FORUM

HEMATOPHAGOUS STRATEGIES OF THE CAT FLEA (SIPHONAPTERA: PULICIDAE)

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ABSTRACT

Hematophagy of the cat flea, *Ctenocephalides felis felis* (Bouche), was investigated. Blood feeding in the adult stages nearly doubled the weight of mixed-sex fleas. However, within 12 h, the gained weight was lost. Protein mass tripled after feeding, but starvation caused a reduction in protein with the percentage protein remaining constant (5%).

Both *in vivo* and *in vitro* rearing of cat fleas was successful in allowing flea survival, feeding, fecal production, and reproduction. *In vivo* rearing, infesting cats with 50 fleas per week, resulted in a mean of 332 fleas per cat. Because 68% were female, male survival times on the host were shorter than those of females. Female fleas produced 1 egg per h, and combined sexes averaged 0.77 mg of feces per day. Average blood ingestion for defecation was 6.97 μl of blood. *In vitro* rearing resulted in lower egg production (12%), feces production (50%), and ingestion of blood for defecation.

Two types of flea feces were found—spherules and coils. Within 24 h of first feeding, almost all feces were spherules <0.07 mm in diameter. After 10 days of feeding, 60-70% of the feces were coils. These adult feces are the natural larval diet of cat flea larvae.

RESUMEN

Se investigo la hematofagia de la pulga gatuna, *Ctenocephalides felis felis* (Bouche). Cuando los estados adultos de ambos sexos se alimentaron de sangre, su peso se duplico. Sin embargo, 12 horas despues, perdieron este peso. La cantidad de proteina se triplico despues de la alimentacion, pero la inanicion causo una reduccion en la proteina, y luego el porcentaje de esta se mantuvo constante (5%).

Tanto la cria *en vivo* como *en vitro* de las pulgas de gatos, fue exitosa y permitio la sobrevivemcia, alimentacion, produccion de materia fecal y reproduccion. La cria *en vivo* en gatos infestados con 50 pulgas por semana, resulto en un promedio de 332 pulgas por gato. Cuando el 68% de la poblacion era femenino, la sobrevivencia de los machos fue menor que la de las hembras.

Las pulgas hembras produjeron un huevo por h, y ambos sexos produjeron 0.77 mg de feces por dia. El promedio de ingestion de sangre para defecacion fue de 6.97 ul de sangre. La cria *en vitro* resulto en una produccion baja de huevos (12%), produccion de feces (50%), e ingestion de sangre para defecacion. Se encontraron 2 tipos de feces de pulga, esferoides y espiroides. Venticuatro h despues de la primera alimentacion, todas las feces fueron esferoides < 0.07 mm de diametro. Diez dias despues, 60-70% de las feces fueron espiroides. Estas feces de adultos sirven de dieta natural para las larvas de las pulgas.

Hematophagous strategies of fleas are of particular interest because during blood feeding they can transmit plague (*Yersinia pestis*; Pollitzer 1960) and murine typhus (*Rickettsia mooseri*; Farhang-Azad & Traub 1985). In addition, flea bites can cause severe pruritus and dermatitis in domestic animals (Kissilett 1938). While scratching and grooming irritated skin, the host can ingest fleas, resulting in transmission of the dog tapeworm, *Dipylidium caninum* (Hamrick et al. 1983).

Cat fleas, *Ctenocephalides felis felis* (Bouche), have been collected from a wide spectrum of hosts and have been found to successfully reproduce on a variety of blood types, although many fleas have very narrow host ranges. Sustained infestations have been reported on cats, dogs, humans, poultry, rodents, artiodactyl livestock, and various wild mammals (Yeruham et al. 1982). Cat fleas feed to repletion in only ten minutes; however rat fleas often feed for up to two hours if left undisturbed (Iqbal & Humphries 1982). Success in obtaining a blood meal is related to the host's grooming efficiency (Waage & Nondo 1982).

Cat fleas and other hematophagous arthropods have refined abilities to locate vertebrate hosts (Rothschild & Ford 1973), behaviors to allow interaction with their hosts (Marshall 1987), and modifications of mouthparts for blood sucking (Hocking 1971). Fleas, like other hematophagous arthropods, locate their hosts by kairomones emitted by the host, including carbon dioxide and other volatiles (Smith et al. 1970, Vale 1984). There are many scents emitted by warm living bodies which allow biting insects to cue in on them (Omer & Gillies 1971), and insects have modifications of their anatomy and physiology which permit them to exploit these signals (Davis & Sokolove 1976). Numerous short-distance chemical cues include heat and moisture (Burgess 1959), lactic acid (Davis & Sokolove 1976), carbon dioxide (Gillies 1980), and other components (Khan & Maibach 1966).

Fleas have a laterally flattened body shape with extensive spination that makes it difficult to groom fleas from the pelage of the host (Karandikar & Munshi 1950). Species with extensive spination, such as cat fleas, are more succesful in remaining on the host than those lacking genal combs (e.g. *Orchopeas howardii*; Amin & Sewell 1977).

Fleas have suctorial mouthparts with strong buccal and pharyngeal muscles, well adapted for piercing the skin and sucking blood (Quick 1972, Sutcliffe & McIver 1984). Daniel and Kingsolver (1983) reviewed the requirements for insect mouthparts capable of piercing the vertebrate skin and sucking blood, with detailed analyses of concentration, viscosity and the mechanical constraints of blood-feeding.

The proventricular armature of fleas (Coluzzi et al. 1982) is used to physically disrupt the blood cells and release intracellular components for digestion by the midgut. Fleas have digestive enzymes specifically adapted to handling blood (Prasad 1979). Levels of the catheptic enzymes, lysosomal carboxy-peptidase, and aminopeptidase have been determined for various times following the blood meal (Houseman & Downe 1983). Reinhardt (1976) has prepared an extensive description of the physiological and morphological changes in *Xenopsylla cheopis*, *Echidnophaga gallinacea*, and *Tunga penetrans* midguts precipitated by blood-feeding. The three flea species had two different feeding strategies—intermittent feeding (temporary parasitic) and continuous feeding (stationary parasitic). Not surprisingly, he found that midgut changes occurring in the intermittent feeders are cyclic whereas the midgut morphology and physiology of continuous feeders after a blood meal is rather constant.

The dramatic alopecia and pruritus of cat flea allergy dermatitis (Kissilett 1938) is considered evidence of the early stages of coevolution in which the host and flea have not yet achieved an optimal adaptation to one another (Girardin & Brossard 1985). Usually it is in the insect's advantage not to irritate the host by feeding, so that it can successfully complete the blood meal and escape to reproduce (Langley 1967). However, flea saliva is irritating to the host. Adult cat fleas readily resume feeding after disruption

and their feces is the main natural diet of cat flea larvae. Consequently it is essential that feces be deposited in the same location as the flea eggs. The irritation of the flea bite may be designed to provoke scratching by the host, thus insuring that eggs and feces will be deposited simultaneously.

The objective of this study was to investigate the hematophagous strategies of the cat flea both *in vivo* and *in vitro*. Three main areas were investigated—the effect of blood-feeding and intervals of starvation on adult weights and protein, the phenomenon of prediuresis and the associated fecal production, and egg production.

Materials and Methods

In vivo feeding. Two adult cats, neutered prior to sexual naturity, were used as hosts for the cat flea. The cats were housed separately in stainless steel cages (45 by 60 by 30 cm high) with screen floors (12 mm mesh). Cats were infested by placing about 50 fleas per week on them.

Flea eggs and feces were collected by removing a tray (43.5 by 61 by 6 cm deep) under the cage and brushing the contents into a Petri dish. Eggs and feces were separated from large debris by sieving (No. 10 U.S.A. Standard, 2.0 mm opening). Numbers of flea eggs were counted daily for two days.

Daily flea feces production was quantified by measuring total hemoglobin using a total hemoglobin test kit (Sigma Chemical, St. Louis, Missouri). Feces and other debris from the tray was dissolved in Drabkin's reagent (5 ml) and filtered. A split beam spectrophotometer (Lambda 6; Perkin-Elmer, Norwalk, Conn.) measured absorbance at 540 nm. Amount of flea feces was determined using a standard absorbance curve for known quantities of flea feces in Drabkin's reagent.

Numbers of fleas on the cats were quantified by serial combing with a fine metal comb (12 teeth per cm). Between combings, cats were returned to cages to collect flea eggs. Combing and egg collections were done until no eggs were recovered, indicating all fleas were removed.

In vitro feeding. Cat fleas were fed citrated bovine blood using a device similar to the one described by Wade & Georgi (1988). The fleas were confined in cages made from a plastic vial (5 by 4.5 cm diam.). The bottom was cut off and the open end was covered with nylon screen (300 um mesh). A hole (3 cm. diam) was cut in the vial lid and covered with screen (500 um mesh). The vial was inverted so that the fleas would insert their mouthparts through the upper fine screen for a blood meal, and eggs and feces would fall through the lower screen.

A thin layer of cat fur was provided as a substrate inside the cage. The fur was suspended against the upper screen with a wire screen (4 cm. diam. and 0.75 cm mesh). The fur provided a substrate for the fleas to cling to while feeding, and posed minimal obstruction for the eggs and feces to fall through the lower coarse screen.

The tubes containing bovine blood were plastic vials (15 dram) with a 0.5 cm hole drilled in the bottom. Plexiglass tubing (1 cm, 0.25 cm inner diam.) was cemented to the hole. The open end of the vial was covered with Parafilm and about 10 ml of bovine blood was added through the Plexiglass tubing.

The blood temperature was maintained at 41°C with an electrical heat band cable (TPI model TPT-6, W. W. Grainger, Chicago, Ill.) connected to a digital temperature controller (Model CN5000, Omega Engineering, Stamford, Conn.). The heat was distributed to the blood using a copper collar.

The flea feeding device (91 by 13 by 12.5 cm) had locations for eight cages. The blood vials were placed on top of the cages so that the fleas could feed by inserting their mouthparts through the screen and the Parafilm to the blood. An aluminum weighing

pan (7 cm diam.) was placed under the cage to collect eggs and feces that fell through the lower screen.

To determine the egg and feces production, 10 fleas were placed in each cage and fed blood continuously for 7 days. Blood was changed every 24 h. Eggs and feces were collected, weighed, and counted daily. The cage was weighed and dead fleas within the cage were counted daily. Because the fleas only began egg production on the third day, the egg production per cage and per female data was calculated only for days 4-7.

To determine the effect of feeding and starvation, 100 fleas per cage were placed in the eight cages. Six to 12 fleas were removed from each cage before feeding, immediately after feeding, and at 12 and 24 h of starvation after feeding. The fleas were weighed in groups of 48-90, and the test was replicated 10-12 times. Types of feces produced following defined periods of blood feeding were examined microscopically, categorized, and quantified.

Protein determinations. Flea eggs, larvae, pupae, and adults were weighed on a semianalytical balance (± 0.01 mg) and ground in a borosilicate tissue grinder with 3.0 ml (6.0 ml for the two fecal samples and the bovine blood) phosphate buffer (pH. 8.0). The homogenate was filtered through Whatman #1 paper. Using Bradford's (1976) method of protein analysis, 0.1 ml of each homogenate was placed in 3.0 ml of reagent, and absorbance of the reaction mixture was read by a spectrophotometer.

Statistical analysis. Data on protein levels, egg production, feces production, and flea longevity were analyzed by analysis of variance (GLM) and means were separated by Duncan's multiple range test ($P \leq 0.05$; SAS Institute 1988).

Results

Body weight of mixed-sex adult fleas increased significantly after blood feeding (Table 1). Before feeding, flea weights averaged 0.192 mg, and weights nearly doubled after access to blood for 24 hours. Starvation for 12 and 24 hours resulted in the loss of all gained weight, with mean weights lower than before feeding, likely due to the expenditure of digestive enzymes.

Protein levels of adult fleas also increased after feeding, but to a greater extent that body weight. Soluble protein content immediately after feeding more than tripled from 0.005 to 0.017 mg per flea. Starvation for 12 and 24 hours resulted in a loss of gained protein, but protein remained at about double the level of unfed fleas. Protein for unfed fleas averaged about 2.6% of body weight, and immediately after feeding was 5.0% of body weight. Even after starvation for 12 and 24 h, the percentage of protein was 5.0 and 5.7%, respectively. Although the amount of protein decreased with starvation, other body constituents were selectively lost during starvation. There is little doubt from the effects of starvation on body weight and protein that fleas must feed at least every 12 h in order to survive and reproduce.

TABLE 1. LIVE WEIGHTS AND PROTEIN CONTENT FOR ADULT FLEAS OF DIFFERENT NUTRITIONAL STATUS.

Feeding status	Hours since last feeding	Mean ± SE	
		Live weight (mg)	Protein (mg)
Unfed	–	0.192b ± 0.012	0.005b ± 0.001
Fed	0	0.343a ± 0.010	0.017a ± 0.002
Fed	12	0.181b ± 0.001	0.009b ± 0.001
Fed	24	0.175b ± 0.012	0.010b ± 0.001

Means within a column followed by the same letter are not significantly different.

Infesting cats with 50 fleas per week resulted in an infestation averaging more than 300 fleas per cat. About 68% of the fleas on the animals were female, indicating longer longevity or survival of female fleas on the host. Osbrink & Rust (1984) found that the lifespan of male fleas (7.2 days) placed in microcells on cats was shorter than that of females (11.2 days). Average flea egg production per cat was 5,577 eggs per cat or 24 eggs per female. Evidently, a healthy female can produce about one egg per hour. Osbrink & Rust (1984) reported that female fleas have six ovarioles in each of two ovaries, and that fleas from cats had an average of six mature eggs in the abdomen. They also found that egg production throughout the female's lifetime averaged 158.4 eggs.

In vitro production was based on about 10 fleas per cage. Egg production began on the third day of the experiment and was markedly less than from fleas released on cats with a daily production that averaged 14 eggs per cage. Assuming that 50% of the fleas in the cages were female, daily egg production was almost 3 eggs per female. Therefore, we concluded that *in vivo* production of fleas is about 8 times more efficient than *in vitro* production.

Feces produced from fleas on cats averaged 254 mg per day or 0.77 mg per flea, in contrast to significantly lower production *in vitro* (Table 2). Fleas on the artificial feeding device excreted about 50% of the amount of feces excreted by fleas on cats. The lower feces production *in vitro* indicates that the system is not yet perfected and flea feeding is lower than that achieved by fleas on cats. The dry weight and specific gravity of blood was used to estimate the total volume of blood consumed to produce feces. Fleas consume about 6.97 ul of blood on a cat to produce feces compared to 2.28 ul *in vitro*.

Two types of adult flea feces are produced, spherules and coils. Spherules can be graded by size as small (<0.07 mm) or large (0.10-0.25 mm). The small spherules are usually cohesive and are stuck to each other like a beaded necklace. Although the cat flea is not considered to have one, the configuration of small spherules is an argument for the presence of a peritrophic membrane. The large spherules are shiny, with little surface decoration, and discrete. The coils average 0.84 mm in length with a diameter somewhat less than the big spherules. The furrows visible on the coils are likely due to the configuration of the rectum, so as moisture is removed from the forming fecal bolus, strata develop.

Almost all the spherules produced by fleas during the first 24 hours of feeding on a host are small (Table 3). However, by the tenth day of feeding, most flea fecal material is excreted as coils. The remaining fecal material is equally distributed as small and large

TABLE 2. FLEA FECES AND EGG PRODUCTION *IN VIVO* AND *IN VITRO*

	Mean ± SE	
	in vivo (per cat)	*in vitro* (per cage)
Number of fleas	332.75 ± 78.62	9.64 ± 0.15
Number of females	226.75 ± 58.87	–
Daily egg production	5,577.00 ± 1,635.45	14.44 ± 2.74
Eggs per female	23.96 ± 0.83	2.92 ± 0.56[a]
Daily feces production (mg)	253.63 ± 59.61	2.60 ± 0.87
Feces per flea (mg)	0.77 ± 0.03	0.38 ± 0.08
Dry weight of blood (g/liter)	109	120
Daily blood consumption[b] (ul)	2,320	22
Blood consumption per flea[b] (ul)	6.97	2.28

[a]Assuming 50% of fleas were females.

[b]Amount of blood consumed to produce feces. Estimated based on the quantity of flea feces produced, and the dry weight per liter and specific gravity of host's blood.

TABLE 3. TYPES OF FLEA FECES PRODUCED FOLLOWING INTERVALS OF *IN VITRO* BLOOD-FEEDING

Days of blood-feeding	Types of feces produced		
	Spherules *0.07 mm	Spherules >0.10 mm	Coils
1	89-90%	<15%	<5%
10	15-20%	15-20%	60-70%

spherules. The two types of fecal conformations produced are distinctive, and the timing of their production is probably of significance, although the actual importance can only be conjectured.

The spherules produced initially have a protein content of 7.4%. Subsequent feces (mostly coils) has a higher protein content of 11.0%. Both protein levels are higher than the 5% protein level of bovine blood that was fed to the fleas in this experiment.

DISCUSSION

Blood consumption and weight gain is quite easy to quantify in ticks and other larger arthropods that take a distinct blood meal (Koch & Sauer 1984). For cat fleas and other continuous feeders, like some fleas and mosquitoes, which exhibit prediuresis, it is inherently difficult to quantify blood consumption and weight gain. Nevertheless, our initial weights (0.19 mg) for cat fleas are similar to Joseph's (1976) weight of female adult *C. felis orientis* (0.18 mg) prior to feeding. He documented that her weight increased to 0.26 mg over 47 min. of feeding on a human, while excreting 0.88 mg rectal fluid. Joseph (1976) also found distinct sexual dimorphism in the weights of these fleas, with females weighing 2.5 times more than males.

Like the *Anopheles* mosquito (Briegel & Rezzonico 1985), cat fleas have prediuretic excretion, i.e., excretion of serum or serum and erythrocytes while blood is ingested, leading to protein concentration in the midgut. Fleas demonstrate an elegant adaptation to this system in that the larval fleas are provided with both the spherules of essentially unhydrolized blood and then later with the coils of partially digested blood. The significance of the two types in the diet of larval fleas has yet to be determined. It may be that the smaller spherules provide a manageable meal for the newly-hatched flea larvae while the larger coils provide sufficient nutrition and are of an appropriate size for consumption by later instars.

Adult flea feces is essentially dried blood; therefore, because flea larvae feed on this dried blood, they, as well as the adults, could be considered hematophagous parasites that depend on the host and conspecifics for their nutrition. Considering the intimate relationship of the larval flea and the host animal, it would not be too surprising to find endoparasitism in some fleas. One unique species of flea is known to exhibit this lifestyle where all stages of development actually occur on or in the host (Williams 1986a).

In species where the larva is free-living, it would be important for the adult to provide adequate nutrition for the development of the larva. By passing through its digestive tract more blood that is less digested, the adult augments the nutrient content of the larval diet. Unlike many other holometabolous, hematophagous arthropods, the male flea is exclusively a blood-feeder. This might be a form of parental care whereby the male contributes to the feeding of the young. Both sexes produce larval food to insure that feces are available for the developing larvae.

The cat flea was unable to successfully develop as a larva without feeding on adult flea feces or dried blood (Strenger 1973, Moser 1989). Other organic materials (Bruce

1948) are suitable for larval nutrition, but it is almost impossible to collect eggs from their contaminated environment without some fecal material adhering to the shell (Hudson & Prince 1958).

The discrepancy between volumes of blood consumed by males or females is of particular interest in the consideration of paternal input in larval nutrition. Iqbal & Humphries (1982) found that the male flea imbibes less than 15% of the blood volume that the female does (0.8×10^{-4} compared with 6.21×10^{-4} mm^3) in a single blood meal. It would be revealing to compare the nutritional components of feces from the two sexes to determine if the female actually produces most larval food. Also of interest are the effects of temperature of the blood on consumption and the fecundity of blood-fed females (Davis et al. 1983).

The integrity and appearance of flea feces may be indicative of a peritrophic membrane. While the typical view is that a peritrophic membrane is produced in insects which consume rough materials, to protect the delicate intima of the midgut, many blood-sucking insects possess peritrophic membranes, as well. It has been demonstrated in mosquitoes that the space between the midgut epithelium and the peritrophic membrane is a compartment for optimal digestion, with a concentration of digestive enzymes (Graf & Briegel 1982). A peritrophic membrane has also been found in *Rhodnius* (Billingsley & Downe 1983).

The blood of most vertebrates is quite similar in composition (Dittmer 1961). This explains why some fleas have such wide host ranges; they are able to adequately exploit the resources of a variety of blood types. For instance, Bacot (1914) found that rat fleas could survive for extended periods fed solely on human blood, but that they were unable to reproduce. Cat fleas can reproduce on calves, but reproductive failure based on ovariole regression is 25% compared to <10% on cats (Williams 1986b). In general, it has been found that hematophagous arthropods have higher fecundity when fed on their normal hosts (Mather & DeFoliart 1983).

In conclusion, it appears that while fleas may have initially been scavengers in animal nests and burrows, they have subsequently evolved nearly complete hematophagy coupled with a range of host association from the perfunctory up to and including endoparasitism (Prasad 1987). The cat flea on the surface appears to be poorly adapted to its hosts because of irritation, pruritis, and allergic responses. In reality, the irritation is an elegant adaptation to insure larval hematophagy. The irritation causes host grooming that dislodges both eggs and adult flea feces into the same environment. The realization that cat flea larvae are also hematophagous will certainly enhance our understanding of flea ecology and behavior.

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