EPIMELETIC (CARE-GIVING) VOMITING IN DOGS: A STUDY OF THE DETERMINATING FACTORS

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Abstract. Epimeletic vomiting fails to occur in a bitch when she is kept in an isolated box apart from her puppies and their nest-pen. However, vomiting is elicited immediately after the bitch is allowed to contact her puppies in the nest-pen. If the contact occurs in a new, unfamiliar place, vomiting is disrupted but reappears again after several contacts in the same place. When after feeding, a bitch is put into her own nest-pen where alien puppies are substituted for her own, their care-soliciting (et-epimeletic) behavior induces in her aggression or avoidance rather than vomiting. Vomiting is not disrupted when some of the exterior features of puppies have been changed. Epimeletic vomiting may occur some days prior to the proestrus of the bitch and, sometimes, even during proestrus and estrus periods. Under special environmental conditions epimeletic vomiting may occur even in male dogs. The appriopriate care-soliciting behavior of properly reared, not satiated puppies, and their own nest-pen are the main factors which elicit epimeletic vomiting in dogs.

INTRODUCTION

As found in my previous study (10), mongrel female dogs that rear their puppies in strictly defined conditions show regular epimeletic vomiting of food. The term "epimeletic" introduced by Scott and Marston (17) is used here to describe intraspecific care-giving behavior. Correspondingly, "et-epimeletic" means care-soliciting behavior. The biological role of epimeletic vomiting in *Canidae* is to supply solid food to the puppies. This phenomenon is known to occur regularly in wild *Canidae* (3, 5, 6, 14, 15, 18, 19, 23). Since it is difficult to study this phenomenon in wild *Canidae* due to their fearfulness and distrust, its

nature and the course it runs are hitherto not known in detail. However, studies on the process of epimeletic vomiting are now rendered possible by the fact that conditions have been recognized in which they appear regularly in domestic dogs (9, 10).

The previous study and the observations now presented were carried out with mongrel dogs, because, as a heterozygotic individuals, they are more close with respect to many biological characters to an average of the *Canis familiaris* species than pure-bred dogs.

Epimeletic vomiting of bitches was regularly observed, on the average, for a period up to the 119th day of the puppies life. Three consecutive phases were distinguished in the development of appropriate behavior of both mothers and their pups. Phase I (preliminary vomiting) — usually consisted of several sporadic vomiting acts of the bitch; this occurred just after delivery, when puppies fed on their mother's milk and showed as yet no interest in solid food. Phase II (transitional phase of vomiting) — began between the 24th and 40th days of the pupies' life; it included few vomiting only for a few consecutive days. Puppies showed increased interest in the food disgorged by the mother and began to manifest et-epimeletic behavior toward her; the bitch and the puppies consumed the disgorged food simultaneously. Phase III (complete epimeletic vomiting), continued for several months. It was characterized by a strong correlation between behavior of the mother and that of the puppies. Et-epimeletic behavior of puppies at that time included a variety of movements and gestures as well as a specific type of vocalization.

All the observed vomiting acts (nearly 1500) always occurred in the nest-pen and close to the bitches' own puppies, though they were fed at a distance from the nest-pen.

Irretrievable removal of all puppies from the mother was immediately followed by the disappearance of epimeletic vomiting in 4 out of the 5 observed bitches.

In the present experiments an attempt was made to study in more detail some of the behavioral mechanisms and ethological relations which are involved in the process of epimeletic disgorging of food in dogs.

MATERIAL AND METHOD

Six related experiments were performed of which five consisted in studying mongrel female dogs and their puppies and the sixth experiment included a study of male dogs with bitches and pups. The bitches in advanced pregnancy were purchased at random without taking into account their morphological exterior and size. The only criteria used were age and health condition. Bitches older than five years of age were

excluded. The age was determined by evaluating the dentition. When admitted, the bitches were treated with piperazine adipinate and vaccinated against rabies and distemper — even though vaccination is not indicated in pregnancy. Puppies were cleared of helminths between the 14–18th day and again between 40–44th day and vaccinated against distemper. Not more than five pups were left with each mother. The care of mothers and pups as well as their feeding were described in an earlier report (10). All the procedures were designed to allow the manifestation of epimeletic vomiting in mothers and et-epimeletic behavior of puppies.

Experiments 1 to 5 were performed with bitches and pups whose behavior was typical at Phase III; in Experiment 6 at Phase II or III.

Additional details of the material and method used in the study are given under the heading of the separate experiments.

EXPERIMENT I

Delayed contact of sated bitches with their puppies and nest-pen

Three bitches and their litters were used in this experiment. Epimeletic vomiting has been observed in these bitches regularly for a long period of time. Puppies were between 63 and 71 days of age. The number of vomiting acts recorded in the bitches Delta, Gamma and Omega during 10 days preceding the present experiment was 27, 19 and 12, respectively. In these 10 days the time interval between start of feeding and the act of vomiting by the bitches were recorded.

The procedure consisted of feeding the mother at some distance from the nest-pen and her pups and of preventing her from coming back to them at the usual time, i.e., within a 4–5 min after the end of feeding. The bitches were kept away from the nest-pen and pups for a period of 10 to 37 min longer than the time intervals between starting of eating and the moment of vomiting in the preceding 10 days (Table I).

Results

Table I presents the time intervals between the moment when the bitches began eating from a distant feeding box and the moment when they were allowed to contact with their pups. For a comparison, the time intervals between the start of eating and the moment of vomiting observed during the preceding 10 days are also presented. As is evident from this Table, there was a wide variation of time intervals between the start of feeding and vomiting in the preceding 10 days period. The-

TABLE I

The effect of delayed contact of the sated bitch with its puppies on epimeletic vomiting

Bitch	10 days preceding the experiment				Experimental observations			
	Number of recorded vomiting acts	Time from start of feeding to vomiting[a] (min)			Age of puppies (days)	Time from start of feeding to contact with puppies (min)	Behavior in feeding box and on way to puppies	Time interval from contact with puppies to vomiting (min)
		Mean	Minimum	Maximum				
Delta	27	10	7	30	65	40	whine, hurry	1
					65	50	took little food	not occurred
					66	55	whine, hurry	1
					66	40	hurry	1
					67	60	whine	not occurred
					68	60	whine, hurry	1
Gamma	19	20	8	35	71	45	whine, vomiting[b]	5
Omega	12	16	10	28	63	44	hurry	1
					64	50	gas release from stomach	20
					67	43	restlessness, hurry	1 / 2 / double vomiting
					68	65	restlessness	5

a Bitch as a rule contacted the puppies within 4–5 min after end of feeding.

b Bitch Gamma vomited in the feeding box 30 min after feeding. The disgorged food was immediately consumed, but was disgorged after entry to the nest-pen. Food disgorged in the nest-pen with puppies present was not taken by the bitch.

refore, the longest interval was taken as a reference point for calculating the experimentally forced delay of vomiting. For example, the bitch Delta (Table I) was allowed to contact with her pups after 40 min in the first trial; compared with the reference point for this bitch (30 min) a 10 min delay is forced. In the second trial it was 20 min, in the third, fourth, fifth and sixth trials — 25, 10, 30 and 30 min, respectively.

Except for one case (Table I, bitch Gamma), in spite of a marked delay in contacts between the sated mothers and their puppies, vomiting did not occur until the bitches entered their own nest-pens and contacted the puppies.

Bitches kept after feeding apart from their puppies and nest-pens behaved in a characteristic manner. Within several minutes they became restless, stayed near the door or showed locomotor hyperactivity, sometimes scratched the door, whined, looked at the experimenter who used to release them from the feeding-box and allow them to join their pups. Particularly characteristic was the speed with which they would run to the pups when freed after a delay and almost immediate vomiting after they entered the nest-pen (Table I). None of these signs of hurry and restlessness were observed when the bitches were freed shortly after feeding: they would willingly leave the feeding-box, but, as a rule, they walked for several minutes before they returned to the nest-pens and their pups.

Discussion

The results obtained suggest that the time interval between feeding and vomiting is not stereotyped and pre-determined. They also indicate that the phenomenon, which consists of a sequence of behavioral acts, is not only associated with interoceptive stimuli and fixed conditioned reflexes. It is suggested that epimeletic vomiting of the bitch occurs when certain additional conditions are met such as: (i) her own, active puppies must be with the mother, and (ii) the bitch must be in her own nest-pen or in close proximity to it. It was already observed in a previous experiment (10) that epimeletic vomiting is inhibited when the puppies are absent (removed from the mother) and when the bitch is out of her nest-pen. In spite of suitable conditions no vomiting was observed beyond the nest-pen.

Delayed vomiting, which corresponds with the delay in contact with the nest-pen and puppies, suggest that exteroceptive stimuli play an important role in the release of the consummatory act itself. Bitches kept after feeding away from the nest-pen and puppies behave in a way which suggests that their appetitive behavior is controlled by a strong drive reflected in their strong tendency to find themselves in the presen-

ce of adequate exteroceptive stimuli (nest-pen and puppies). It shows, therefore, the characteristic signs of appetitive behavior — as described by Tinbergen (20).

One of the results obtained with the bitch Gamma is worth mentioning in this context (Table I, Note b). First vomiting occurred 30 min after feeding, away from the nest-pen and in the absence of her puppies. This might indicate that, in this bitch, pre-established conditioned reflexes to the time lapse (e.g., visceral reactions) appeared effective enough and stronger than the inhibitory effect produced by the absence of her pups and her stay away from the nest-pen. During the 10 days preceding the present experiment Gamma vomited on the average after 20 min (8–35 min) after start of feeding. However, when reflexive vomiting did occur Gamma immediately consumed the disgorged food and then she vomited again upon re-entering the nest-pen with the puppies present and left it to be eaten by the pups. Immediate consumption of her own disgorged food has not been previously observed in Gamma nor has she ever vomited out of the nest-pen. This case, in which the return of the bitch to the nest-pen and puppies was intentionally delayed strongly suggests the existence of adaptive mechanisms which ensure that the biological aim — food supply to the puppies — is attained, even under unfavorable circumstances.

EXPERIMENT II

Change of place at which the sated bitch contacts the puppies

This experiment was performed with four randomly selected bitches that reared their puppies under circumstances which were favorable to epimeletic vomiting. Their litters were 53 to 72 days of age. Vomiting of the bitches and the corresponding et-epimeletic behavior of their puppies reached Phase III. In the 10 days which preceded the experiment the bitches, after feeding, always met their puppies in their own nest-pens and vomited regularly at least 14 times.

During present experiment the contact between sated bitches and their puppies took place in a box (always the same) which was furnished differently than the nest-pen and at a distance of several meters from it. The experiment consisted of six trials at the rate of one trial per day. The puppies were put into the new box several minutes before the sated bitch entered it. During each trial the animals were observed for 35 min, starting from the bitch's entry into the box. When the observation was concluded, the animals were transferred to their own nest-pen and left there till the next trial on the following day.

Results

The results are presented in Table II. On the first and the second trial vomiting occurred in none of the four bitches observed. On the Trial 3 one bitch vomited, on the Trial 4 — two, on the Trial 5 and 6 — three.

TABLE II
Epimeletic vomiting of bitches after the place of
contact with puppies was changed

Bitch	Age of puppies on Trial I (days)	Presence or absence of vomiting						Et-epimeletic behavior of puppies
		Trials						
		1	2	3	4	5	6	
Alfa	64	—	—	—	+	+	+	normal
Beta	72	—	—	+	+	+	+	normal
Lambda	53	—	—	—	—	+	+	normal
Sigma	58	—	—	—	—	—	—	normal

In the fourth bitch (Sigma) the modified circumstances of contact with her puppies inhibited for all six trials the vomiting beyond the nest-pen, in spite of normal et-epimeletic behavior of all litters. No significant change was seen in the et-epimeletic behavior of the pups.

Discussion

The results of the second experiment suggest the possibility that epimeletic vomiting did not initially occur due to two groups of factors. The first group might include the lack of adequate releasing or facilitating stimuli, the second would consist of stimuli which are inhibitory. The first group is, thus, associated with the lack of stimuli coming from the familiar nest-pen and its close neighborhood. The second might involve stimuli that evoke an orienting reaction of the bitch to the new place and, thus, inhibit the epimeletic vomiting response.

The occurrence of vomiting in three bitches as late as on the fifth trial might indicate that this belated behavior was mainly due to inhibitory effect of the orienting reflex to the new box. It might also be supposed that on later trials, when the orienting reaction of the bitches became weaker or disappeared, the presence and the adequate et-epimeletic behavior of puppies were sufficient to evoke epimeletic vomiting of the bitch away from her nest-pen.

From the first trial away from the nest-pen, the puppies showed normal et-epimeletic behavior when joined by their mothers. This sug-

gests a high stability of care-soliciting behavior or a strong hunger drive as well as prompt habituation to novelty both of which might be expected of young animals.

EXPERIMENT III

Contact of the sated bitches with alien
hungry puppies in their own nest-pen

Three randomly selected bitches were used that reared their puppies in circumstances favorable for epimeletic vomiting. During the 10 days which preceded the present experiment all three bitches vomited regularly at least 13 times. Both mothers and their litters were in Phase III (complete epimeletic vomiting). The puppies were between 71 and 90 days of age. The difference in age between the mothers' litters and alien puppies did not exceed 9 days and the two groups of pups were matched as closely as possible with respect to body size. The nest-pen where pups and bitch made contact was the own nest-pen for the bitch but was unfamiliar for the puppies and, moreover, was a nest marked with the odor of another dog family. To avoid any possible interference with et-epimeletic behavior of the pups, they were allowed for 10 min on 3 consecutive days to get acquainted with an emptied foreign nest-pen in which experimental observations were to take place.

Alien puppies were substituted for the mothers' litters once a day for 3 days. They were waiting in the nest-pen of the bitch while she was fed in a distant box. After feeding, the bitch entered her own nest-pen where she met with the same alien puppies on each trial.

From that moment on, the animals were observed for 20 to 25 min, then the alien pups were taken away and the bitch's litter was put into the nest-pen. The observation was continued for the next 20 min. If the bitch was too aggressive towards alien pups they were separated from her by a wire mesh (Fig. 1).

Results

The results are presented in Table III. The presence of alien puppies in the mothers' own nest-pen interfered with epimeletic vomiting. When these pups were exchanged for their own litter the bitches vomited readily. Frequently, aggression occurred against alien puppies (Fig. 1), especially in response to their insistent et-epimeletic behavior which all of them showed initially towards alien bitches.

Discussion

The absence of vomiting was not due to a lack of et-epimeletic behavior on the part of the alien puppies. If aggressive responses of the bitch
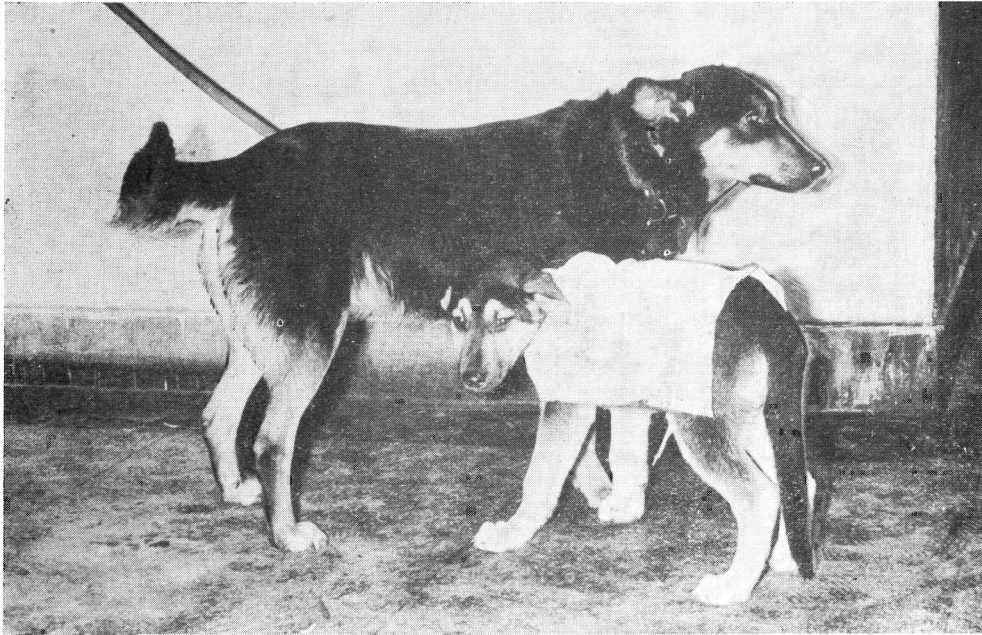
Fig. 2. A bitch with a "masked" puppy.

Fig. 1. The reaction of a bitch to et-epimeletic behavior of a strange puppy.

were not too vigorous, their et-epimeletic behavior resembled that which they showed towards their own mother. The initially full-blown et-epimeletic activity of puppies became weaker or ceased altogether as a result of the bitches' aggression or — later — because of the lack of success of their activity (Table III, Zeta, Trial 3).

TABLE III

The effect of substitution of alien puppies for their own on epimeletic behavior of bitches

Bitch	Age of own puppies on consecutive trials (days)	Behavior of bitch					
		With alien puppies			With her own puppies		
		Trial 1	Trial 2	Trial 3	Trial 1	Trial 2	Trial 3
Delta	77, 78, 79	aggression, no vomiting	aggression, no vomiting	aggression, no vomiting	vomiting	no vomiting	vomiting
Zeta	71, 72, 73	weak aggression, no vomiting	weak aggression, no vomiting	escape reaction, no vomiting	no vomiting	vomiting	vomiting
Gamma	88, 89, 90	aggression, no vomiting	aggression, no vomiting	aggression, no vomiting	no vomiting	vomiting	vomiting

The lack of vomiting in the bitches contacted by alien puppies may be interpreted in at least two ways. Either the presence and et-epimeletic behavior of alien puppies were a source of stimuli inhibiting the vomiting reactions (i.e., stimuli evoking aggression) or alien puppies failed to provide the necessary stimuli pattern which releases vomiting. The both possibilities are of interest since it is known from breeding practice that, as a rule, alien pups, until to 1 or 2 week of age, can be successfully given early post-partum to bitches that easily "adopt" them as their own.

The present experiment indicates that in a later period after the end of lactation or, possibly, with the growth of the pups, the "adoption" process becomes difficult or may be quite impossible. The following aspects should be taken into acount in interpreting of different reactions of mothers to 1-week old puppies as opposed to 10-weeks old ones. In early maternity, presumably under strong care-giving drive, as well as very strong key stimuli emitted by newborn pups, the mother does not distinguish between alien and her own pups. Later, the endogenous care-giving drive might become weaker, and the stimuli provided by older puppies (especially alien ones) may not correspond to the stimuli which, during the post-partum period were critical for evoking the mother care-giving behavior.

EXPERIMENT IV

The effects of the change in the puppies' appearance

Two bitches (Delta and Gamma) and their litters, both in Phase III (complete epimeletic vomiting) were used. During the 10 days preceding this experiment, Delta and Gamma vomited 11 and 13 times, respectively. The day in which the experiment began, one litter was 89 and another 99 days of age. The appearance of pups was changed by dressing them in white overcoats (Fig. 2). For 3 days preceding the experiment the pups were adapted to wearing the overcoats (15 to 20 min, twice a day) and were separated from their mothers during this pretraining. On all subsequent trials the pups waited, as usual in their nest-pens for the mother, and were dressed 15 min before her return from the feeding box.

Results

Beyond a brief period of sniffing the coats, there were no essential changes in the behavior of mothers. The lapse of time between the return to the nest-pen and the act of vomiting was 14 min for Delta and 11 min for Gamma.

It may be concluded, therefore, that even a considerable change, at least from the observer's point of view, in appearance of the puppies failed to modify the normal epimeletic behavior of the mother.

EXPERIMENT V

Estrus cycle and epimeletic vomiting

This experiment was aimed at a clarification of some effects of hormonal factors associated with physiological estrus cycle on the incidence and course of epimeletic vomiting. Another aim was to get some information as to the effect of increasing sexual drive, and consequently decreased care-giving drive, on epimeletic vomiting. It was expected that the hormonal background of endogenous care-giving drives would be different during lactation than during proestrus, estrus, ovulation and early postestrus period.

Material and method

Five bitches were selected that still vomited when their puppies were 110 days old. In healthy female dog in our climate estrus usually occurs every 6 to 6.5 months. Pregnancy lasts 60 to 65 days (usually 61 to 63). Thus, the next estrus is expected 4 to 4.5 months after delivery at the time when her puppies are about 122 to 135 days of age.

In this experiment all epimeletic vomiting instances were recorded which took place within 25 min after the sated mothers' return to their pups and nest-pen. Starting from the 110th day of the puppies' life, the bitches were gynecologically inspected every 2nd day to detect early signs of proestrus and estrus. Proestrus was considered to begin when bloody-serous excretion was found in the vaginal vestibule. Estrus and incipient ovulation was considered to start on the day when the bitch admitted the male to coitus. Male dogs were allowed to contact the bitches every 2nd day, starting from the 5th day of proestrus.

Results

It can easily be calculated from Table IV that Bitches 1 to 4 began proestrus 8, 38, 12, 8 days respectively, after the last vomiting, whereas the Bitch 5 began proestrus 24 days before last vomiting. It is striking that in this bitch vomiting occurred twice during proestrus and six times during estrus or immediately thereafter (Table IV, Note c). Counting

TABLE IV

Estrus cycle and epimeletic vomiting of bitches

	Age of puppies (days)			Time lapse (days) from preceding to observed ovulation by mothers
Bitch	On day of last vomiting recorded	On 1st pro-estrus day in mother	On 1st ovu-lation day in mother	
1	150	158	168	230
2	129	167	172	234
3	144	156	165[a]	--
4	122	130[b]	136	198
5	170[c](!)	146	154	216

a The bitch admitted the male but coitus was no complete.

b By Bitch 4 signs of proestrus was weak.

c By Bitch 5 vomiting occurred two-fold in proestrus on days 149 and 150 of puppies life, and during estrus and postestrus repeated on days 156, 160, 165, 168, 169 and 170 of puppies life. At the same time the behavior of the bitch included aggression against her own puppies.

from the 1st day signs of proestrus, estrus and ovulation started after between 5 (Bitch 2) to 10 (Bitch 1) days. The interval between the previous ovulation and the first ovulation after epimeletic vomiting was 6.6 to 7.6 months (198 to 234 days) (Table IV). The period of regular epimeletic vomiting, which lasted in these bitches until the 4th to 5th months or more of the puppies' life, might be responsible for such prolonged interestrus period.

The time interval between the previous ovulation and ovulation which is coming during epimeletic vomiting period or shortly after it are given in Table IV. The data are only approximate, since the animals were purchased pregnant and the date of previous ovulation was unknown. For calculation the date of delivery was taken into account and it was accepted that pregnancy lasted 62 days on average. The day of previous fertilization was accepted as the date of incipient previous ovulation (as usually occurs in the bitches living in the open air in the country). Assuming that pregnancy lasted 1 day more, or 1 day less, and that fertilization took place usually on the 1st or the 2nd day of ovulation, the error was not greater than 2 to 3 days.

During proestrus and just before it, the mothers came back re-lunctantly to their puppies after having been feed and often had to be led there on a leash. This would suggest a suppression of the appetitive behavior of bitches by other actually predominant drives.

Discussion

Hormonal changes in female dogs are known to progress rapidly during several days preceding proestrus. Due to neurohormonal factors, they are usually manifested in a modified intraspecific behavior of the animals and changes visible in the vaginal region. In proestrus, these changes are especially profound and reach their peak in estrus. In *Canidae* the corresponding behavioral changes in the female are, in general, very clear. Therefore, the present findings may prove that epimeletic vomiting may occur in bitches in different physiological conditions, i.e., at different concentrations of the hormones of the system hypophysis–hypothalamus–adrenal cortex–gonads–uterus.

There is enough evidence that vomiting, although it may occur in various hormonal conditions, occurs only when the mothers are under direct influence of adequate exteroceptive stimuli provided by their puppies and their own pen. As reported by Koller (7) even non-fertilized mice without their own litter, build a nest for pups only if they can touch and carry the alien newborns.

It can be also supposed that acquired appropriate responses involved in the epimeletic vomiting behavior are determinants of the occurrence of epimeletic vomiting during the hormonal unfavorable conditions (on days preceding proestrus, during proestrus, estrus and postestrus). The state of fixed sequences of this behavioral pattern seems to be reached if preceded by a sufficiently long period of regularly epimeletic vo-miting in which both vegetative and somatic reactions are repeatedly reinforced. It is known that specific behavioral reactions in mammals

persist in spite of the absence of an appropriate hormonal background for the drive which underlies this behavior. Horses castrated late in life, which were previously mated, show sexual behavior toward females but not if they have not copulated previously. Urich (21) reported habitual fights between male mice that were castrated after they reached sexual maturity while such fights were not observed if males were castrated before they reached maturity.

The effect of learned responses involved in the epimeletic disgorging of food seems to be essential especially in the final period of the phenomenon under study. In this period the action of stimuli pattern is probably effective enough if there is cooperation of previously acquired and fixed elements of the bitch care-giving behavior. Strongly fixed behavioral sequences may compensate for weaker hormonal background of care-giving toward adolescent puppies in particular. It should be assumed that, in the period when gonadotropic hormones and estrogens increase in concentration, care-giving drive has to decrease under the influence of other drives which predominate in that period (8). The reactivity of bitches to sexual stimuli increases while their reactivity to other stimuli decreases.

Directly before proestrus, as well as during proestrus and estrus, the bitches took usually less food than during diestrus period. After feeding, when they were conducted to the nest-pen and pups, they often refused to go and had to be forced to enter the nest-pen. It is likely, therefore, that in this period the care-giving appetitive behavior of bitches decreases considerably. However, the vomiting act itself may occur in the presence of adequate visceral and environmental stimuli.

Such concepts would agree with the interpretation of background for defined animal behavior (method of dual quantification by Lorenz (13)). They would also be in agreement with the principle of heterogeneous summation of stimuli suggested by Tinbergen (20). The acquired elements, which most probably exert an effect on epimeletic vomiting during hormonally unfavorable periods, suggest the important role of learning in care-giving behavior of higher mammals, including *Canidae*. This, in turn is in accordance with Lehrman's (12) emphasis on the role of acquired elements in the formation of instinctive behaviors.

The observed sporadic vomiting some days before proestrus, during proestrus and estrus, in spite of lower care-giving drive, may be taken as evidence that exteroceptive stimuli are decisive in releasing the vomiting act (the consummatory reflex). The results of Experiments I–III as well as my previous observations (10), also support such an interpretation. However, the related appetitive behavior of bitches (their tendency to contact the puppies at a defined time — Experiment I) seems

to be primarily influenced by interoceptive stimuli (e.g., visceral) or previously acquired and fixed responses.

It should be added that the domestic dog seems to be a suitable model for studies on the effect of hormonal factors on care-giving behavior of *Canidae*. Compared with the wolf (*Canis lupus*), fox (*Vulpes vulpes*), blue fox (*Alopex vulgaris*) or jackal (*Canis aureus*), all of which are monoestrus animals, inter-estrus periods in domestic dogs are usually twice as short. A situation obtains, therefore, in which puppies are young enough for care and can provide an adequate stimulus pattern while their mother enters already the next estrus.

EXPERIMENT VI

Epimeletic vomiting in male dogs

An attempt was made to produce epimeletic vomiting in males and to get preliminary information as to the circumstances which can favor it. At the same time, the production of at least some epimeletic vomiting in males might be an important complement to the data obtained in Experiment V and might yield additional information about the nature of the drive involved in epimeletic vomiting in *Canidae*.

Grzimek (6) in 1969, referring to Goddard's data, reported that four male cape hunting dogs fed and reared under natural conditions suckling puppies of a dead mother. He also wrote that both females and males in a given group of cape hunting dogs take part in supplying solid food to puppies; feeding is performed by disgorging the food from the stomach. The phenomenon was also observed by Sosnowskii (18) in cape hunting dogs in a zoo. Scott and Fuller (15) suggest that male domestic dogs seldom show interest in puppies, while in wolves epimeletic vomiting occurs in both males and females. These authors quoted the data obtained by Louis Crissler, who observed two groups of Alaska wolves and found that both female and male yearlings fed younger puppies.

No detailed data are available in the current literature on course of epimeletic vomiting of male in wild *Canidae* and, in particular, of the domestic male dog. I am inclined to agree with Scott and Fuller (15) and Scott (16) that in domestic dogs, males are only exceptionally interested in puppies. This could be due, however, to the possible absence of some important exteroceptive stimuli patterns and situations which might elicit their care-giving behavior toward the pups. The reasons for the lack of epimeletic vomiting in male dogs may be similar or the same as those in the female (10), in whom epimeletic vomiting has been observed only exceptionally and sporadically (5, 17) until now (10). This behavioral pattern in bitches could be obtained in its fully developed

form under specially designed living and feeding conditions as I have previously shown (10).

Epimeletic vomiting has a biological aim which can be fulfilled by both males and females. We may suppose, therefore, that patterns of adequate care-giving behavior which were phylogenetically transmitted into females and persisted in them up-to-date — should be potentially present in domestic male dogs too.

The aim of the present experiment was, thus, to create such living conditions for male dogs and to design such experimental procedures as to induce in them the anticipated patterns of care-giving behavior.

It was assumed that the decisive stimulus to evoke epimeletic vomiting would be presence of puppies suitably trained to show active et-epimeletic behavior.

Material and method

Three male dogs aged from 1 to 5 years were selected randomly and used in this experiment. The age of the animals was evaluated approximatively by the state of dentition. Five litters of suitably trained puppies were also used, and were of varying age. They were bred by five different mothers that were selected randomly. All puppies were in Phase III or at least in Phase II of et-epimeletic behavior toward their mothers.

The experiment was designed so as to allow hungry puppies to contact the male soon after he ate in separate feeding-box. The contact took place in the nest-pen of the puppies or in a close neighborhood with which they were familiar. The animals were observed for 20 min (in one case for 45 min) from the moment of contact. Since the situations were not quite identical for the three dogs, details will be provided for each dog, separately.

Results

Dog 1

Mongrel, about 1 year of age, weight 14 kg. He resided permanently in the nest-pen of the puppies, starting from the 14th day of their life, in July and August. As was the mother of the puppies, the male was fed in a feeding-box that was inaccessible to the puppies and, after feeding, it was put again into the nest-pen.

At the age of 45 days the puppies began to manifest clear et-epimeletic behavior toward both their mother and the male. Towards the male this behavior continued up to 51 days of the puppies' life, then disappeared probably because the male did not react with vomiting

and was, instead, inclined to play. With the mother, who vomited regularly, et-epimeletic behavior persisted up to the end of the 5th month of the puppies' life. The male resided in the nest-pen for 62 days, i.e., up to 76 days of the puppies' life. The result of the experiment with Dog 1 was negative, vomiting was never observed.

Dog 2

Mongrel, 3 to 4 years of age, weight 8 kg. Observation was carried out throughout January, February, and March. The dog was in contact with one litter of puppies. It was introduced permanently into a pen adjacent to the nest-pen as late as on 68th day of puppies' life. The two pens were separated by a solid wall with the front walls of the two neighboring pens made of wire mesh. Thus, the male in its pen could not see the bitch and the puppies. For the next 16 days direct contact between the male and the pups was only sporadic and accidental when they were free on the corridor. From the 84th day of the puppies' life (16 days of the male's residence in the neighboring pen) they were allowed to go into the male's box, for 20 min daily, before the mother was fed and immediately after the male was fed. Then the puppies returned to their nest-pen and the mother entered it after she was fed. The animals were observed for 30 min starting from the moment in which they are allowed to contact with sated male, and for following 30 min after contact with sated mother. At the age of 84 days the pups were markedly larger than the male, which seemed to be an unfavorable circumstance.

The puppies' behavior. Et-epimeletic behavior of the puppies towards the mother was highly insistent and always accompanied by loud typical vocalization. During daily contacts with the male they also showed toward him active though less insistent et-epimeletic behavior which disappeared, however, after 13 days. The appropriate behavior towards the mother persisted about 35 days longer. The mother vomited regularly, often two or even three times a day.

The behavior of the male. Starting from the 14th day of his stay in the neighboring box (82nd day of the puppies' life) the following observations were made. When the sated male was alone in his box and the sated mother came back to the hungry puppies, the male stayed near the wall separating the two boxes (the puppies behaved typically vocalizing loudly), remained motionless for a while, pricked his ears, bowed his head and then become hyperactive, walked around the box, and, finally, stopped near the wall which separated him from the bitch and the puppies, and vomited. Sometimes he ate the disgorged food after about 20 to 30 min. This behavior of the male and his vomiting

in the absence of the pups were observed 11 times, on the 82, 83, 86, 87, 89, 90, 91, 94, 95, 97 and 101 days of the puppies life. When starting from 84 days of their life the pups were allowed daily to go into the male's box he became aggressive. However, he vomited five times when the puppies were with him: on the 84, 85, 87, 100, and 125 days of their life. After vomiting, the male did not allow the pups to eat the disgorged food at once, only several minutes later. A total of 16 epimeletic vomiting incidents was recorded, between the 68th and 134th days of the puppies life.

Dog 3

Age approximately 5 to 6 years, weight 17 kg. The dog resembled a chow-chow. Trials were performed in contact with three different litters: with Litter I in May and Litters II and III in October. The box of the male was between the nest-pens of Litters I and II.

Trials with litter I. From the 40th day of pregnancy of the bitch, the male was kept permanently in a box next to its nest-pen. The two boxes were separated only by loose iron bars through which the male could directly contact by touch the bitch and the pups when they began to come out of the kennel. The latter, where the bitch gave birth to the litter and reared it, was placed near the bars of box occupied by the male dog.

On days 52, 59, 60, 61 and 62 of the puppies' life, at usual time of feeding the bitch went out of the nest-pen and the male, fed some minutes earlier, joined the hungry puppies. On all five trials the puppies showed toward the male highly active et-epimeletic behavior. During 30 min of observation, vomiting of male was recorded only twice — on days 58 and 59 of the puppies' life. Such vomiting took place after 4 to 6 min of strong locomotor activity of the male. After vomiting the male took some steps back and the pups at once ate the disgorged food.

Trials with litter II. The location of the male's box was the same as mentioned above. Direct contact of the male with the pregnant bitch started as early as on the 20th day of pregnancy, through the bars which separated the two boxes. The bitch gave birth to and reared her litter in a kennel placed near the bars.

On days 32, 35, 36, 37 and 38 of the puppies' life the mother was not fed at the usual time and the sated male was allowed to enter the nest-pen in which the bitch and puppies were together.

On day 32 of the puppies' life, i.e., on the first trial, their et-epimeletic behavior was not very much in evidence but they ate greedily the food disgorged by the male. So did the mother. Et-epimeletic behavior of puppies' became more pronounced on subsequent trials.

During all five trials the male showed an increased locomotor activity in response to et-epimeletic attacks of the puppies. Such locomotor hyperactivity was observed for 7 to 16 min. Then, on all trials, except the last one, the male remained quiet for a while and following some contractions of the abdominal muscles he disgorged a considerable amount of food and allowed the pups to eat it. Thus, vomiting of the male was observed on four of the five trials.

Trials with litter III. The nest-pen of the bitch and puppies of Litter III was 16 m away from the male box and the animals could not see each other. Prior to the experiment no touch contact was allowed between the male and Litter III and their mother. Instead, on all trials with Litter III, the male contacted by touch the puppies of Litter II whose nest-pen was close by.

On days 79, 80 and 87 of the puppies' life, the mother was not fed at the usual time and instead the male was allowed to go into the nest-pen after it had been fed. On days 79 and 80 it was allowed in, immediately after feeding, and on day 87 after an 18-min delay.

On all three trials et-epimeletic behavior of puppies toward the male was very active, lasted in bouts of several minutes with only brief intervals. On all trials the male showed strong hyperactivity when attacked by the puppies. On the first two trials the male vomited after 7 and 9 min following contact with the pups, and on the third trial (87 day) he vomited after 45 min. This was preceded twice by urination and defecation and extremely strong locomotor activity.

Discussion

We could have expected that epimeletic vomiting may occur in male dogs, since it had been previously seen (10) in many females as part of a care-giving pattern and since it is known to occur in male wild *Canidae* (6, 14, 15, 18, 19). However, it was not easy to induce. There are some important biological differences between the wild *Canidae* and the domestic dog. For example, wolves are monoestrus animals and are active in reproduction only once a year. Therefore, hormonal state of male wolves, especially 3 to 4 months after coitus, may be quite different from the state of male dogs whose reproductive activity (*potentia coeundi et generandi*) continues for a whole year and, in females, estrus occurs not once but usually twice a year.

Vomiting in male dogs can be taken as evidence that epimelectic vomiting in dogs is not solely a consequence of the hormonal states associated with pregnancy, delivery, and lactation. This was demonstrated in wolves and cape hunting dogs by the authors cited previously.

Referring to L. Crisler's data, Scott and Fuller (15) expressed the

view that, since care-giving occurs in adolescent wolves of both sexes, the patterns of care-giving behavior are not produced by hormones. The present experiments do not provide conclusive proof of such statement in relation to dogs. In Dogs 2 and 3 vomiting occurred several days after they began to stay in the neighborhood of the nest-pen and puppies. This period might be necessary for inducing in a male animal a necessary hormonal condition which might be obtained only after a prolonged influence of a pattern of exteroceptive stimuli provided by the puppies, the nest-pen, and the nursing mother. An analogous situation was observed in male pigeons and turtledoves (Ring Dowes) that could produce "alimentary milk" (a secretion of their crop) and feed the nestlings, if they had previously participated at egg incubation or observed, even through a glass, a female incubating eggs in the nest (11). The fact that lactation can be induced in heifer cows by systematic milking lends further support to the notion of the importance of exteroceptive stimuli for inducing a necessary hormonal condition. Therefore, occurrence of epimeletic vomiting in yearling (or even younger) wolves of both sexes cannot be proof that vomiting is independent of hormone action. For example, prolactin, which is present in both sexes, may affect care-giving behavior not only by females and possibly affects the appearance or course of such reaction in response to appropriate stimulus patterns.

The development of care-giving behavior in dogs, including males, seems to involve also socialization — determination of the relation to other dogs. According to Dobzhansky et al. (2) socialization in dogs develops between the 3rd and 13th weeks of life. This process is presumably essential for later care-giving behavior in parents toward puppies. Possibly, the negative results obtained with Dog 1 and the surprising behavior of Dog 2 would be easier to explain if their individual history were known. The surprising behavior of Dog 2, that showed aggression toward puppies (they were markedly larger than the male) and vomited while affected only by acoustic and olfactory stimuli suggests that his specific behavior was, possibly, a consequence of course of his socialization. At the same time, his behavior suggests that visual or even tactual stimuli may not be indispensable. The restricted role of visual stimuli in inducing vomiting in the bitches can also be inferred, to some extent, from Experiment IV.

In spite of the small number of male dogs that were tested, the epimelectic vomiting reactions might not be an exceptional phenomenon. Manifestation of this behavioral pattern may depend to a great extent on suitable environmental circumstances, and probably, on the course of socialization in early age.

GENERAL DISCUSSION

An attempt will be made now to characterize in detail the phenomenon of epimelectic vomiting.

The whole behavioral acts associated with epimeletic disgorging of food in dogs is a complex process which is controlled at different levels of the CNS, and there might be important sex differences.

In females Phase I and the beginning of Phase II of epimeletic vomiting is an unconditioned reaction which occurs in bitches even after the first delivery (10). Interoceptive stimuli alone might be probably sufficient to induce the drive and result most probably from the neuro-hormonal condition of the bitch during the post-partum period. Exteroceptive stimulus patterns (the nest and puppies that are, as yet not interested in solid food) may act in Phase I and II as additional facilitating stimuli. Of particular interest are some of my earlier observation of the behavior of two bitches as well as those by E. Stajudowa's (personal communication). After imaginary pregnancy and soon after imaginary delivery, bitches disgorged food several times when they came to a fictitious nest which had never contained any pups.

During the long Phase III, especially after the reduction of lactation, the role of intero- and exteroceptive stimuli appears to undergo a change. The hormonal background seems less important though visceral stimuli, as a consequence of large ingested amounts of food (10), still have some importance. Conversely exteroceptive stimuli — especially those provided by active puppies — become decisive for both the release of vomiting itself and some others aspects of appetitive behavior. Probably the increased role of exteroceptive stimuli is due to multiple reinforcements, and fixed conditioned reactions. The behavior of bitches is repeatedly reinforced either negatively by their state of restlessness and excitation induced by the et-epimeletic quasi-aggressive behavior of the pups and, positively, by the performance of the consummatory reflexes. The reversal of the relative role of intero- and exteroceptive stimuli in the vomiting process seems to correspond to Lorentz's principle of "dual quantification" (13) as well as to Tinbergen's "heterogenic summation of stimuli" (20). The accquired elements in this instinctive behavior are consistent with Lehrman's hypothesis (12), which assumes that instinctive behavior includes more than the strictly inherited elements.

In male dogs the consummatory reaction and appropriate appetitive behavior might also be unconditioned during the initial phase of epimeletic vomiting. The drive state seems to be under the influence of specific hormonal conditions induced mainly by the durable presence of exteroceptive stimuli. And, in turn, the puppies more and more active

and insistent in their et-epimeletic behavior, constitute a strong un-conditioned stimulus which interacts with the hormonal background. According to the hypothesis accepted, the subjective power of action of these exteroceptive stimuli depends on hormonal condition of adult dogs.

Independently, the intensity of exteroceptive stimuli and the time of their action on the male dog may play an essential role in later stages. When puppies grow larger, they probably do not correspond precisely with the key stimulus pattern which, normally, induces care-giving behavior. In such a situation, the behavior of the adult male dog towards puppies might be determined by acquired responses. Among these, the following should be taken into account: (i) the beginning and the length of the period during which the dog was influenced by the presence of puppies, nestling bitch, and possibly the nest itself; (ii) the et-epimeletic activity of the puppies; (iii) acquired behavioral properties of the dog, i.e., the degree to which behavioral patterns of epimeletic vomiting have been developed and fixed as well as other acquired features of its intra-specific behavior. The latter would involve mainly the process of so-cialization in the juvenile male. The provoking behavior of puppies should not induce aggression in the dog, since it might affect et-epimele-tic behavior which, in turn, might disturb care-giving behavior of the adult dog toward puppies. The level of socialization of the dog is, there-fore, important, and so is body size of the puppies compared to that of the dog. More doubtful, though not negligible might be also the effect of previous sexual activity of the dog.

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When characterizing the process of epimeletic disgorging of food, it should be contrasted with vomiting that occurs in pathological conditions. The latter form is a defense reaction of the organism (repulsion reflex) aimed at elimination of toxic, irritating, indigestible, or useless sub-stances. Such vomiting occurs as a vegetative reaction evoked by the stimulation of visceral and other chemoreceptors.

Epimeletic disgorging of food in Canidae cannot be qualified as a defensive reflex because of its biological role and — in spite of apparent similarity — because different physiological mechanism are involved. Since in dogs of both sexes the behavior under discussion is aimed at the supply of food to the young, it should be classified as a protective function. It is a specific "prolongation of the lactation activity", which is short in Canidae and — as lactation — it is necessary for the survival of the species in natural biotopes. Therefore, it must be considered as allotropic, social, and care-giving behavior.

Vomiting as repulsion reflex, is stereotyped and induced almost entirely by the action of interoceptive stimuli. Since a delay is generally impossible it bears all the signs of a vegetative reaction controlled mainly by lower levels of the CNS. On the other hand, epimeletic disgorging of food, in its fully developed form (Phase III) is a much more complex process. Exteroceptive stimuli begin to play a predominant part and both past (10) and present observations emphasize that there must be specific conditions which are essential for the manifestation and reliable occurrence of the phenomenon. As suggested, higher nervous centers are involved in the process. This is also indicated by the fact that delayed vomiting occurs until the bitch contacts the puppies, and her explicit tendency to establish early contact. Additional support for this notion comes from the fact that the mothers distinguished between their own and alien puppies, and that vomiting did or did not occur depending on such differentiation.

The effect of higher cortical centers on the occurrence and course of epimeletic vomiting suggests some analogy with vomiting which occurs in humans who are healthy but are suddenly emotionally excited by exteroceptive stimuli or sometimes even by imagination. Both are a consequence of psychical process.

According to Świętorzecki (19) and Eisfeld (4), in wolves the vomiting act may occur at any time under the influence of strong fear. It may occur when sated wolf escapes quickly, frightened by man. These data suggest that in *Canidae*, when the stomach is full, vomiting may be the result of some emotional state accompanied by active locomotion, and is neither a pathological sign nor an epimeletic act; it is a type of defense reaction which makes the escape easier. Circumstances under which such vomiting occurs show some analogy with the restlessness and locomotor hyperactivity manifested by both male and female dogs prior to epimeletic vomiting (10, and Experiment VI in present paper). In both situations there is thus a state of emotional stimulation and active locomotion with a full stomach.

Previous results (10) as well as the present data indicate that only the act of disgorging food — the actual consummatory act — is stereotyped. On the contrary, the whole complex process of appetitive behavior may be variable, what appears for instance in the manifestation of the tendency of sated mother to be in contact with the adequate stimuli patterns (see Experiment I). It was observed in one trial that the sated bitch, instead of waiting until the door will be opened and taking the usual route to her nest, jumped over a 1.5 m hedge, so as to be sooner with the puppies.

The biological role of epimeletic vomiting is determined by all the

characteristics discussed above. If the appetitive behavior were a stereotype and in consequence the consummatory act were performed only after a defined and invariable time, the dog ancestors and contemporary wild *Canidae,* that hunt far from the nest, might not reach in time their nests and pups and might discharge the precious food store too early. If, in turn, the consummatory act might occur without adequate exteroceptive stimuli (puppies), food were disgorged anywhere by action of interoceptive stimuli alone.

Finally, it seems possible that the learned and fixed elements of vomiting behavior promotes an optimal course of such behavioral responses in later period, when hormonal background decreases and stimuli producible by adolescent puppies are not so effective as earlier, i.e., when they were younger (the peak of frequency of epimeletic vomiting responses by mothers appears between 40 and 80 day of the puppies life).

In evaluating the role of the pups as the most important stimuli patterns, in Phase III of the phenomenon, three aspects of their effect on the parents appear to be fundamental: (i) induction of the specific restlessness of sated mother, i.e., signs of drive behavior when the puppies are far away, and this urges the bitch to join them; (ii) constitution of a complex stimulus pattern which induces in the bitch both the drive and the vomiting reaction itself; (iii) suppression of the hunger drive and aggression in the mother and male, which normally allows the puppies to take the disgorged food. In some cases, for example, when a second vomiting occurred 3 to 5 min after the first one, the bitch did not give up disgorged food and shared it with puppies. Such behavior was probably due to only partially fulfilled hunger which suppressed the antagonistic epimeletic drive.

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