Some Abiotic Factors Affecting the Survival of the Cat Flea, *Ctenocephalides felis* (Siphonaptera: Pulicidae)[1]

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ABSTRACT Some abiotic environmental factors influencing the survival of the cat flea, *Ctenocephalides felis* (Bouché), in semi-arid and temperature climates were studied. Pupae survived outdoors throughout most of the year except July and August, when temperatures often exceeded 35°C. As temperatures increased, the time required to kill larvae exposed to 12 and 33% relative humidity (RH) decreased. At 27°C, 16-h exposures to 12% RH and 24-h exposures to 33% RH provided 100 and 97% mortality, respectively. Larvae survived only when the RH was >50% for several consecutive days or the microhabitats provided substantially higher than ambient humidity. Soil moistures of 1 to 10% permitted larval development even when larvae were held at 12 ± 2% RH. Soil moistures from 20 to 50% were deleterious. Emerged and preemerged adults survived short exposures to low temperatures but were killed by 10-day or 5-day exposures at 3 and −1°C, respectively. Exposures to 3°C for 5 days killed all immature stages.

The cat flea, *Ctenocephalides felis* (Bouché), is a seasonally abundant and cosmopolitan ectoparasite of many feral and domestic animals in urban situations. Although most of the *Ctenocephalides* species are endemic to the Ethiopian and Oriental regions (Hopkins and Rothschild 1953), the widespread distribution of *C. felis* may partly be explained by its preference for domestic cats and dogs as well as skunks and opossums, by human migrations, and possibly by its less restrictive environmental requirements (Lewis 1972). In spite of its veterinary and medical importance as a causal agent of severe pruritus and dermatitis in dogs and cats (Kristensen 1976, Nesbitt and Schmitz 1978) and localized allergic reactions in humans (Hudson et al. 1960), a vector of dog tapeworm, *Dipylidium caninum* (Chen 1934), a potential vector of murine typhus (Traub et al. 1978), and plague (Pollitzer 1960), little is known concerning the abiotic factors affecting the survival of the cat flea.

Bruce (1948) reported that cat fleas reared at 21 to 32°C and 80% relative humidity (RH) provided 90 to 99% survival, whereas RHs at or below 45% resulted in no adult emergence at 32.2°C. Silverman et al. (1981) reported on the effects of continuous exposure to various combinations of temperature and RH on the development of each stage of the cat flea. The upper and lower temperature limits for development were 32 and 13°C, respectively. RHs from 50 to 92% resulted in >80% egg hatch, 100% larval development, and >90% survival in the pupal cocoon.

The pronounced effects of temperature and humidity on cat flea development reported by Silverman et al. (1981) do not explain the success or distribution of this pest in semi-arid and temperature climates. In the semi-arid areas of southern California, adult fleas have been collected throughout the year and are particularly abundant in the late spring and summer (Osbrink and Rust, unpublished data). Reported herein are some effects of ambient environmental conditions of semi-arid southern California, such as low RH, dry soil, and highly fluctuating temperatures, on the development of cat fleas. Those developmental stages likely to survive unfavorable conditions are emphasized.

Materials and Methods

All stages of *C. felis* used in these experiments were obtained from a stock culture reared as described by Hudson and Prince (1958) and modified by Silverman et al. (1981). A screen was used to separate flea eggs from debris collected beneath cages containing infested cats. Eggs used in the tests were carefully aspirated into glass shell vials and to specified containers. The remaining eggs placed in larval rearing media (20:3:2 wt/wt/wt pulverized dry dog chow, dried beef blood, and whey-grown yeast) were incubated at 75% RH and 22 ± 1°C. After 4 to 5 days, 2nd- and 3rd-instar larvae were aspirated into glass shell vials from the media for tests, and the remaining larvae were allowed to pupate. About 7 days after eggs were placed into the media, pupal cocoons were separated from the media with a 6.3-mesh/cm screen.

Influence of Ambient Temperatures and RH on Development

The development of *C. felis* was studied throughout 1980 on campus in an open-air structure designed to provide shade and partial protection from precipitation but not to alter the ambient temperature or humidity. At the beginning of each month, 20 1-day-old eggs, 2nd- and 3rd-instar larvae, and 2- to 4-day-old pupae were placed in individual tin containers (6 cm in diameter by 2 cm) covered with 19.7-mesh/cm screen lids. Five replicates were tested for each stage. Eggs and larvae were provided ca. 1 cm^3 each of sand and rearing media. All stages were exposed to ambient and 75% RH in the outdoor structure. Constant 75% RH, optimal for development of immature fleas, was maintained in a tightly covered, stainless-steel pan containing a saturated solution of aqueous NaCl (Winston and Bates 1960).

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Outdoor temperatures and humidities were monitored with a recording Thermohumidograph (Bristol Co., Waterbury, Conn.) and were confirmed with data provided by the U.S. Department of Commerce, Weather Bureau, University of California, Riverside Station. At the end of each month, each container was examined and the number of adults was counted. The containers with immature fleas were transferred to chambers maintained at 22 ± 1°C and 75% RH in the laboratory to allow for completion of development. Survival was determined by counting the number of emerged adults.

Influence of Brief Exposures to Low RH at Various Temperatures

Larvae were exposed for short periods to low relative humidities at various temperatures to determine their effects on larval development. Ten 3rd-instar larvae (three replicates), held in uncovered glass vials (2 cm in diameter by 8 cm) containing ca. 1 g of sand, were placed inside sealed chambers for 4, 8, 16, and 24 h and exposed either to 12 ± 2% or 33 ± 1% RH provided by saturated LiCl and $MgCl_2$ solutions, respectively (Winston and Bates 1960), over a range of temperatures from 10 to 43°C. After each exposure the larvae were removed and placed in sealed chambers (22 ± 1°C and 75% RH) for 24 h to determine if there were any latent effects from the test condition.

To determine if larvae were capable of absorbing water vapor after brief exposures to dry air, 10 3rd-instar larvae were placed in small aluminum weighing pans, weighed, and held in a desiccator maintained at 12% RH and 27°C. When the larvae had lost 8% of their original body weight, the pans containing the larvae were removed from the desiccator and placed in a chamber maintained at 100% RH. After 24 h, the pans and larvae were removed and weighed again to determine the change in larval weight.

Survival in Protected Microhabitats

To determine if certain outdoor microhabitats might provide suitable conditions for development, cat fleas were placed in several locations around a home in Riverside. The locations selected were sites where flea eggs might be dropped from infested animals frequenting such areas. Ten 2nd-instar larvae reared from laboratory colonies were held in glass vials (2 cm in diameter by 2 cm) with ca. 1 g of sand. Each vial was covered with paper toweling to prevent ants from killing and removing the larvae. Five vials were placed in each microhabitat. Larvae were placed in a dense 15-cm-deep mat of groundcover (ice-plant, *Mesembryanthemum crystallinum* L.) which completely shaded the soil, in the shade underneath a shrub with low branches ca. 15 cm above the ground with limited air circulation, at the base of a tree which provided continuous shade and good air circulation, and within a 2- to 3-cm-high lawn of hybrid Bermudagrass which was in full sunlight. Temperature and RH were monitored at each site during the test with a Digitec three-channel thermistor thermometer. The unit was modified into a psychrometer by wrapping the tip of one of the stainless-steel temperature probes with wet cotton gauze and then blowing air over it with a rubber bulb to provide a wet bulb reading. A second dry probe was used to simultaneously record temperature. The accuracy of this device was verified at high and low humidities with a sling psychrometer. Cobalt thiocyanate papers (accurate to within 10%) were also used to supplement psychrometer readings. To maximize differences in RH between ambient air and each microhabitat, the tests were conducted when the air was dry (25% RH). Larval mortality was assessed after 24- and 48-h exposures.

Effects of Soil Moisture on Larval Survival

The effect of soil moisture on the survival of larvae was studied by confining larvae to sand, sandy clay, and silty clay containing known amounts of water inside chambers with three different humidities. Soil composition was determined by differential sedimentation as described by Foth and Jacobs (1964). The soils were passed through a 40-mesh screen and dried at 110°C for 24 h. Distilled water was added to each soil to provide moistures of 1, 5, 10, 20, 30, 40, and 50%, and 20 g of each soil type and moisture were placed into each of three plastic vials (3 cm in diameter by 8 cm). Ten 3rd-instar larvae placed on top of the soil in each vial were placed inside chambers held at 12, 55, and 95% RH provided by LiCl, $Na_2Cr_2O_7$, and Na_2SO_4 saturated solutions, respectively (Winston and Bates 1960). After 24 h, the soil was removed from the vials and the number of dead larvae was counted.

Influence of Low Temperature on Survival

The effects of low temperature on the survival of cat fleas at constant high humidities were assessed by exposing 20 1-day-old eggs, 2nd- and 3rd-instar larvae, prepupae, pupae, or adult fleas in plastic vials (3 cm in diameter by 8 cm) to −1, 3, and 8°C. Eggs and larvae were provisioned with rearing media. All stages for each of three replicates were held at 75% RH for 1, 5, 10, 20 or 40 days at each temperature. After each exposure period, the immature stages were transferred to chambers held at 27°C and 75% RH for 21 days to allow for development to the adult stage before mortality was assessed. The number of dead adults exposed to the various temperatures was counted after each exposure period.

Results and Discussion

Outdoor temperatures were favorable for survival of *C. felis* larvae and pupae held at constant 75% RH for most of 1980 (Fig. 1C and D). However, maximum daytime temperatures often exceeded 35°C from May to September (Fig. 1A), with occasional temperatures as high as 43°C in July and August. When the temperature surpassed 35°C for more than 40 h/month, there was complete mortality of larvae and pupae (Fig. 1C and D).

When pupae were exposed to ambient RH, the level of adult emergence was similar to that of pupae maintained at 75% RH (Fig. 1C). One noticeable exception

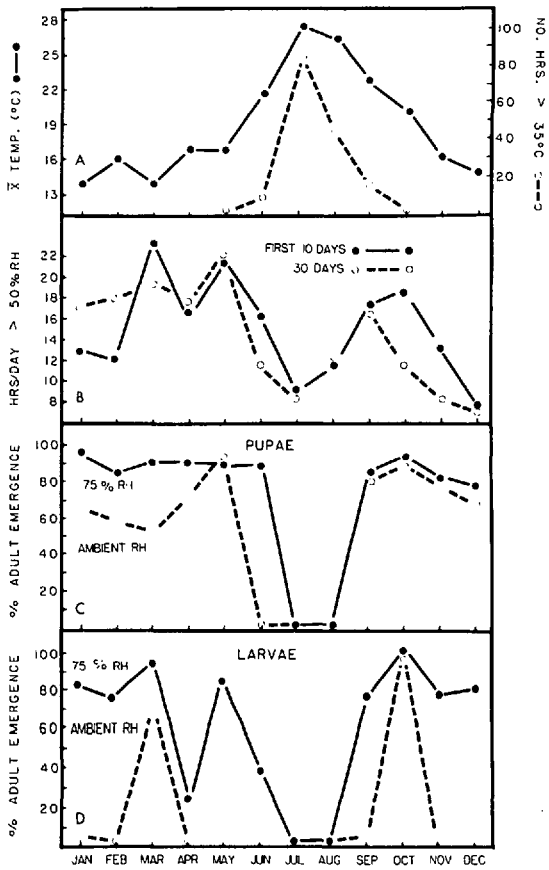

FIG. 1. Monthly survival of larval and pupal stages of *C. felis* exposed outdoors during 1980 in Riverside, Calif. (A) Mean stages of daily temperature (____) and number of hours per month exceeding 35°C (-----); (B) average number of hours per day at RH > 50%; (C and D) pupal and larval survival at 75% RH (____) and ambient RH (-------), respectively.

was the combination of increased daily temperatures and decreased RH during June which resulted in 100% mortality of pupae exposed to ambient conditions. Although many larvae survived at 75% RH for much of the year, drier ambient conditions elicited higher mortality (Fig. 1D). Larval survival in March at ambient RH was attributed to favorable humidity conditions during the first 10 days when the larvae were placed outdoors. During this time there were more than 22 h/day when the RH was >50% (Fig. 1B); thus, most larvae pupated. These pupae were able to survive the decrease in humidity occurring later in March. Larvae survived ambient conditions in October, even though the number of hours per day of RH >50% was less in October than it was in May. Since the mean monthly temperature was higher in October than it was in May, there could have been an accelerated development to the desiccation-resistant pupal stage, thereby reducing the time of larval exposure to the low RH.

Although flea eggs are more tolerant to desiccation than larvae, newly hatched larvae would be subjected to dry conditions longer than 3rd-instar larvae were in previous studies (Silverman et al. 1981). When tests were begun by holding eggs at ambient RH, the eclosed larvae never developed into adults.

Silverman et al. (1981) found that continuous exposure of *C. felis* pupae to 35°C and larvae and eggs to 38°C was lethal. In addition, pupae could resist desiccation, whereas larvae died when exposed continuously to RHs below 50%. Amin (1966) reported that fewer adult *C. felis* were collected from dogs in Cairo, Egypt, after extended periods of low RH. Desiccation of larvae during these dry periods may explain the subsequent decrease in adult numbers. In the present study, ambient RH fluctuated between 10 and 100% throughout the year, with an average <75%. Consequently, larvae survived only during infrequent periods when RH was greater than 50%. Pupal survival was mediated much more by temperature than RH.

Influence of Brief Exposure of Larvae to Low RH

As temperature increased, the exposure period necessary to kill larvae at 12 and 33% RH decreased (Table 1). Even though continuous periods of <50% RH rarely persisted outdoors for longer than a week in the previous test, daily fluctuations between 20 and 80% were common. Even though larvae were probably not subjected to desiccating conditions for more than 8 h/day, larval mortality was high (95 to 100%) most of the year. Knülle (1967) reported that the larvae and prepupa of *Xenopsylla cheopis* may absorb water vapor, thereby rehydrating after partial desiccation. In the present study, 3rd-instar *C. felis* larvae were dehydrated to 92% of their original body weight at 27°C and 12 ± 2% RH and lost an additional 3% of body weight even when held at 100% RH for 24 h, with death ensuing within 72 h. Cat flea larvae apparently could not absorb atmospheric moisture at high RH to compensate for water lost during periods of low RH.

Survival in Protected Microhabitats

Although *C. felis* larvae are unable to survive low RHs and high temperatures, adults are found infesting domestic pets throughout the year in many semi-arid and temperate climates. Since the chorion of flea eggs is smooth and eggs readily fall from the host during oviposition, larval distribution largely depends upon the location of the host. Only eggs disseminated in microhabitats with relatively moist air or soil will hatch into larvae and reach maturity. The suburban microhabitats listed in Table 2 represented locations of varying temperature and humidity where feline and canine hosts of *C. felis* frequently visit. Within the dense mat of ground-covering plants or beneath the shrub, larvae pupated within 48 h because the RH in these locations never dropped below 45% for extended periods even during the hottest part of the day. In open areas such as under the tree, or within a Bermuda lawn, the RH was similar to ambient RH and consequently most larvae desiccated within 48 h. Therefore, the most likely outdoor sources of flea infestations are shaded and wind-protected areas

Table 1. Effects of brief exposures of larval *C. felis* to low humidities at various temperatures

RH (%)[a]	Exposure time (h)	% Larval mortality at the following temp (°C)[b]						
		10	16	21	27	32	38	43
12 ± 2	4	—	—	—	—	—	20	100
	8	—	—	0	17	63	70	100
	16	0	13	60	100	—	—	—
	24	3	57	97	100	—	—	—
33 ± 1	4	—	—	—	—	0	10	100
	8	—	—	—	—	7	50	100
	16	—	3	17	63	87	100	—
	24	0	27	90	97	100	—	—

[a]Saturated solutions of LiCl and $MgCl_2$ provided 12 ± 2 and 33 ± 1% RH, respectively.
[b]Mortality differences were significant between all temperatures, all exposure times and both RHs ($P < 0.05$; ANOVA, arcsin transformation).
—, Temperature and exposure period not tested.

Table 2. Effects of continuous exposure in outdoor microhabitats on *C. felis* larval survival during conditions of low ambient RH (25%) and an average daily temperature of 21°C

Location	Highest temp (°C)	Lowest RH (%)	% Larval mortality at:	
			24 h	48 h
Ground cover	27	70	0	0
Beneath shrub	27	45	0	0
Under tree	29	35	0	65
Within lawn	30	25	100	—

visited by the host. Kristensen et al. (1978) considers temperature and RH to be limiting factors in the development of cat and dog fleas in northern Europe. The increased indoor humidity inside structures in Denmark, as a consequence of energy conservation, has contributed to favorable conditions for larval development resulting in a northerly spread of *C. felis*.

Effects of Soil Moisture on Larval Survival

When some moisture was added to soil, larvae were able to survive even in dry air (12% RH), as shown in Table 3. Larval mortality was reduced from 100 to 0% by merely increasing the moisture of sand or sandy clay from 0% to 1%. Mortality remained at 100% with silty clay containing 1% moisture because clay readily absorbs water, making it unavailable at low moisture levels. Also, various dry clays exhibit desiccating properties by absorbing wax from insect cuticle (Ebeling and Wagner 1959). Mortality of larvae decreased significantly ($P < 0.05$) when the moisture of silty clay was raised to 5%. Larvae were found on the soil surface when moisture was increased to 10% for all soil types, a consequence of the interstitial soil spaces becoming saturated, thus blocking gaseous transfer. At higher moisture levels (20 to 50%), a surface film of water developed which killed some larvae. The mortality of larvae held at 55 and 95% RH was similar (±10%) to that of larvae at 12% RH when exposed to the same soils and moisture levels above 10%. Trimble and Sherrard (1935) reported that the number of adults of the rodent flea *Leptopsylla musculi* decreased outdoors following an increase in rainfall. The adverse effect of high soil moisture on *C. felis* larvae may explain this decline.

Influence of Low Temperatures on Survival

In addition to RH and soil moisture, temperature influences the variety of habitats in which *C. felis* can survive. As discussed earlier, the critical upper temperature threshold for development ranges from 35 to 38°C. The lower temperature limits for survival of each stage are shown in Table 4.

There was a significant difference in survivorship at each temperature ($P < 0.05$; analysis of variance [ANOVA]). Survivorship decreased significantly with increasing exposure time except after 20 days. Cold

Table 3. Influence of soil moisture and composition on the survival of *C. felis* larvae when held for 24 h in chambers maintained at 12% RH and 22 ± 1°C

Soil composition	% Larval mortality at the following % soil moisture[a]:							
	0	1	5	10	20	30	40	50
Sand	97	0	0	0	13	90	90	—[b]
Sandy clay	100	0	0	0	3	43	50	70
Silty clay	100	100	17	0	7	37	90	90

[a]Overall mortality was significantly higher on silty clay than sand or sandy clay ($P < 0.05$; ANOVA, arcsin transformed).
[b]Soil unable to retain more than 40% water.

Table 4. Percent survival of *C. felis* after continuous exposure to low temperatures and 75% RH[a]

Stage	Exposure (days) at[b]:									
	8°C					3°C			−1°C	
	1	5	10	20	40	1	5	10	1	5
Egg	55	35	0	0	—	35	0	—	3	5
Larva	85	85	45	0	—	63	0	—	7	0
Prepupa	97	42	17	0	—	63	0	—	0	—
Pupa	95	75	35	0	—	78	0	—	0	—
Preemerged[c]	100	97	82	38	28	88	20	0	28	0
Adult	100	100	100	45	30	100	65	0	80	0

[a]Survival expressed as individuals attaining adult stage after exposure period.
[b] —, Exposure period not tested.
[c]Quiescent adult within pupal case.

tolerance of each life stage was as follows: Adult > preemerged adult > pupa = larva > prepupa > egg ($P < 0.05$; ANOVA, arcsin transformation). It has been demonstrated that gradual chilling of insects increases their survivorship at low temperatures (Salt 1961). Eggs and prepupae cooled from 21 to 3°C—6°C every 3 days—did not survive any longer than did unacclimatized fleas. Emerged adults and quiescent adults within the cocoon were best able to tolerate long exposures at 8°C, but neither could withstand 10 days at 3°C or 5 days at −1°C. However, the geographical range of *C. felis* includes many areas where prolonged subfreezing winter conditions occur (Hopkins and Rothschild 1953). Daniels (1973) reported 41% adult survivorship of *Ctenophthalmus agyrtes agyrtes* (Haller) in Czechoslovakia in mammal burrows 30 to 40 cm deep, where temperatures never dropped below 0°C, versus no survival on the frequently frozen ground surface. Kristensen et al. (1978) collected *C. felis* adults throughout the year from dogs and cats in Denmark. Since survival under subfreezing conditions was low in our study, it is likely that *C. felis* endures harsh winter conditions by living either on their host (domestic or feral) as adults or in the shelter of their host.

In conclusion, habitats favorable for continuous development of *C. felis* should: (1) provide greater than 50% RH, (2) contain soil of less than 20% moisture content, and (3) protect against temperatures above 35 and below 4°C. Further research to evaluate the dynamics of *C. felis* populations in protected habitats is necessary and requires the development of methods for sampling field populations of immature and adult cat fleas.

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