

SPECIES-CHARACTERISTIC RESPONSES TO CATNIP BY UNDOMESTICATED FELIDS¹

J.O. HILL,² E.J. PAVLIK,^{1,3} G.L. SMITH III,³
G.M. BURGHARDT,^{2,3} and P.B. COULSON^{1,2}

² *Departments of Psychology and Zoology
University of Tennessee
Knoxville, Tennessee 37916*

³ *Knoxville Zoological Park
Knoxville, Tennessee 37915*

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Abstract—Thirty-three large felids belonging to six different species were exposed to catnip and catnip extract. The species-characteristic response to catnip and the sensitivity of the response to various concentrations of catnip were examined. Putative relationships between catnip sensitivity, species range, age, estrous cycle, and behavioral complexity are discussed. The behavioral response to catnip shown by the domestic cat is seen in several different large felids. Lions and jaguars were extremely sensitive to catnip compared to tigers, cougars, and bobcats, who gave little or no response. Both males and females of the same species tested alike. Reproductive-age adults were more sensitive than either aged or immature animals. It was quantitatively demonstrated that catnip responsiveness is not limited to the domestic cat, that it is not limited to the female, and that it varies dramatically between species and age of felids.

Key Words—catnip, olfaction, behavior, threshold response, felines, sensitivity.

INTRODUCTION

The first record of the domestic cat's peculiar response to catnip (*Nepeta cataria*) is lost in time. It is well known, however, that catnip stimulates an "innate releasing mechanism" (IRM) in domestic cats that elicits a predictably

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“playful” behavior pattern apparently independent of experience and learning (Ewer, 1973 and Leyhausen, 1975). *Cis, trans*-nepetalactone (Waller *et al.*, 1969; McElvain *et al.*, 1942; McElvain and Eisenbraun, 1955) is reported to produce this behavioral response and to be metabolized by cats. Other reports assign activity to *trans, cis* nepetalactone (Bates and Siegel, 1963). It has been verified by Todd (1963) that the response to catnip is mediated by olfactory and not gustatory stimuli. Catnip sensitivity has been related to a dominant autosomal gene and to the estrous cycle by Todd (1962). These reports indicated that catnip elicits certain behavioral responses in some of the domesticated as well as undomesticated cats, but these responses have not been shown to be species specific, typical of, or limited to the female sex. In addition, it has been suggested (Todd, 1963) that catnip mimics a pheromone found in cat urine; however, evidence supporting this theory is scant.

An unpublished attempt to relate the catnip response to different felids (Todd, 1963) utilized catnip leaves and recorded stereotyped behavioral responses. There are shortcomings in this approach. Qualitative descriptions of behavior are often inadequate criteria by which to assess sensitivity to catnip.

The present experiments were designed to investigate the qualitative and quantitative aspects of catnip sensitivity by testing undomesticated felids with respect to control and experimental (catnip-containing) objects. In addition, catnip extracts sprayed onto targets objects were employed in order to carefully control the amount of stimulating material and study felid sensitivity to reduced amounts of material.

The types of behavior which occur as positive responses to catnip were first identified and described. Two experiments were then performed to determine species differences in the response to catnip. Finally a procedure for demonstrating sensitivity thresholds was developed.

EXPERIMENT 1: THE RESPONSE OF FELIDS TO CATNIP-FILLED BOXES

Animals were presented with stimuli attached to the outside of their cage in a way that allowed them to approach the experimental and control stimuli but eliminated touching or tasting the sample.

Methods and Materials

The behavioral response and sensitivity to catnip of the undomesticated felids at the Knoxville Zoological Park was examined in thirty-three cats of various ages maintained in cages (Table 1). All experimental animals had been born and raised in captivity. The cats were tested during the months of March

TABLE 1. LIST OF FELIDAE^a INCLUDED IN THE SURVEILLANCE FOR CATNIP SENSITIVITY^b

Scientific name	Common name	Male number (Age in months)	Female number (Age in months)
<i>Lynx rufus</i>	Bobcat	1 (Adult)	1 (Adult)
<i>Panthera leo</i>	Young lion	2 (10)	3 (10)
<i>Panthera leo</i>	Lion	2 (36, 50)	
<i>Panthera leo</i>	Lioness		5 (24-36)
<i>Panthera leo</i>	Lion cub	1 (6)	
<i>Panthera onca</i>	Jaguar	1 (39)	2 (39, 41)
<i>Panthera pardus</i>	Spotted leopard	1 (32)	1 (27)
<i>Panthera pardus</i>	Spotted leopard cubs	1 (8)	1 (6)
<i>Panthera pardus</i>	Spotted leopard	1 (120-180)	1 (120-180)
<i>Panthera pardus</i>	Black spotted leopard	1 (21)	1 (26)
<i>Panthera tigris</i>	Tiger	1 (62)	1 (55)
<i>Panthera tigris</i>	Tiger		2 (26, 27)
<i>Panthera tigris</i>	Tiger cub		1 (6)
<i>Puma concolor</i>	Cougar	1 (24)	1 (11)
<i>Puma concolor</i>	Cougar	1 (25)	1 (25)

^a The term "felid" will be used routinely in this study in order to include all living *Felidae* (Ewer, 1973) including the three subfamilies *Pantherinae* (the so-called greater cats: lion, tiger, leopard, jaguar, etc.), *Acynonychinae* (the cheetas), and the *Felinae*s (the so-called lesser cats: lynx, cougar, bobcats, domestic cats, etc.).

^b Ages are expressed where known and approximated by ranges in other cases. Animals are listed on the basis of enclosure.

through June early in the morning and after closing hours to avoid visitor distractions. Attempts to involve two adult cheetas in the survey were unproductive, since they never approached catnip or control objects.

Two Plexiglass panels were constructed approximately 28 cm square by 1 cm thick. Four holes (5 cm diameter) were drilled through each piece of plexiglass. The holes of the experimental panel were filled with dried catnip leaves (Hartz Mountain) and the control panel was left empty. Cardboard was taped to each side to contain the catnip. Both the control and experimental panels were then wrapped in black electrical tape, and small slits were cut in the tape and cardboard so that the catnip scent could easily be released. Metal hasps were attached with wire to each end of the panel so it could be attached to the cage.

A behavioral check-list was devised for characterizing the responses of the cats to the experimental versus the control panels. The list was initially based on observations made on the domestic cat (Todd, 1962; Palen and Goddard, 1966; Hatch, 1972) and was altered as necessary during the first exposure of

B. Behavioral response to rocks sprayed with catnip

1. Biting in mouth 2. Carrying in paws 3. Licking between paws 4. Holding in paws 5. Carrying in paws 6. Pouncing on face on rock 7. Rubbing face on rock 8. Kicking and pursuing 9. Play (one cat jumping over the other, who rolls over) 10. Lying/ sitting beside 11. Rolling over 12. Total specific responses

Female lions (G.L.)	+	+	+	+	+	+	+	+	+	+	+	10
Female lions (J)	+	+	B	+	+	+	B	+	+	+	+	9
Female jaguars	+	+	B	+	+	+	+	+	+	+	+	7
Lion (J)	+	+	B	+	+	+	+	+	+	+	+	5
Jaguar (S)	+	+	B	+	+	+	+	+	+	+	+	4
Young lions	+	+	B	+	+	+	B	+	+	+	+	4
Spotted leopards	+	+	+	+	+	+	+	+	+	+	+	4
Male tiger	+	+	+	+	+	+	+	+	+	+	+	4
Spotted leopard cubs			B	+	+	+	B	+	+			3
Black spotted leopards			B	+	+	+	B					2
Female tiger			B	+	+	+	B					2
Spotted leopards (old)			B	+	+	+	+					1
Female cougar			+	+	+	+	B	+				1
Tigers (field)			B	+	+	+	+					1
Lion cub (male)			+	+	+	+	+					1
Tiger cub (female)			+	+	+	+	+					1
Cougars (paired)			+	+	+	+	+					1
Male cougar												
Bobcats (paired)												

* The length of the test period was 10 min. Behavior observed to the experimental box only (+). Behavior observed to both experimental and control (B). Both experimental and control were presented simultaneously.

each animal to catnip. This first test consisted of a 15-min exposure to the experimental box alone. Any new type of behavior was recorded and added to the check-list. Several days later each animal was presented with both control and experimental panels simultaneously. The panels were attached to the outside of the cages approximately 45 cm above ground level and about 70 cm apart. The test period was reduced to 10 min since most animals either lost interest in the first 10 min or remained interested for the full 15 min.

Types of behavior toward control and experimental panels were recorded on check-lists for individual animals. The total time with each panel was recorded. When more than one animal was present in a cage, the response of the first animal to be attracted to either panel was recorded.

Results

Table 2 lists the behaviors that were recorded during the test periods for each species. Certain types of behavior can be seen to occur in response to both panels in almost every animal. Thus, these types of behavior were not specifically elicited by catnip. Other types of behavior occur almost exclusively in response to the experimental panel but are seen on occasion in response to the control panel (Table 2).

It is noticeable that some animals perform several different types of behavior in response to the experimental stimulus, while other animals respond with only one or two types (Table 2: A6–A12 and B4–B7 and B9–B11). Animals can be ranked according to total number of different behavior patterns performed in response to the experimental treatments (Table 2: A13 and B12).

A relative index was calculated weighing the difference between experimental and control conditions by normalizing scores in terms of the time spent elsewhere (Table 3, E). This relative index rates the animals with respect to the length of their behavioral response to catnip. The relative index is defined as equal to $[\% (\text{time at catnip minus times at control})/\% \text{ elsewhere}] \times 100$. The percentage of time spent elsewhere was limited to a minimum of 0.1%; thus, the range for the relative index becomes 0–999. This relative index can distinguish between an increased general arousal and an attraction to catnip, since it normalizes in terms of time spent at an activity other than time spent at the catnip-containing panels. It is clear that certain felids (i.e., lions and jaguars) are attracted more easily than others to catnip-containing panels (Table 3, A and B), as shown by the time spent during exposure to catnip versus control boxes.

The two adult male lions (housed with different prides) gave variable responses. The oldest lion (G.L.) scored low (Table 3) on several occasions. This older lion was housed in a very large enclosure, which may have encour-

TABLE 3. DURATION OF RESPONSE TO CATNIP AND CONTROL PANEL^a

	A	B	C	Δ	E
	Catnip time (sec)	Control time (sec)	Time elsewhere (sec)	Delta	Relative index
Positive responders					
Female lions (J, 2)	540	60	0	80.0	800
Female jaguars (2)	538	62	0	79.4	794
Female lions (G.L., 3)	355	21	124	55.7	269
Male jaguar (S)	310	174	116	22.7	117.6
Partial responders					
Spotted leopards (paired)	251	11	338	40.0	71.1
Young lions (2 male, 3 female)	182	25	393	21.6	39.8
Spotted leopard cubs (paired)	128	40	432	20.6	28.6
Lion cub (male)	143	73	384	11.6	18.1
Nonresponders					
Spotted leopards (old pair)	28	12	560	2.7	2.9
Tigers (field, 2)	95	86	419	1.5	2.2
Female tiger	4	0	596	0.7	0.7
Male tiger	2	0	598	0.3	0.3
Bobcats (paired)	2	2	596	0	—
Cougars (paired)	0	0	600	0	-0.2
Male cougar	37	37	524	-0.3	-0.3
Black spotted leopards (paired)	161	169	270	-1.4	-1.4
Female tiger cub	42	81	477	-6.5	-6.5
Male lion (G.L.)	140	210	250	-11.7	-28.1
Female cougar	155	325	120	-28.4	-142.0

^a Each test lasted 600 sec. $\Delta = (\text{time at catnip} - \text{time control})\%$. The percentage of time spent elsewhere is limited to a minimum of 0.1%; thus, the range of the relative index is 0 to 999. $\text{Relative index} = (\Delta / \%$ elsewhere) $\times 100$. Animals are listed on the basis of the decreasing relative index scores in column E.

aged his indifference to events on the exterior. In checking zoo records, however, it was also found that he had a recent history of illness and medication which might also explain his lack of responsiveness during these tests. The young male lion (J) scored high on the first tests (Table 2 and 4) but was frequently distracted by his pride during other tests.

EXPERIMENT 2: THE FELID RESPONSE TO CATNIP EXTRACT

Since catnip leaves mounted on the outside of enclosures may generate

behaviors different from the unrestrained situation, experiments were included in which the felids were permitted access to experimental and control objects. It was necessary to use a catnip extract applied to indestructible objects since all attempts to build a sturdy catnip receptacle proved futile.

Tests were performed in which cats were permitted access to experimental and control objects placed inside their enclosure and their behavior was recorded.

Methods and Materials

“Catnip Extract” (Hartz Mountain), an aerosol spray made from filtered catnip leaves, was used in order to allow sprayed objects to be placed inside the cage with the animals. Spraying was conducted in the same manner each time by “brushing” the aerosol on the object (moving can at 15–20 in. distance) until an opaque film covered the surface.

River rocks were selected, sprayed, and placed in the cages. The rocks were generally prolate (8 cm × 10 cm) with a thickness of about 2 or 3 cm.

As in Experiment 1, each animal received an initial 15-min exposure to only the catnip-sprayed rock. Types of behavior were recorded on separate check-lists. Several days later each animal was given a 10-min simultaneous test period with a catnip rock and control rock placed inside the cage approximately 3 ft apart. Data similar to that of Experiment 1 were recorded. A detailed determination of half-life of the volatile attractant was not made, however, for lions the catnip rock was still identifiable 7 days later.

Results

Table 2 (B) shows the types of behavior recorded and how each animal responded when it had access to a catnip-sprayed rock.

A variety of behaviors were elicited in addition to behavior that involves rolling. Subsequent actions by the animal were directed toward maintaining contact with the catnip-sprayed rock. Such action paralleled the results of Experiment 1 with the animal positioning itself and its activity near the catnip-containing receptacles. While sniffing and licking behavior were demonstrated towards both fixed catnip panels and catnip-sprayed rocks, biting was only occasionally demonstrated toward the rocks. Biting actions may represent attempts to gain access to foreign objects on the exterior. Aggressive behavior was rarely observed and when displayed was of extremely short duration. A lack of biting/chewing and aggression was reported by Palen and Goddard (1966) for the domestic cat. The total time spent with each rock as well as the relative index, are recorded in Table 4.

The animals were ranked on the basis of their attraction to the catnip

TABLE 4. DURATION OF RESPONSE TO ROCKS SPRAYED WITH CATNIP EXTRACT^a

	A	B	C	Δ	E
	Catnip time (sec)	Control time (sec)	Time elsewhere (sec)	Delta	Relative index
Positive responders					
Female jaguars (2)	550	50	0	83.1	831
Male jaguar (S)	420	2	168	69.7	248.9
Female lions (G.L., 3)	290	0	310	48.3	93.4
Partial responders					
Male lion (J)	245	4	351	40.1	68.6
Young lions (2 male, 3 female)	197	10	393	31.1	47.5
Black spotted leopards (paired)	170	20	350	25.0	42.9
Spotted leopards (paired)	130	30	440	21.2	28.9
Lion cub (male)	116	49	435	11.1	15.3
Male tiger	65	0	535	10.8	12.1
Nonresponders					
Spotted leopard cubs (paired)	56	3	541	8.8	9.8
Female cougar	72	36	492	6.0	7.3
Tiger cub (female)	52	43	505	1.5	1.8
Spotted leopards (old paired)	15	10	575	0.8	0.8
Female tiger	3	0	597	0.5	0.5
Cougars (paired)	0	0	600	0	0
Male cougar	0	0	600	0	0
Bobcats (paired)	0	0	600	0	0
Tigers (field, 2)	5	16	519	-1.9	-2.2

^a Each test period lasted 500 sec. Terminology and rank ordering are as described in Table 3.

rock versus control as expressed in the relative index (column E). When the animals are divided into arbitrary categories as responders ($E = 80$ or above), partial responders ($E = 10$ or above), and nonresponder, it is apparent that most of the individual animals fall into the same category as in Experiment 1, Table 3.

EXPERIMENT 3: SENSITIVITY TO CATNIP

Two sets of behavior for the animals and two relative indices have been developed to rank felid response to catnip. The frequency and intensity of behavioral responses to catnip, which have already been described, may not

necessarily reflect the olfactory threshold or sensitivity to catnip. The final experiment was designed to distinguish the level of olfactory "sensitivity."

Methods and Materials

Six identical metal rods were used (25.5 mm diameter). These objects were selected because they were indestructible, their surface area could be easily calculated, and thus the area sprayed with catnip extract could easily be varied. Masking tape was used to cover the parts of the rod not being sprayed.

Four rods were sprayed with catnip extract to give different total areas of experimental stimuli. The remaining two rods were used as controls. One-half of the first rod was sprayed with catnip extract to give an exposed surface area of approximately 20 cm². Other rods had sprayed surface areas of approximately 10, 4, and 0.25 cm² each. All animals were exposed to the three larger doses. The fourth dose (rod area = 0.25 cm²) was only used with the adult African lions.

The sensitivity experiment was performed in the evenings after the zoo closed. The animals were distracted by the calls of a keeper while the rods were placed in the cage at the opposite end. One experimental rod with a small identifying mark and two control rods were used for each test. The rods were placed side by side on the floor of the cage approximately 3 ft apart. Four data records were made: (1) length of time to find the catnip rod, (2) length of time first attraction to the catnip rod lasted, (3) total time at the catnip rod, (4) total time at either control rod. The test period was again 10 min. All the animals were first tested with dose 1. Several days later they were tested by dose 3 and then by dose 2. All animals were tested with one dose before any were tested with the next dose.

Results

There is a general decrease in response to decreasing doses of catnip with the exception of the lionesses in the G.L. pride (Figure 1). Lions consistently exhibited sensitivity to catnip greater than any other species tested even at a dosage that was 16 times lower (0.25 cm² area) than the next lower dose (4.0 cm² area) responded to by any other species (Figure 1).

With regard to time spent at the catnip, the relative index was selected as the most valid means of ranking the animals, since it distinguishes animals that demonstrate attraction to catnip from animals with a high general activity level, which may give spuriously high attraction to catnip. The lists in Tables 3 and 4 were ranked according to the relative index. For these rankings, the animals were divided into three arbitrary groups. A relative index of 80 or greater was taken as a clear positive response, while less than 10 was considered

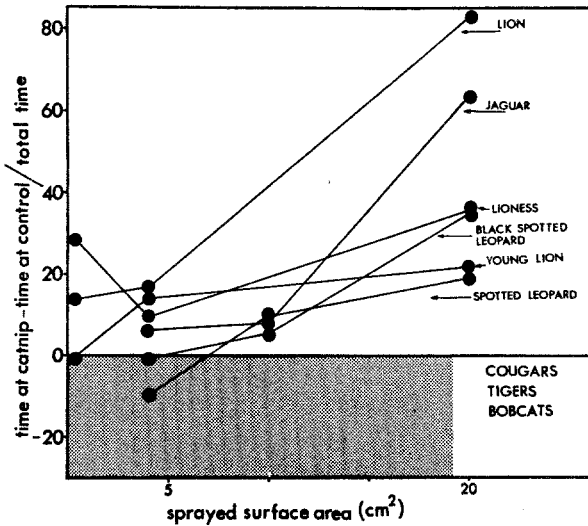


FIG. 1. Sensitivity to decreasing doses of catnip. The length of each test period was 600 sec. Values are representative of single animals. The shaded area corresponds to negative responses. Each individual animal of a species in the shaded area tested negatively on all three doses (5, 10, and 20 cm²).

equivalent to no response. It can be seen that most animals are in the same group in both tables. Sensitivity and performance can be ranked visually in Figure 1. Thus, five different methods of ranking have scored the species response to catnip with the result that only a small variation in hierarchy occurs.

The lions (except for a cub, Little Josh) and the jaguars were the most sensitive (Figure 1). The adult spotted leopards, the lion cubs, the spotted leopard cubs, and the black spotted leopards comprised a “borderline” response group. The tigers, cougars, bobcats, and old spotted leopards were all at or below zero.

In Figure 1 it appears that the adult lions (male and female, but not young lions) are sensitive to a dose of catnip (0.25 cm² surface area) 16 times lower than that responded to by any other species. Since lions were used as a reference for dose effectiveness, every catnip bar dose was first checked against the lions. Other animals demonstrated a sensitivity to a sprayed surface area of 4 cm², which was lower than the sensitivity of lions and jaguars.

The dose sensitivity of the young lions, along with the fact that the lion cub consistently responded less positively than the aged lions, could perhaps be correlated with reproductive maturation. Young lions experienced a decreased response at a higher catnip concentration than adult lions.

Age might also account for differences in sensitivity in the spotted leopard (Table 4). Leopard cubs responded less positively than the adults, who were more positive than very old adult leopards. Studies on young adults castrated at an early age might be able to distinguish whether or not catnip sensitivity is related to sexual maturity at the neural or hormonal level. Castration after sexual maturity did not block the response to catnip in domesticated cats (Palen and Goddard, 1966).

GENERAL DISCUSSION

Responsiveness to catnip in undomesticated felids involves sets of behavior in such a way that the intensity of the behavioral response is only a general indicator of sensitivity. Adult lions and jaguars routinely responded positively to catnip, with the adult lions (male and female) showing the greatest sensitivity to low doses. Tigers, cougars, and bobcats routinely gave very low to zero response to catnip. Therefore the olfactory attractant in catnip is differentially effective and species specific in large fields.

Palen and Goddard (1966) observed that in the domestic cat "rolling over" behavior was associated with the response to catnip as well as with behavior during hormonally induced estrus. In the present experiments the male jaguar that was found sensitive to catnip never demonstrated a copulatory "after reaction" such as the routine "rolling over" that is seen with the lions (Pavlik, unpublished observations). Positive responses to catnip were observed in naive, reproductively immature animals (young lions, lionesses, and black-spotted leopard) as well as in pregnant lionesses and in male lions. "Rolling over" behavior occurred in many undomesticated felids that were either positive responders or nonresponders to catnip. It was even observed in response to the control boxes (Table 2, black leopard). A correlation was not found between "rolling over" behavior to catnip and "rolling over" behavior by large felids in estrus.

The results indicate that no one specific behavior of felids can be considered the response to catnip. Most prominent in the set of behavioral events elicited by catnip were sniffing, licking, sustained contact, and often play (which is defined here as the interaction between individuals demonstrating such behaviors as biting, pawing, jumping and rolling over). The four types of catnip responses (I. sniffing, II. licking and chewing with head shaking, III. chin and cheek rubbing, IV. head-over rolls and body rubbing) described by Todd (1963) were also evident in these studies; however, the "head-over roll" was not often observed when the animal had access to the sprayed objects. The head-tuck behavior by jaguars reported by Todd (1963) was not observed in these studies. In addition, the catnip response in large felids could be seen

to continue almost indefinitely (once as long as 60 min.) without an observable period of decay. In general, an animal could lose interest in the object but would return within 1 or 2 min. In contrast, the domestic cat exhibits a response which rarely exceeds 15 min in duration, and it is accompanied by a 1-hr refractory period (Todd, 1963).

With the exception of a single male lion, G.L. (a nonresponder, Table 3) no sexual differences within a species were found. No differences were noted in animals caged alone compared with those caged in pairs or groups; however, this comparison is difficult to make since there were some species in which no members were caged individually. Todd (1963) reported that a tiger cub actively avoided the catnip and actually ran away from it. No such response was found in our observations. While the tiger cub in this study did not respond positively to catnip, he did not avoid it either.

The fact that some species would not encounter *Nepeta cataria* (Youngken, 1950; Slife, 1960) in their natural habitat might explain the species differences in response. Lions and jaguars would not ordinarily encounter catnip (which is endemic to North America and Europe, but not to the southern hemispheres) and yet they responded positively to it. Bobcats and cougars showed no response even though they would encounter catnip in their natural habitat. Within the limits of our survey, species sympatric with *Nepeta cataria* do not respond, while allopatric species do respond or partially respond (leopards) to catnip. These observations may not have any evolutionary significance; alternatively, sensory adaptation may have displaced this response. Such adaptation may occur in the domestic cat, where the response rarely exceeds 15 min in duration and is accompanied by a refractory period (Todd, 1963). This idea is in contrast to the hypothesis that *no* relationship exists between the distribution of *Nepeta* and catnip sensitivity (Todd, 1963).

Todd (1962) attributed the predisposition to respond to catnip to a dominant autosomal gene occurring in 65% of domestic cats. He classified subjects as responders or nonresponders according to whether they displayed "rolling-over" behavior. Our observations indicate that the response to catnip is comprised of sets of behavior. In species other than the domestic cat, "rolling-over" behavior may be an insufficient criteria for determining responsiveness to catnip since it ignores other frequently elicited behaviors as well as aspects of the response that are described in this paper by dose sensitivity. Since diverse complex responses describe sensitivity to catnip, it is likely that any complete response is polygenic and relies on genetic specificity determining type and number of sensory receptors, sensory afferent communication, central integration, and efferent response pathways.

Recently, Cambell et al. (1969) have shown that catnip can change the pattern of single-unit discharge in the hypothalamic ventromedial nucleus.

The catnip response appears to be linked to peripheral nicotinic mediation with central muscarinic and serotonergic facilitation complete with a prominent voluntary component. Inhibition seems to involve central muscarinic and nicotinic mechanisms (Hatch, 1972). Thus, behavioral responsiveness to catnip requires that each participating process be completely functional. Age-dependent catnip sensitivity may originate from one or several undeveloped participating processes. Todd's behavioral genotype may in reality be a phenomenon comprising multiple integrated genes. Any one gene mutation might ultimately interrupt the total response by blocking a single essential component and thus suggest the operation of a single dominant gene.

The present study confirms Todd's observations (Todd, 1963) that responsiveness to catnip is not sexually dimorphic, and that felids can be categorized as "responders," "partial responders," and "nonresponders." In addition we have observed distinct species variation occurring with respect to the catnip behavioral response and olfactory sensitivity to it.

Finally, the catnip response is always *observationally* clear-cut. Our efforts to quantify this response in order to understand the relationships between behavioral intensity and olfactory threshold do not entirely reflect a numerical distinctiveness, and because of the limited numbers of each species they cannot have a statistical interpretation. These efforts should be regarded as descriptions of the extent of responses by the individual and as precedents by which animals can be grouped and tested in subsequent experiments involving replication. Lastly, this paper illustrates how zoo animals can be manipulated in the study of behavior.

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