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Water balance and humidity requirements of house dust mites

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ABSTRACT

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The house dust mites, *Dermatophagoides farinae*, *D. pteronyssinus* and *Euroglyphus maynei*, are prevalent in homes in humid geographical areas throughout the world. These mites thrive in humid environments in human dwellings where there is no liquid water to drink. However, their bodies contain 70–75% water by weight, which must be maintained in order to reproduce. Their primary source of water is water vapor which is actively extracted from unsaturated air. At relative humidities above 65–70%, adequate amounts of water can be extracted from unsaturated air to compensate for that lost by all avenues. Active uptake is associated with ingestion of a hyperosmotic solution which is secreted by the supracoxal glands. Active mites do not survive longer than 6–11 days at RHs \leq 50%. They survive extended dry periods by forming a desiccation-resistant protonymphal stage which can survive for months at RHs below the critical humidity for active stages. Feeding rate and allergen production is directly influenced by RH. Mites feed, multiply, and produce more fecal matter at higher RHs than at lower ones.

INTRODUCTION

Water is as basic to life as oxygen for terrestrial metazoan animals. Most terrestrial animals are more than 70% water by weight. Water molecules constitute more than 99% of all molecules (structural and in solution) which comprise living animals. It is the major constituent within all living cells and serves as a matrix in which cells function. Because of its hydrophilic, hydrophobic and hydrogen-bonding interactions with other molecules, water is responsible for the three-dimensional configuration of macromolecules. Water

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is also responsible for bioelectrical currents associated with the diffusion of ions, movements of nutrients, wastes and metabolic intermediates by diffusion or bulk flow, lubrication of reproductive, digestive and other surfaces, and participation in chemical reactions. Expressed as a chemical potential or mole fraction, body fluids of most animals have a water activity (a_w) of greater than 0.99. Although terrestrial animals have different tolerances to hydration and dehydration, the a_w of body fluids normally ranges between 0.990 and 0.996. Expressed as osmolarity, body fluids range between 250 mOsm and 700 mOsm (Wharton and Richards, 1978; Arlian and Veselica, 1979). In order to maintain normal physiological integrity, both body water content and concentration must be maintained within tolerance limits by balancing the water gain and loss over time. Therefore, the availability of water and adaptations for obtaining and conserving water limits the prevalence and distribution of animals both geographically and within geographical areas where liquid water may be scarce or absent in specific habitats and microhabitats. In spite of the need to maintain water balance, some animal species live and breed in habitats where there is no liquid water (e.g. kangaroo rats and some species of insects and mites). These dry areas, habitats, and microhabitats are permanently populated by species that have morphological, functional, and behavioral adaptations (mechanisms) that regulate water uptake and loss so that a critical water mass is maintained. The allergen-producing house dust mites *Dermatophagoides farinae* (DF), *D. pteronyssinus* (DP) and *Euroglyphus maynei* (EM) are such species. These mites thrive in humid environments in human dwellings where there is no liquid water to drink. They are cosmopolitan inhabitants of homes throughout the world.

House dust mites, like other small arthropods, have large surface-to-volume ratios that favor the rapid evaporative loss of water. However, these animals exhibit adaptations that allow them to conserve sufficient water in these dry habitats so that gain, by means other than drinking, is sufficient to compensate for this loss. Most important among these adaptations is an impermeable integument (exoskeleton) that encases the body and impedes the evaporative loss of water from the body surface. For example, a drop of water the size of a house dust mite's water pool ($< 10 \mu\text{g}$) would evaporate in seconds in an atmosphere at 75% relative humidity (RH). By contrast active dust mites can survive 24 h or longer and the quiescent protonymphal life stage can survive for months at 0% RH because of the impermeable exoskeleton and minimal loss associated with body processes (excretion, reproduction, feeding, etc.). At higher humidities such as 75% (25°C) the mites reproduce rapidly when food is available. An impermeable integument and reduced water loss by other avenues coupled with a remarkable adaptation for obtaining water from unsaturated air allow them to maintain water balance and to survive.

Because of their role in house dust mite allergy, the water balance physiolo-

ogy of house dust mites and its ecological implications are of particular interest and have been extensively studied. The purpose of this paper is to review what is known about the water requirements and water balance physiology for the common species of house dust mites, DF, DP and EM.

Major source of water

Generally, terrestrial arthropods obtain water by drinking it, ingesting it with moist food, passively absorbing it from unsaturated ambient air, and as a product of metabolism. For most, direct drinking, sucking plant juices and/or ingestion of plant material with high water contents (e.g. leaves) are the usual sources of water. Relative to their total water requirements, house dust mites obtain only small amounts of water by the usual routes; these include imbibition (if free water is available), ingestion of moist food, as a product of the oxidation of organic molecules and by passive absorption from unsaturated air. Liquid water is usually not available for imbibition. The mites have low metabolic rates and oxidative water does not significantly contribute to the maintenance of water balance (Arlan, 1975a). Water gained by passive sorption and ingestion of moist food contributes little to the total water requirements. Instead, their primary source of water is water vapor that is actively extracted from unsaturated air (Arlan and Wharton, 1974; Arlan, 1975b, 1977). This is the reason RH is so important to the occurrence and prevalence of these mites. House dust mites have a system (adaptation) for extracting water from unsaturated air to replenish their body water. It is an energy-requiring active mechanism in which water is moved against a chemical gradient (potential) into the body water pool that is at $0.99 a_w$. At least three other mite species, *Acarus siro*, *Tyrophagus putrescentiae* and *Laelaps echidnina*, and several tick species possess similar adaptations (Knülle, 1965, 1967; Devine, 1969; Cutcher, 1973; Devine and Wharton, 1973). The mechanism is still poorly understood for all mites and ticks. It is this adaptation coupled with adaptations that minimize water loss that allows these mites to thrive in environments where there is usually no liquid water. Enough water can be gained from unsaturated air to compensate for water loss by all avenues.

Avenues of water loss from the body

Water is lost from arthropods by diffusion from permeable surfaces (respiratory and general body), by secretions of digestive, reproductive and defensive fluids, and during oviposition, defecation and excretion. The primary avenues of water loss are evaporation from the general body surfaces and during ventilation of moist air. Unlike most terrestrial insects and mites, dust mites lack an organized respiratory system and associated opening. Therefore, little water is lost by ventilation. Most water is lost by dust mites during

egg production, by evaporation (transpiration) from the general body surface, with body secretions and through defecation/excretion.

Fresh weight and water content

Fresh weights of standardized *Dermatophagoides farinae* (DF) females held at 75% RH (25°C) range from 8–13 µg (Arlian and Wharton, 1974; Arlian and Veselica, 1981b). Data for specific studies are given in Table 1. Similarly, the standardized fresh weights of DP females are about half of that for DF (Table 1) (Arlian, 1975b). EM females are about 2/3 the weight of DP females. Males of each species are much smaller than females. The normal water contents of DF, DP and EM females and males are 71–76% by weight. However, the weights and water contents of these mites vary depending upon the availability of water (RH) and the condition and physiological activities of the mites (Arlian and Wharton, 1974; Arlian 1975b; Arlian and Veselica, 1981b, 1982). For example, in one study the fresh weights of 16 groups of DF ($n=323$) taken from different cultures ranged between 7.9 ± 0.32 and 13.2 ± 0.4 µg (Arlian and Veselica, 1981b). Likewise, in two other studies the mean water masses of different groups of DF also taken from different cultures ranged from 5.82 ± 0.65 to 7.56 ± 0.78 µg ($n=113$) (Arlian and Veselica, 1982) and 8.5 ± 0.57 to 10.8 ± 0.98 µg ($n=52$) (Arlian and Wharton, 1974). Presumably, the water contents (as percent of body weight) of the larvae, protonymphs and tritonymphs are similar to the adults.

Ingestion of water with food and effect of RH on feeding and allergen production

Relative humidity, water balance condition and water content of food may influence or induce feeding by mites. For example, in studies on hematopha-

TABLE 1

Fresh weights and water masses of fasting *D. farinae* (DF), *D. pteronyssinus* (DP) and *E. maynei* (EM)^a

Species	Sex	Fresh weight (µg)	Dry weight (µg)	Water mass (µg)	Water mass (%)
DF	F	10.7±2.3	3.1±0.6	7.6	71
	F	13.0±0.5	3.3±0.2	9.7	75
	M	4.1±1.0	1.0±0.3	3.1	75
DP	F	5.8±0.2	1.5±0.3	4.3	74
	M	3.5±0.2	1.0±0.1	2.5	72
EM	F	1.9±0.4	0.5±0.2	1.4	76
	M	0.6±0.2	0.2±0.1	0.4	73

^aData from Arlian and Wharton (1974), Arlian (1975b), Arlian and Veselica (1981b, 1982) and Arlian unpublished.

gous or plant-feeding mites it was found that feeding was induced when the mites were subjected to dehydrating conditions (Wharton and Cross, 1957; Cross and Wharton, 1964). In these cases, imbibition of blood or plant fluids replaced water that was being lost. As a consequence of increased feeding and fluid intake, there was also an associated increase in nutrient uptake. Plant-feeding mites which were induced to feed more at lower RHs also produced more eggs (Rodriguez, 1954; Boudreaux, 1958). Therefore, there can be an important relationship between fecundity and feeding to maintain water balance.

Dust mites in contrast to hematophagous and plant-feeding mites feed on material that is predominantly biomass and contains little water. The food that dust mites consume equilibrates with the moisture content of the air around it. Therefore, the moisture content of the food dust mites eat is proportional to the ambient RH in which the food is equilibrated. Then, the quantity of water obtained by feeding mites is proportional to the quantity of food consumed and its water content (Arlian, 1977).

Arlian (1977) found that feeding rate and water intake with food by DF and DP was directly influenced by ambient RH (Table 2). At 85% RH or greater, mites consumed a quantity of moist food per day that was greater than 42% of their body weight. In contrast, food consumption at 75% RH was only 8.4 and 10.3% of body weights for DF and DP, respectively, a significant reduction from that consumed at 85% RH (Table 2). Heavy fecal accumulation that was proportional to the feeding rate was observed on and around the food for mites feeding at these high RHs at or above 75%. Mites held at RHs below the critical equilibrium humidity (CEH) fed sparingly and produced little fecal material. Likewise, water gained as a result of feeding amounted to

TABLE 2

Feeding rates and water consumed by DF and DP when fed on yeast equilibrated at specific RHs^a

RH	Food consumed/day/mite				Water obtained (μg)	
	DF		DP		DF	DP
	(μg)	% of body wt.	(μg)	% of body wt.		
22.5	0.17(0.16)	1.3	0.05(0.05)	0.9	0.01	0.003
65.0	0.48(0.42)	3.7	0.28(0.25)	4.8	0.06	0.035
75.0	1.08(0.92)	8.4	0.60(0.51)	10.3	0.16	0.088
80.0	3.61(3.04)	28.0			0.57	
85.0	5.52(4.57)	42.8	2.95(2.44)	50.9	0.95	0.510
95.0	7.60(6.05)	58.9			1.55	

^aData from Arlian (1977).

Between parentheses: dry weight of food consumed.

only 4–16% of total water gain at 75–85% RH (Table 3). Water gained as a result of feeding for mites held below 75% RH amounted to less than 5% of the total water requirement to maintain water balance. Therefore, in terms of maintaining water balance, particularly under dehydrating conditions, water gained by feeding was insignificant.

The high feeding rates observed at high RHs have significant implications. Normally, it is not practical to reduce RH in a home to a level that will kill mites (e.g. from 85% RH to 55% RH). However, with the use of dehumidifiers and air conditioners it is practical to reduce indoor RH by 10–15% (e.g. 85% down to 75% RH). Because of the influence of RH on feeding rate, a 10–15% reduction can have a dramatic effect on the rate in which allergen is produced. First, the higher feeding rates observed at higher RHs result in production of more fecal pellets and thus more allergen of fecal origin at high RH compared to lower RHs. A reduction of RH from 85 to 75% reduced feeding by 80% with a concurrent reduction in fecal production for both DF and DP (Table 2). Secondly, with reduced feeding there is also reduced nutrient intake. Presumably there was a concomitant reduction in egg production as a result of the reduced nutrient intake. Therefore, lowering the RH in homes, even if it is not below the CEH, may have a beneficial effect in reducing fecundity and mite population size and therefore mite antigen levels. Egg production by DF, DP and EM at different humidities has not been studied but in view of this relationship it would be of interest.

Critical equilibrium humidity and survival

Because metabolic rates are low and oxidation of biomass is insignificant, weight change in fasting dust mites (no drink or food) is a good measure of

TABLE 3

Water gain by DF females when fed on bakers' yeast equilibrated at specific RHs and by sorption from unsaturated air (25°C)^a

RH (%)	Water gain		
	Sorption ($\mu\text{g}/\text{h}$)	Feeding ($\mu\text{g}/\text{h}$)	Total ($\mu\text{g}/\text{h}$)
22.5	0.007	0.0004 (5.3)	0.008
65	0.058	0.0025 (4.2)	0.060
75	0.166	0.0070 (4.1)	0.173
80	0.187	0.0240(11.4)	0.211
85	0.212	0.0400(15.9)	0.252
95	0.261	0.0650(19.9)	0.326

^aData from Arlian (1977).

Between parentheses: % of total water uptake.

net loss or gain of water from the atmosphere. Thus, the critical equilibrium humidity for DF and DP has been determined by simple gravimetric techniques (Larson, 1969; Arlian, 1975b). Mites were exposed to dry air (0% RH) where no active and passive sorption was possible. The mites slowly dehydrated which was evident by a reduction of body weight and collapse of the body (Fig. 1). The partially dehydrated mites were individually weighed and then exposed to a graded series of water vapor activities. After a specific time interval (usually 24 h), the mites held at each RH were individually weighed again. The mean weight changes for each group of mites held at specific RHs were plotted against the RH. The lowest RH at which no weight change occurred (gain or loss) was the CEH. Mites lost additional weight (water) in proportion to the RH when held at humidities that were below the CEH. A weight gain occurred for mites held at RHs above the CEH. Under hydrating conditions the partially dehydrated mites eventually fully hydrated and came to an equilibrium weight (constant weight) (Fig. 1).

Using this gravimetric technique, the CEHs for fasting DP and DF were determined to be 73% and 70% RH, respectively, at 25°C (Larson, 1969; Arlian, 1975b). The CEH is influenced by temperature. For example, fasting dehydrated DF can gain water at humidities between 55 and 75% depending on the temperature (Table 4) (Arlian and Veselica, 1981a,b). This temperature relationship coupled with the fact that feeding mites do gain small amounts of water with food explain why active mites are often found in environments where RH is a little below 70%. The CEH for EM has not been determined, but it is less than 75% RH since this species can be cultured at 75% RH (25°C).

Adult mites gradually dehydrate and die when held at humidities below the CEH. Survival time under dehydrating conditions is proportional to the temperature and RH (Table 5) (Arlian, 1975b; Brandt and Arlian, 1976). Males dehydrate faster and die sooner than females when held at similar dehydrating RHs. Only half (LT_{50}) of DP females assayed survived 2.1 to 3.2 days when held at 40 or 50% RH and 28–34°C. Likewise, LT_{50} for males held at the same conditions was only 1.8 to 3.4 days. The LT_{50} values for DF females and males are 2.1 to 3.2 and 1.3 to 2.1 days, respectively, at 40 or 50% RH, 28–34°C. However, in these conditions some males and females were more resistant to dehydration and survived 6–10 days and 4–6 days for DF and DP, respectively.

The water content of dehydrating DF females has been measured just prior to death (Arlian and Wharton, 1974). The normal water content may be reduced by at least 52% (59% of fresh weight) without lethal effects. Similar studies have not been conducted with DP or EM. However, DP survives at least a 17% loss in body water content (Arlian, 1975b).

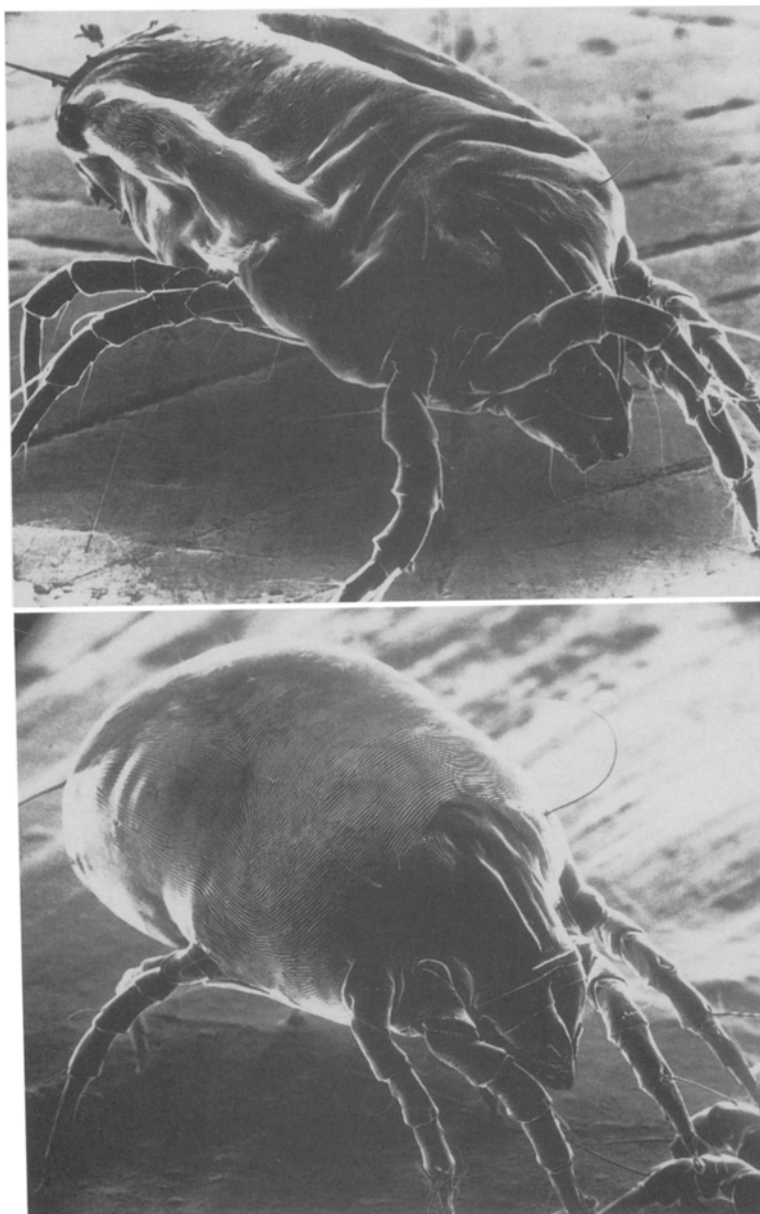


Fig. 1. (Top) Dehydrated *Dermatophagoides farinae* female. Mite was held for 16 h at 0% RH. (Bottom) Rehydrated *D. farinae* female. Mite was dehydrated for 16 h at 0% RH, then held for 18 h in water vapor above 75% RH (Arlian, 1976; with permission of Marcel Dekker, Inc., NY).

TABLE 4

Relative humidity (RH) at which pre-desiccated *D. farinae* females gained or lost water mass after a 24-h exposure at specific temperatures^a

Temp. (°C)	Lost water (% RH)	Gained water (% RH)
15	45	55
25	55	65
30	55	65
35	65	75

^aData from Arlian and Veselica (1981a,b).

TABLE 5

Time (days) required to kill 50% (LT₅₀) and 100% (LT₁₀₀) of test populations of DF and DP females when held at specific RHs and temperatures^a

Temp. (°C)	Species	LT ₅₀		LT ₁₀₀	
		40%RH	50%RH	40%RH	50%RH
25	DF	3.66	3.98	11	11
28	DF	2.65	3.19	8	8
	DP		3.24		10
31	DF	2.31	2.61	6	7
	DP		2.93		8
34	DF	2.05	2.26	5	6
	DP	2.07	2.19	6	6

^aData from Arlian (1975b) and Brandt and Arlian (1976).

Survival during dry periods

Many studies show that the density of mites in homes in humid temperate geographical areas such as Ohio fluctuates sharply with seasonal variations of indoor and outdoor RH (Arlian et al., 1982, 1983; Arlian, 1989)¹. High mite levels occur during the humid summer months (July to October). During this peak period, the number of live mites/g of dust greatly exceeds the number of dead mites in dust. During the heating season (December–April) when RH is low, mite density drops by 80% or more. Few or even no living mites can be found in the dust samples collected by vacuum cleaners during these dry periods. Active mites die from dehydration and little or no breeding occurs because RH is below the CEH for extended periods. Similar less-pronounced seasonal cycles that parallel seasonal changes in RH occur in warmer southern parts of the U.S. In these warmer humid climates more live mites

¹Leupen and Varekamp, 1966; Spieksma and Spieksma-Boezeman, 1967; Domrow, 1970; van Bronswijk and Sinha, 1971; Spieksma et al., 1971; van Bronswijk, 1973; Dusbábek, 1975; Hughes, 1976; Furumizo, 1978; Lang and Mulla, 1978; Lustgraaf, 1978; Murray and Zuk, 1979; Arlian et al., 1982, 1983; Carswell et al., 1982.

occur in homes during the winter months than in northern climates and peak mite periods exist for longer periods of time (June to December) (Arlian, 1989). However, significant numbers of active mites may occur year-round in these geographical areas.

In dry climates (outdoor RH below 30%) such as Arizona, Colorado, Texas, New Mexico and Southern California, use of swamp coolers during the hot summer months, may raise indoor RH sufficiently in some homes so that breeding mite populations occur (Arlian, unpublished). Also, few if any active mites are found in these homes when swamp coolers are not in use (heating season).

In temperate climates, indoor RH may be less than 50% for several months during the heating season. These dry periods are sufficiently long that no active life stage can survive. In spite of this, mite populations persist in homes from year to year. Apparently a desiccation-resistant quiescent protonymph is formed during dry periods of the year (Arlian et al., 1983). This life stage provides the major source of breeding mites for population growth when conditions are favorable. The normal life cycles (from egg to adult) for DF and DP are temperature dependent and require 18–35 days to complete at 20–30°C (Table 6) (Furumizo, 1975; Andersen, 1988; Hart and Fain, 1988; Arlian et al., 1990). Following copulation, females deposit eggs. The active stages in sequence which follow are larvae, protonymphs, tritonymphs and adults (Fig. 2). An active larva emerges from the egg, feeds for a few days and then eventually becomes quiescent (motionless). Metamorphosis occurs inside the exoskeleton of the quiescent larva and a pharate protonymph (motionless) develops. When the development is complete the protonymph emerges from the larval exoskeleton. Again, following a feeding period the active protonymph becomes quiescent, a pharate tritonymph develops inside the quiescent protonymphal exoskeleton and then an active tritonymph emerges and feeds. This metamorphosis is repeated for the quiescent tritonymphs and pharate adults and eventually the adults emerge.

The durations of the quiescent/pharate periods between each active instar

TABLE 6

Developmental times of *D. pteronyssinus*^a

Temp. °C	Sex	<i>n</i>	Days ^b $\bar{x} \pm \text{s.d.}$
16	♂, ♀	24	122.8 ± 14.5
23	♂, ♀	43	34.0 ± 5.9
30	♂, ♀	62	19.3 ± 2.5
35	♂, ♀	51	15.0 ± 2.0

^aData from Arlian et al. (1990).

^begg to adult at 75% RH.

are normally shorter than the durations of each preceding active period and short relative to the duration of the entire life cycle (Fig. 2). The three quiescent/pharate periods are also about equal in length (Arlan et al., 1990). At 23°C the durations of the quiescent larvae, protonymphs and tritonymphs are 4.0 ± 1.4 , 3.2 ± 1.0 and 3.4 ± 1.5 days, respectively, for DP (Arlan et al., 1990). Likewise, the durations of the quiescent periods following the active larvae, protonymphs, and tritonymphs for DF are 2.8, 2.7, and 3.3 days, respectively, at 22.2–28.8°C (Furumizo, 1975). However, under some conditions, slow development or diapause of the quiescent protonymph may occur so it may last for months before metamorphosis of the pharate tritonymph and emergence (Ellingsen, 1974, 1975, 1978; Arlian et al., 1983). Ellingsen (1974, 1975) has reported that the quiescent protonymphs of DF last 143.8 days at 15.6°C. Uninterrupted development of DP takes only 123 days for the entire life cycle at this temperature (Table 6) (Arlan et al., 1990).

The factors that induce formation of the prolonged protonymphal stage are not known but it is probably induced by multiple independent or interacting factors. The prolonged quiescent protonymphal stage is prevalent in mature laboratory cultures maintained at 75% RH. In cultures they can be observed firmly glued to the substrate. Interestingly, in DP studies in which development of an individual was followed from egg to adult under optimal conditions (food and RH) this stage did not form (Arlan et al., 1990). Therefore, RH is not the only inducing factor.

Quiescent protonymphs have a significantly reduced metabolic rate compared to active protonymphs and they are extremely resistant to desiccation (Ellingsen, 1975, 1978). For example, active protonymphs consume 28.5 times more O_2/h than quiescent protonymphs (Ellingsen, 1978). Likewise,

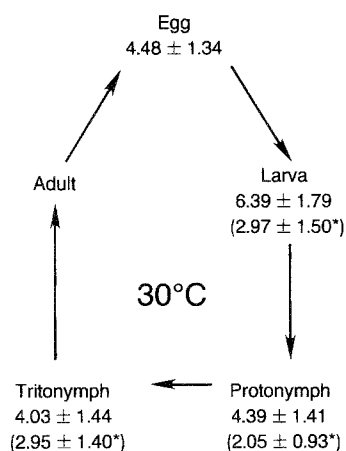


Fig. 2. Life cycle of *D. pteronyssinus* at 30°C and 75% RH (duration in days). *Duration of quiescent period of each life stage.

the half-life of body water exchange for DF quiescent protonymphs is 3833 h (159.7 days) compared to only 20.4 h for active protonymphs and 27.7 h for adult females at 75% RH, 25°C (Arlian and Wharton, 1974; Ellingsen, 1975). Thus, the prolonged quiescent protonymph is desiccation-resistant and well-adapted for survival during extended dry periods.

In their natural environment, protonymphs may become quiescent when the ambient RH is below the CEH. It is likely that quiescent protonymphs survive these dry periods and serve as the source of breeding mites when the RH in homes is optimal. The diapausing quiescent protonymphs which are firmly glued to the substrate are not removed when vacuuming carpets and other surfaces during the winter. Analyses of the life stage composition of mites in dust samples collected monthly over a 2-year period from homes in Ohio support this hypothesis (Arlian et al., 1983). Regardless of the mite density, during most times of the year adults were the most abundant life stage. However, during early spring when the population was low but had started to increase, there was a surge in tritonymph density so that tritonymphs were the most numerous life stage. Presumably these tritonymphs emerged from the quiescent protonymphs (glued to the substrate) as the RH in the homes became more favorable. The surge in tritonymph density was followed by an increased abundance of adults that emerged from the tritonymphs. Subsequently, an increase in the number of larvae was observed as eggs produced by females began to hatch.

Relative humidity in the microhabitat

Many investigations have monitored ambient RH and temperatures in homes in parallel with determining mite prevalence. Rarely have the climatic measurements been taken in the microhabitat where mites live and breed. However, significant differences in RH and temperature between ambient air and air in the microhabitat may exist in some locations where mites live. This is particularly true for floors. Surface temperatures of floors over cool basements or crawl spaces and concrete slab floors over earth, which is normally about 13°C, are lower than ambient temperatures. Lower floor temperatures (carpet) can increase the RH (degree of vapor saturation) of room air as it is circulated over these cool surfaces and is cooled (Fig. 3, Table 7). In a study by Arlian et al. (unpublished data) the temperature and RH in carpets and in the room air above it were monitored in five homes with high mite levels. It was found that the RH in the carpet was $9.6 \pm 3.4\%$ higher and temperature was $3.7 \pm 2^\circ\text{C}$ lower than for ambient air 1–2 meters above the floor. Because of this temperature relationship, the RH in a carpet may be sufficient to support mites while ambient RH is not. For example, ambient room air at 27°C and 56% saturated with water vapor (56% RH) becomes 79% saturated (79% RH) when cooled to 20°C (Table 7, Fig. 3). In the laboratory, mites

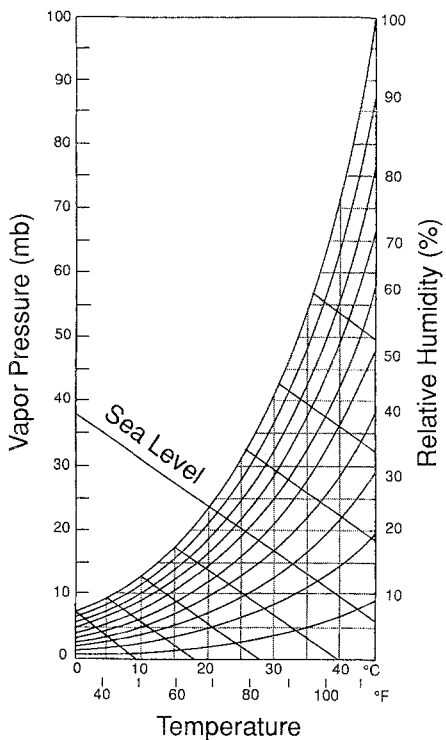


Fig. 3. The relationship of temperature, relative humidity and vapor pressure.

TABLE 7

Relationship between temperature, relative humidity and absolute water in air

Temperature		Relative humidity (%)					
°F	°C	16	24	31	45	57	100
86	30	16	24	31	45	57	100
80	27	17	27	37	56	70	
75	24	21	34	45	66	82	
68	20	28	42	54	79	100	
65	18	33	50	63	89		
61	16	36	53	69	100		
55	13	49	69	85			
50	10	52	77	100			
43	6	67	100				
32	0	100					
Water vapor (g H ₂ O/m ³ air)		4.85	7.27	9.41	13.65	17.31	30.4

can maintain water balance and can be cultured at 20°C and 79% RH. But, mites die and cannot be cultured at 27°C and 56% RH. However, the absolute amount of water in air is the same for both sets of temperature and RH conditions (Table 7). This clearly demonstrates that maintenance of water balance and survival of mites is not a function of the absolute amount of water in air as some have suggested. Rather, sorption and transpiration fluxes for water by mites are driven by the chemical potential of water and this is related to temperature as described by an Arrhenius function (Arlian and Veselica, 1982) as follows:

$$k = A \exp(-E_a/RT) \quad (1)$$

where k is the rate constant for the water flux, E_a is the activation energy, R is the gas constant, and T is absolute temperature.

Mechanism for active uptake of water from ambient air

The active uptake mechanism has been studied for DF. Presumably the related mites DP and EM have a similar mechanism but this remains to be confirmed. Active uptake is thought to be associated with the secretion of a hyperosmotic solution by the paired supracoxal glands (Wharton and Furumizo, 1977; Wharton and Richards, 1978; Wharton et al., 1979; Wharton, 1985). These glands are located internally just above and posterior to the dorsal coxae of legs I. The fine structure of these glands is typical of secretory tissue and exhibits infoldings of the cell membranes and concentrations of mitochondria which are characteristic of such tissue (Brody and Wharton, 1970; Brody et al., 1972, 1976). Ducts carry the glandular secretions to openings located just above legs I. A trough termed the podocephalic canal leads from this opening, across the base of the palps and into the preoral cavity located beneath the chelicerae. The coxal glands produce and secrete a hygroscopic fluid that flows from the gland's opening via the podocephalic canal into the preoral cavity. The hygroscopic fluid absorbs water from humid air as it flows. The water-enriched secretion is pumped by the pharyngeal pump, from the prebuccal cavity through the pharynx and esophagus to the gut. Water and salts are passed from the gut into the hemolymph. The supracoxal glands which are bathed by the hemolymph absorb and recycle the salts. At humidities below the CEH, this secretion dries and blocks the openings of the glands. Low-energy laser-generated x-ray scans of the plugs show they contain sodium and potassium chloride and other materials. When mites are held at humidities above the CEH the salt plugs will deliquesce as water is absorbed from air and the flow of brine is resumed. Apparently, the brine contains detergent-like material to reduce surface tension and keep the solution flowing.

Kinetics of water exchange

As previously noted, house dust mites constantly exchange body water with the water vapor in their environment by absorption and evaporation. These exchanges are key to their survival. The kinetics for these exchanges between unsaturated air and the mites' body water pool for DF and DP have been investigated by following the movements of tritiated water (Arlian and Wharton, 1974; Arlian, 1975a; Arlian and Veselica, 1981b, 1982). A similar technique has been used to determine the water fluxes and the appropriate mathematical models that describe the water exchange kinetics for a few other mites, ticks and insects. For background and complete details on this topic, I refer the reader to reviews and other papers by Knülle (1965, 1967, 1984), Wharton and Devine (1968), Devine (1969, 1977, 1982), Wharton and Arlian (1972), Devine and Wharton (1973), Rudolph and Knülle (1974, 1978, 1982), Arlian and Eckstrand (1975), Wharton (1978), Wharton and Richards (1978), Arlian (1979), Arlian and Staiger (1979), Arlian and Veselica (1979), Wharton et al. (1979), Toolson (1980), and Needham and Teel (1991). Only a brief review of the kinetics of water exchange for DF and DP is given here.

These studies of the kinetics of water exchange between the dust mites' water pool and unsaturated air have utilized fasting mites so that gain and loss of water associated with feeding, excretion and defecation are negligible. Thus, the gain and loss of water are limited to active and passive sorption (influx) and transpiration (efflux). The one-way flux of water from the mites' water pool to the surrounding air has been termed transpiration. This flux includes direct evaporation through the cuticle as well as evaporation of secretions or other body products. Likewise the one-way flux of water from the environment into the mites' water pool has been termed sorption. Except at 0% RH, the two water fluxes occur independently and simultaneously. Since there is no water in the environment at 0% RH only the transpiration flux occurs.

A net change in total body water mass results when the total water from one flux exceeds the other for a specific period of time. When the transpired amount of water exceeds that which is sorbed, there is a net loss in body water. A net gain results when sorption exceeds transpiration. Water mass remains constant when the fluxes are equal. It should also be kept in mind that highly variable transpiration and sorption fluxes can result in the same net water mass change (either a gain, a loss, or no change). That is, water turnover rate may vary but the net change in body water mass may not.

The driving force for the uptake of water from the unsaturated air is the number of water molecules impinging on the uptake surface (Wharton and Arlian, 1972; Arlian and Wharton, 1974; Arlian and Veselica, 1979). Since at a given RH the driving force for water uptake is constant, sorption will occur at a constant rate in time and follow a zero-order kinetic relationship. The

number of water molecules impinging on the exchange surface per unit of time is directly proportional to the RH. Therefore, under constant temperature and pressure conditions and no change in the exchange surface or mechanism, the active and passive uptakes of water at any RH above 0% are directly proportional to the RH. Mites sorb more water per increment of time at a higher RH than at a lower one. As a consequence, pre-desiccated mites rehydrate faster at 95% RH than at 70% RH.

The driving force for transpiration from a dust mites' body is the concentration of water in the body (Arlian and Veselica, 1979). The rate constant for water loss is determined by the permeability of the exchange surface. Therefore, under constant temperature and pressure conditions and no change in permeability of the cuticle, transpiration rate constants are independent of ambient RH (Arlian and Wharton, 1974). That is, the rate constants for transpiration at any RH will be the same. Because the body water pool decreases in size, the actual amount of water transpired per unit of time decreases in time according to a first-order relationship (Arlian and Wharton, 1974).

It is important to understand that mites dehydrate faster at a lower RH than a higher one (e.g. 25% RH compared to 55%) because the amount of water sorbed per unit of time is less at the lower RH than at the higher one. Since an equilibrium water mass is maintained at RHs above the CEH and sorption is proportional to the RH, in actuality transpiration will also be proportional to the RH to compensate for the increased water gain by sorption. The rate constants for transpiration for DF and DP were found to be proportional to the RH at humidities above the CEH (Table 8) (Arlian and Wharton, 1974). In contrast, rate constants for transpiration are independent of RH at humidities below the CEH (Arlian and Wharton, 1974).

Transpiration fluxes were determined by first loading the mites' water pool with tritiated water (HTO) and then following its disappearance in time when the mites were held in environments that served as large sinks to trap the transpired HTO. Actual rates of water sorption at any RH must be calculated using rate constants for transpiration (tritium loss) and the virtual equilib-

TABLE 8

Transpiration rate constants ($-k_T$) and water sorbed for fasting DF females held in different RHs^a

RH	$-k_T$ (h^{-1})	Water mass sorbed ^b ($\mu g/h$)
75	0.0221	0.215
85	0.0235	0.228
92.5	0.0249	0.242
100	0.0262	0.254

^aData from Arlian and Wharton (1974).

^bAssumes an equilibrium water mass (m_∞) of 9.71 μg . Water mass sorbed ($\mu g/h$) = $k_T(m_\infty)$.

rium water mass (described later). The kinetic models that describe transpiration and sorption for house dust mites follow.

When female mites containing HTO are exposed to air with a RH above the CEH, HTO will disappear according to the first order relationship

$$\ln T_t = \ln T_0 - k_T t \quad (2)$$

where T_t is the tritium quantity in the water pool at any time t , T_0 is the initial tritium content at time 0, and $-k_T$ is the rate constant for loss of tritium (rate constant for transpiration). Rate constants for transpiration ($-k_T$) for DF females ranged from 0.0221 to 0.0262 for relative humidities between 75 and 100% (Table 8). No net change in body water mass will occur when the mites are held at RHs above the CEH because the amount of water transpired (efflux) is replaced by an equal amount of water sorbed (influx). The mites maintain an equilibrium water mass (m_∞). Therefore, the amount of water transpired (m_T) for a time t at equilibrium can be calculated as follows:

$$m_T = m_\infty (-k_T t) \quad (3)$$

where m_∞ is the equilibrium water mass and $-k_T$ is the rate constant for transpiration (water loss). For example, with a $-k_T$ of 0.0221 h⁻¹ and an equilibrium water mass of 9.11 μg, DF transpires 0.215 μg of water h⁻¹ at 75% RH (Table 8) (Arlian and Wharton, 1974). Since equilibrium is maintained, an equal amount of water is sorbed from unsaturated air at this RH.

When DF or DP containing tritiated water were exposed to RHs below the CEH, they lost weight due to a net water loss and tritium content loss. That is, the net quantity of water lost by transpiration was not compensated for by sorption (passive and active combined). A semi log plot of HTO content or water mass versus time gave a curve with gradually decreasing slope (decreasing k value with time). Such a curve suggested that when the mites dehydrated, water was lost from two compartments at two different rates, one was fast and one was slow. The loss of HTO from the mite is defined by

$$T_t = T'_0 \exp(-k'_T t) + T''_0 \exp(-k''_T t) \quad (4)$$

where k'_T and k''_T are the rate constants for water loss from the fast and slow compartments, respectively, T_t is the total ³H in the animal, T'_t and T''_t are the ³H at time t in compartments ' and ', respectively, at time t , and T'_0 and T''_0 are the initial ³H contents of each compartment. Under dehydrating conditions above 0% RH mites show a net water loss in time; however, as the mite dehydrates the water mass curve will asymptotically approach an equilibrium value (m_∞). This value is termed the virtual equilibrium value because the mite dies from dehydration before it is actually achieved. The water content of a dehydrating mite is described by:

$$(m_t - m_\infty) = (m'_0 - m'_\infty)\exp(-k'_T t) + (m''_0 - m''_\infty)\exp(-k''_T t) \quad (5)$$

where m'_0 and m''_0 are the original water masses of the fast and slow compartments, m_t is the mite's water content at any time t , $(m_t - m_\infty)$ and $(m_0 - m_\infty)$ are the exchangeable water contents at the initial and any time t , respectively, and $-k'$ and $-k''$ are the rate constants for the change in water contents of the fast and slow compartments, respectively.

A virtual equilibrium water mass is approached because the amount of water being transpired decreases (first-order kinetics) as the water mass decreases while the amount of water sorbed by diffusion is constant. At some theoretical point water passively sorbed and water transpired during the same time interval become equal and an equilibrium water mass (m_∞) is maintained. The mite dies from dehydration before m_∞ is actually achieved. The virtual equilibrium mass (m_∞) can be determined by curve stripping and extrapolation using a least-squares regression analysis of equation 5. Once m_t , m_0 , $-k'_T$ and $-k''_T$ are known, m'_∞ and m''_∞ can be calculated by rearranging equation 5. Sorption rate (m_s) can then be calculated as described:

$$m_s = -k'_T m'_\infty + -k''_T m''_\infty \quad (6)$$

As one can see, determination of water mass sorbed at dehydrating conditions is a complex process.

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