effects. One is that when females develop in-utero between two males, they are partially masculinized by diffusion of androgens through the amniotic membranes (Clemens et al., 1978; vom Saal and Bronson, 1978). This

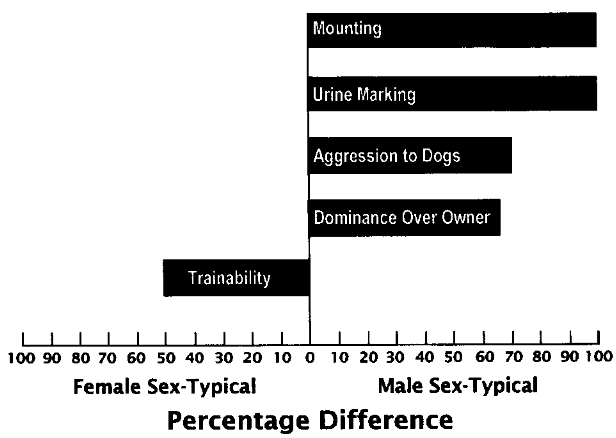

Fig. 1. Degree of sexual dimorphism of behavioural characteristics of dogs as represented by the projected consensus of canine behaviour authorities as to whether a behavioural characteristic was more prominent in male or female dogs. Data taken from Hart and Hart (1985a); Beach (1974); Beach et al., 1982 and Beach and Kuehn (1970). A rating of 100 in either the male sex-typical or female sex-typical direction implies virtually unanimous consensus; a rating of 0 implies that authorities either rated neither sex stronger on that trait or as many rated males stronger as females (see Hart and Hart, 1985a for calculating details). Only traits scoring at least 50 in either the male or female direction by this procedure are listed.

mechanism has been supported by studies on mice and gerbils (Clark et al., 1990; vom Saal, 1981). The other mechanism is that because uterine blood flows from the cervix rostrally, androgens from caudally-located male fetuses may androgenize rostrally-located females through the fetal blood supply (Meisel and Ward, 1981). Support for this mechanism exists for rats, hamsters and ferrets (Houtsmuller and Slob, 1990; Richmond and Sachs, 1984; Vomachka and Lisk, 1986; Krohmer and Baum, 1989).

These studies raise the interesting possibility that the occurrence of objectionable masculine behaviour seen in a small proportion of female cats or dogs could be due to intrauterine position. This possibility has not been tested experimentally in cats or dogs but was explored to a limited degree in a clinical survey involving interviews of cat owners who were familiar with the litters from which their cats were adopted (Hart and Cooper, 1984). In this survey of those owners who knew the littermate composition of their cats, two of the five female cats who urine sprayed frequently, and four of the 14 females that fought frequently, came from all female litters. Since all-female litters could not supply any androgen to adjacent fetuses or up-stream fetuses for masculinization, these data are not consistent with the fetal masculinization effect. Furthermore, of 22 female cats that did not spray or fight, eight came from litters in which there were three or more male littermates (average litter size of six), a condition where masculinization was at least possible. Until more information is available, these results suggest that the tendency for some cats to engage in male sex-typical urine spraying or fighting is not due to intrauterine masculinization.

3. Behavioural effects of castration on sexual behaviour

One of the behavioural patterns most readily affected by castration is sexual behaviour, including mounting, copulatory intromission, and the display of the ejaculatory pattern. These behavioural patterns are readily measured in the laboratory and can be easily evoked in experimental animals. Thus, there is considerable experimental literature on the effects of castration on sexual behaviour in a variety of mammalian species including rats, cats, dogs, rhesus monkeys, and goats. In all of these studies, changes in the behaviour, such as increased latency in response (mounting) to the female, are apparent soon after castration (Hart, 1974). The behaviour that is first lost is that of the ejaculatory pattern followed eventually in some animals by loss of mounting and even interest in females. A comparison of a variety of animals reveals considerable species differences in the rate at which the ejaculatory pattern is eliminated (Fig. 2). According to the studies that were cited in preparing Fig. 2, within 5 weeks following castration, 50% of male cats will no longer showed the copulatory pattern, whereas in male dogs, 80% still showed the pattern, at least occasionally, 15 weeks after castration. The change in sexual behaviour of male rats was about the same as male cats, whereas, goats resembled dogs; rhesus monkeys were intermediate. An evolutionary explanation of these differences in response to castration has been offered (Hart, 1974).

As is apparent from these data, there is considerable individual variation within species in the persistence of sexual behaviour following castration. Thus, in male cats, 20% of animals were still responding to females with the copulatory pattern 15 weeks

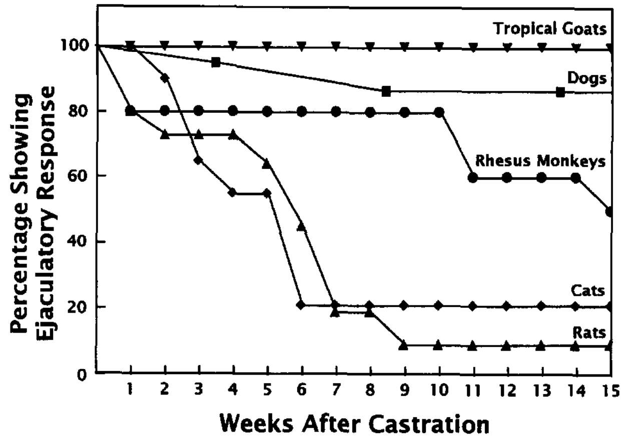

Fig. 2. Species comparisons of differences in persistence of ejaculatory response as a function of duration of time since castration (data from Hart, 1974; Hart and Jones, 1975).

after the operation while 80% no longer responded. In male dogs, 80% were still responding with the copulatory pattern 15 weeks after castration, and 60% one year later (Hart, 1968).

Finding individual differences in response to castration raises the issue of the role of copulatory experience in the loss of copulatory behaviour. This issue has been directly addressed in dogs and laboratory rodents. In a study on dogs designed to explore this issue, animals in the inexperienced group were allowed no copulations prior to castration but were habituated to females by being allowed to mount them. Animals of the experienced group were allowed 30 copulations prior to castration. In tests starting the week after castration and continuing for one year, there was no difference in any parameter of sexual behaviour between the two groups (Hart, 1968). Similar results have been reported with rodents (Hart, 1974). From these laboratory studies and data represented in Fig. 2, three important concepts are established that can probably be extrapolated to clinically relevant behaviour of companion dogs and cats: (1) there are pronounced species differences in behavioural changes after castration; (2) there are pronounced individual differences within a species after castration; and (3) experience in performing the behaviour in question appears to have no predictive ability as to whether or not the animal will change its behaviour.

4. Behavioural effects of castration on objectionable behaviour of male cats

The objectionable behavioural patterns shown by adult male cats that are generally recognized as sexually dimorphic are fighting with neighborhood males, urine spraying and roaming. A retrospective clinical survey (interview of owners) was conducted for 42 gonadally-intact adult male cats presented for one or more of these behavioural patterns (Hart and Barrett, 1973). Castration was effective in eliminating the problem behaviour in 80–90% of the animals (Fig. 3). According to the clients surveyed, in about one-half

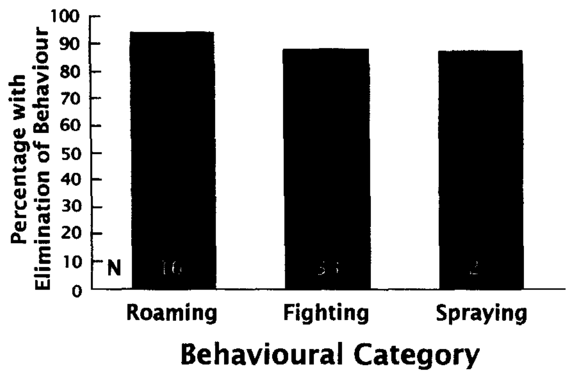

Fig. 3. Percentages of adult male cats in which objectionable roaming, fighting with neighborhood males, and urine spraying in the house were eliminated (problem resolved according to owner's report) following castration. The N is shown at base of bars (from Hart and Barrett, 1973).

of the cases involving aggression towards other males, the cats changed rapidly (within a week or two after castration) with the other half showing a more gradual change. The same was true of roaming behaviour. For cats engaging in urine spraying, most of the animals seemed to undergo a rapid change in the behaviour. Although the clients said the problem behaviour was resolved or eliminated, it is entirely possible, if not likely, that some occurrence of the behavior in question went unnoticed. When cats were presented with more than one of the problem behaviors, an elimination of one behavior did not predict a change in the other problems. The only other behavioural change reported was that 25% of cat owners mentioned their cats became more docile. There was no indication, judging by the age of the animals at the time of castration, that the animals which were older, and presumably more experienced in performing the problem behaviour, were affected any less than the younger, presumably less experienced, males. For example, the median age at time of castration of the cats which showed no decline in spraying was 12 months compared with 18 months for cats that showed either a rapid or gradual elimination of the behaviour.

5. Behavioural effects of castration on objectionable behaviour in male dogs

As mentioned above, the most dimorphic behaviour patterns in dogs are urine marking, mounting, aggressive dominance towards owners and aggression towards other male dogs. A retrospective clinical survey, similar to the one conducted for adult male cats, was conducted on 42 gonadally intact male dogs presented for: urine marking in the house; mounting other people or dogs; intermale fighting and/or roaming (Hopkins et al., 1976). According to the owners, urine marking, mounting and fighting were markedly reduced or eliminated in 50–60% of the animals (Fig. 4). Interestingly, roaming was reduced in 90% of dogs. Data were also available on eight dogs with territorial aggression and four with fear-related aggression but there was no change in any of these dogs. Aggressive dominance directed towards the owners was not included

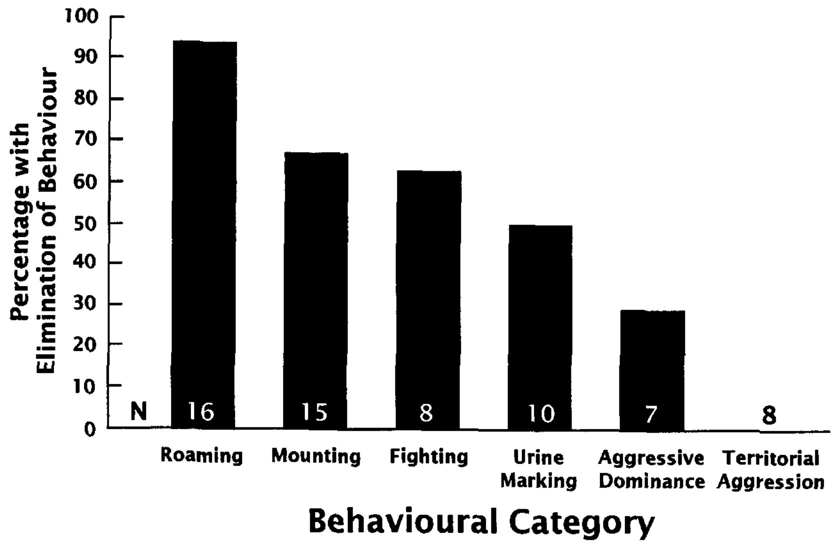

Fig. 4. Percentages of adult male dogs in which objectionable roaming, mounting of people or other dogs, fighting with non-household male dogs, urine marking in the house, aggressive dominance towards the owner and territorial aggression towards strange people were eliminated (problem resolved according to owner report) following castration. The N is shown at the base of the bars (data from Hopkins et al., 1976 and unpublished preliminary results for aggressive dominance).

in the original survey but a recent preliminary study has shown that of seven male dogs presented for this problem, castration resulted in resolution of the behaviour in 2 individuals. These recent data are included in Fig. 4. As with cats, there was no indication that dogs castrated later in life were more likely to persist in the behaviour following castration than those castrated earlier. Even with aggressive dominance involving the owner, experience seemed to play no role as a determinant in response to castration. Of the two dogs that responded to castration, the problem aggression had existed for 5–6 years; in the five dogs that did not appear to respond, the problem aggression had existed for a median of 3 years (range 2–5).

The results of the clinical survey are in line with what would have been extrapolated from laboratory studies on the effects of castration on sexual behaviour. With the exception of roaming, castration was effective in a smaller proportion of dogs than cats, and experience appeared to play no predictive role in which animals changed after castration. The rather uniform effect of castration on roaming in dogs is puzzling. Perhaps, roaming was affected in such a high proportion of dogs because it is a sexually motivated behaviour, and a decrement in sexual motivation which consistently follows castration, may result in major reduction in roaming (even though copulatory performance may still occur).

There are two possibilities for differences in the response of various males to the effects of castration, neither of which has been tested. One is simply genetic differences among individuals related to the sensitivity of neural tissue to the withdrawal of androgenic support (Hart, 1974). Some indication of this possibility might be revealed by a study of genetic relatedness and persistence of problem behaviour after castration. A second possibility for such differences may reflect the fact that in fetal life some males experience greater exposure to testosterone from other male fetuses located more caudally in the uterus, an effect that has been shown to enhance male sexual behaviour in male rats (Houtsmuller et al., 1994).

The persistence of undesirable male behaviour following castration is apparently not due to any residual amounts of testosterone. It has been documented in a number of laboratory species (e.g. Resko and Phoenix, 1972) and cats (Hart, 1979) that testosterone is metabolized within hours after removal of the testicles. The persistence is not due to compensatory adrenal androgen secretion. Sexual behaviour, for example, persists even after adrenalectomy (Hart, 1974).

6. Behavioural effects of castration before adulthood

It is customary to castrate male cats before they reach full sexual maturity, that is, sometime between 6 and 10 months of age, to prevent fighting, roaming and urine spraying. This practice brings up the question of differences in the effects of castration performed at this earlier age versus after puberty. This question was addressed in a retrospective clinical survey of 134 male cats castrated between 6 and 10 months of age (Hart and Cooper, 1984). Spraying and fighting on an occasional basis occurred in 29 and 44%, respectively, of the cats as adults. Ten percent of the male cats became frequent urine sprayers later as adults revealing that the proportion of male cats that take up frequent spraying as an adult is about the same as the proportion of male cats that persist in urine spraying once they have started the behaviour as adults and are then castrated (Fig. 3).

The mean age of castration for those that sprayed and/or fought occasionally was 8.5 months and for those that engaged in neither behaviour 8.2 months. This small and statistically insignificant difference is consistent with the concept of no relationship within the early castrated animals of age of castration and occurrence of problem behaviour. The same study found that 5% of ovariohysterectomized female cats became frequent urine sprayers as adults, demonstrating that females do engage in male sex-typical behaviour, albeit at a lower probability than castrated males. The only study of prepubertal castration in dogs is one of sexual behaviour in males which found that males castrated prepubertally had the same frequency and tendency to mount females as those castrated as adults (LeBoeuf, 1970). The question of whether cats or dogs castrated well before puberty, for example as early as 2 months of age, will differ from those castrated at 6–10 months of age is yet to be fully tested. The preponderance of evidence revealing no effect of experience and no relationship within the 6–10 month age range between time of castration and later behavioural effects, suggests that no further effect on problem behaviour will be found with very early castration. Early castration of male cats does have permanent effects on morphology, especially in reducing the size of cheeks and jowls. Thus, cats castrated before puberty are visibly different than tom cats and Turner (1995) has suggested this may play a role in evoking male sex-typical behaviour in males castrated as adults. As a general rule, cats should be castrated before adulthood for best management of problem behaviour.

7. Treating male sex-typical behaviour in gonadectomized males and females

A word should be said about clinical approaches to dealing with objectionable male behavioural patterns of animals previously castrated. With feline urine spraying, eliminating olfactory stimuli that might evoke the behaviour by cleaning up the marked areas with an enzymatic cleaner and blocking visual stimuli from cats outside the home may prove useful. Discouraging marking of previous target areas through the use of remote punishment, or feeding and watering the cats at target areas, has also been recommended (Hart and Hart, 1985b). Although some behavioural therapists have reported a high degree of success with such behavioural measures (Turner, 1995), others find the behaviour difficult to control (at least in the homes of most clients) and pharmacological approaches to this problem have been favored by veterinarians. This treatment has evolved over the last two decades starting with the use of progestins (Hart, 1980) and moving more recently to drugs that enhance gamma-aminobutyric acid (e.g. diazepam) or serotonin (e.g. buspirone). Both diazepam and buspirone suppressed spraying in a higher percentage of animals than progestins (Cooper and Hart, 1992; Marder, 1991; Hart et al., 1993). In prospective studies, both diazepam and buspirone resulted in 55% of cats showing an elimination or marked reduction in the behaviour, but buspirone did not have the undesirable side effects associated with diazepam of transient sleepiness, ataxia, appetite stimulation, and dependency with long-term use (Hart et al., 1993). Although with buspirone and diazepam the proportion of male and female cats responding was not significantly different, with buspirone more cats from multiple-cat households responded than did those from single-cat households. With progestin therapy a higher proportion of male cats than female cats responded.

The treatment currently recommended with buspirone is 5–7.5 mg per cat given twice daily for 1–2 weeks as a trial to see if the drug will eliminate or markedly reduce the behaviour. If the behaviour is altered, it is recommended that the cat be treated 8 additional weeks before gradually tapering off over the ensuing week or two. About half the cats can be expected to resume spraying after the drug is discontinued (Hart et al., 1993). Those that resume spraying can be placed on long-term treatment for another 6–12 months with the expectation that after the drug is then tapered off some animals will continue to be suppressed while others will resume spraying and may be continued on indefinite treatment. A major difference is seen between buspirone and diazepam in the tendency for cats to resume spraying once drug treatment is discontinued. In one study with diazepam, 90% of animals that were on 8 week treatment began spraying when the drug was tapered off (Cooper and Hart, 1992), compared with 50% with buspirone (Hart et al., 1993). The resumption of spraying with diazepam may be because diazepam produces behavioural and physiological dependency, and taking animals off the drug, even gradually, undoubtedly produces some rebound emotional effect that may predispose the animal to resume spraying.

Both buspirone and diazepam may suppress spraying in cats that were previously treated with progestin but did not respond. Based upon the fact that progestins utilize different receptors and perhaps even a different neurological pathway than antianxiety drugs, a model of urine spraying was proposed consisting of two neurological systems, one relating to male sexuality and one to anxiety. Progestin administration, which presumably suppresses neural elements that are normally activated by testosterone, may work with those cases where urine spraying is more of an expression of male sexuality. Antianxiety drugs may suppress urine spraying related to anxiety-provoking situations such as introduction of new cats or moving to a new house. With regard to treatment of objectionable male sex-typical behaviours other than spraying, there is some indication that progestin administration may alter intermale aggressive behaviour in castrated male dogs (Hart, 1981).

8. Behavioural effects of ovariectomy

There is little clinical or experimental research relevant to the behavioural effects of ovariectomy. As mentioned previously, during prenatal and neonatal development of females, there is no behaviourally significant amount of estrogen or progesterone secreted and the organization of feminine responses occurs as a function of development without testosterone.

Among dog handlers and trainers, one may hear of references to calming (or mellowing) effects of allowing female dogs to experience one or more estrus periods or even parturition and care of a litter of puppies. The degree to which removal of female gonadal hormones might result in permanent changes in behaviour was explored in a

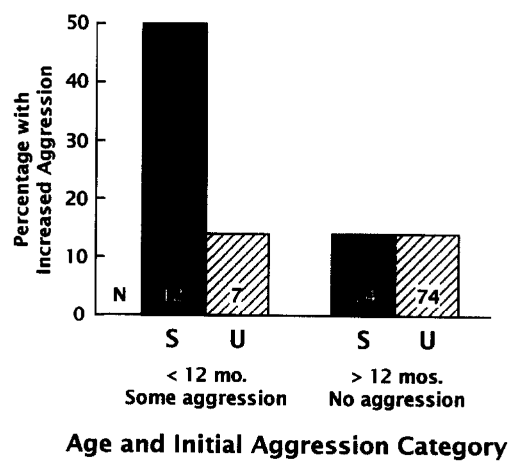

Fig. 5. Percentages of female dogs showing increased aggression after ovariohysterectomy (spay) as a function of age at time of the operation (less or greater than 12 months) and whether they showed signs of some aggression prior to the operation. Only dogs that were spayed (S) at less than 12 months of age and showing some aggression exhibited an increase in aggression compared with unspayed controls (U) who also showed some aggression (from O'Farrell and Peachey, 1990).

study of 150 spayed and 150 unspayed female dogs by O'Farrell and Peachey (1990). Owners were interviewed via questionnaire at the time the female dog was spayed and 6 months later. Owners of a control group of age-matched unspayed dogs were also interviewed twice at an interval of 6 months. In both groups there were changes over time in some dogs but the only two behaviour patterns in which spayed females showed a change that differed significantly from the control group was in aggressive dominance towards owners and in indiscriminate eating. The increase in aggression was only apparent in females spayed at less than 12 months of age and that already showed some aggression (Fig. 5). Females that were older than 12 months at time of being spayed presented no risk of increase in aggression.

One possible explanation of these results is that spaying removes the source of progestin production if done shortly after estrus. Female dogs that cycle twice a year are in a progestational state for about 2 months following each estrus period. Given that progesterone has some calming influences, removal of progesterone in some animals may increase aggressive or irritable tendencies especially if the dogs are spayed when progesterone levels are high producing a sudden change in this hormone. Once a female has gone through more estrous cycles, and perhaps been disciplined for aggressive behaviour, spaying may have less of an impact.

9. Conclusions

This review reveals the complexity of the role of gonadal hormones in companion animal behaviour and in the alteration of these hormones for changing objectionable behaviour. Two overriding concepts should be very apparent: (1) gonadal hormones have pronounced effects on behaviour and must be taken into account in any program designed to treat or manage problem behaviour; and (2) the alteration of gonadal hormones, particularly castration of males, does not affect all dogs or all cats similarly. One cannot extrapolate from experience with one or two dogs or cats in predicting the effects of castration or ovariectomy. There is a need for additional research in understanding the basis of such pronounced individual differences in the effects of hormones on behaviour.

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