Temperature and Humidity Effects on Off-Host Survival of the Northern Fowl Mite (Acari: Macronyssidae) and the Chicken Body Louse (Phthiraptera: Menoponidae)

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ABSTRACT Off-host survival of the northern fowl mite, *Ornithonyssus sylviarum* (Canestrini & Fanzago) (Acari: Macronyssidae), and the chicken body louse, *Menacanthus stramineus* (Nitzsch) (Phthiraptera: Menoponidae), was studied at 12 combinations of temperature (15, 21, 27, and 33°C) and humidity (31, 65, and 85% RH). Mite protonymphs and louse third instars survived longer on average than the respective adult stages. Higher temperatures significantly reduced survival of adult and immature stages of both ectoparasites, whereas relative humidity had significant effects on *O. sylviarum* (especially protonymphs) but not *M. stramineus*. The LT₅₀ values for adult northern fowl mites ranged from 1.9 (at 33°C, 31%RH) to 8.3 d (at 15°C, 85%RH), LT₅₀ values for mite protonymphs ranged from 2.0 (at 33°C, 31%RH) to 18.1 d (at 15°C, 85%RH), LT₅₀ values for adult lice ranged from 1.2 (at 33°C, 31%RH) to 1.7 d (at 15°C, 65%RH), and LT₅₀ values for nymphal lice ranged from 1.2 (at 33°C, 65%RH) to 3.3 d (at 21°C, 31%RH). Maximum survival of the northern fowl mite was up to 35 d for adults and 29 d for protonymphs. Maximum survival for the chicken body louse was 3.3 d for adults and 5.8 d for nymphs. The data provide minimum guidelines for leaving poultry houses vacant long enough to allow ectoparasites to die before introduction of subsequent new flocks.

KEY WORDS Ornithonyssus sylviarum, Menacanthus stramineus, survival, temperature, humidity

The Northern fowl mite, *Ornithonyssus sylviarum* (Canestrini & Fanzago) (Acari: Macronyssidae), is the most economically important ectoparasite of commercial poultry in the United States (DeVaney 1978, Axtell and Arends 1990, Hinkle and Hickle 1999). The chicken body louse, *Menacanthus stramineus* (Nitzsch) (Phthiraptera: Menoponidae), is also an important and damaging ectoparasite of caged layers (Derylo 1974, DeVaney 1976). Both organisms complete their entire life cycle on the host.

The northern fowl mite has two blood-feeding stages: protonymph and adult (Sikes and Chamberlain 1954). Adult females lay an average of two to three eggs within 48 h of a bloodmeal, and they have a generation time of as little as 5–12 d (Sikes and Chamberlain 1954), leading to very high mite loads on commercial hens. The northern fowl mite presumably spreads by direct host contact, has been observed to disperse from hen-to-hen by walking on cage wires across empty cages (Mullens et al. 2001), or potentially can be transported within or between houses by other vertebrates (Hall and Turner 1976, Miller and Price 1977). Transmission also can occur through movement of contaminated personnel and equipment (egg crates, egg flats, and manure removal equipment) (Kells and Surgeoner 1996), which requires that mites are capable of surviving off the host for periods of time.

A few researchers have examined off-host survival of northern fowl mites under a very limited range of conditions; in general, studies suggest that maximum northern fowl mite survival is 2-4 wk at operating hen house temperatures (21-27°C) (see DeVaney and Beerwinkle 1980). Two studies examined northern fowl mite survival in more detail. Abasa (1969) examined humidity effects on adult northern fowl mite survival at a single temperature (25°C) and observed longer survival at higher humidities. DeVaney and Beerwinkle (1980) followed survival of roughly estimated numbers of mixed age northern fowl mites (50-200 per replication on feathers), at unspecified time intervals, in temperatures ranging from -15 to 49°C with uncontrolled relative humidity and from 0.3 to 38°C in a desiccator (75% RH). Survival was better (up to 57 d at 4°C) at lower temperatures and higher humidities.

The chicken body louse tends not to leave the host body, and it has been conjectured to live <24 h off host (Furman 1962), although to our knowledge that has not been studied. The body louse is dislodged or thrown from hosts at times (B.L.C. and B.A.M., unpublished data). It thus may end up in the environment and on people or equipment, where it might

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persist and later reacquire a host. Three other biting lice [Columbicola columbae columbae (L.), Campanulotes bidentatus compare (Burmeister), and Bonomiella columbae (Emerson)] survived for 3–11 d when kept off-host at room temperature ($20-30^{\circ}$ C) and uncontrolled relative humidity (Rem and Zlotorzycka 1981). The sheep body louse, Bovicola ovis (L.), showed similar survival (5–10 d) at a lower temperature (18– 20° C) (Scott 1952). Under some environmental circumstances, however, off-host survival of biting lice may be much higher. Crawford et al. (2001) documented survival of B. ovis nymphs up to 29 d on unscoured wool at 36.5°C, and they calculated an LT₉₀ value of 24.1 d (with access to wool as possible food) off-host at 25°C.

Caged layer flocks typically are kept through one to two laying cycles of \approx 45 wk of production each (Bell and Weaver 2002). Between flocks, houses are disinfected and left vacant for a short period before new hens are introduced. In California, those vacancy periods often are ≈ 2 wk. Documenting mite and louse survival rates at different temperatures and humidity may provide commercial poultrymen with valuable guidelines for controlling ectoparasites by knowing the vacancy period necessary to eliminate them. To date, no one has tested off-host survival of both adult and immature mites and lice thoroughly and at a full range of representative temperatures and controlled humidities. The following study was performed to characterize the ability of the northern fowl mite and chicken body louse to survive off their host.

Materials and Methods

Temperature and Humidity Control. Twelve individual humidity chambers were created using clear polystyrene plastic containers (15 by 15 by 5 cm) with tight-fitting lids. Temperatures and humidities were selected to cover the expected seasonal range characterizing vacant southern California poultry houses. Three different saturated salt solutions were used to provide an environment with constant relative humidity. The containers contained 100 ml (≈ 0.5 cm in depth) of the saturated solution and provided a relative humidity of 31% (MgCl₂), 65% (NaNO₂), and 85%(KCl) (Winston and Bates 1960). The supersaturated solutions were allowed to cool and then poured into their respective containers. Three containers (one container of each humidity) were placed into each of four constant temperature incubators (15, 21, 27, and 33°C). Temperature stability was ±0.3–1.0°C. Each incubator was maintained at a photoperiod of 12:12 (L:D) h by using a 15-W fluorescent light source. Each container had a screen shelf to hold glass containers with ectoparasites suspended above the solution.

Ectoparasite Stages and Maintenance. Populations of lice and mites were maintained on White Leghorn (Hy-Line W36 strain) hens in caged-layer poultry houses at the University of California Agricultural Experiment Station in Riverside. Ectoparasites were removed periodically as needed for the experiments.

Northern fowl mite populations typically increase for a period on a host, but later decline due to host immune responses (e.g., Matthysse et al. 1974). To generate data on survival that would represent the range of likely off-host movement, mites were removed at selected time periods after infestation. Beaktrimmed hens (normal commercial hens) were infested with ≈ 50 mites and monitored visually at weekly intervals. Mite numbers on hosts were estimated by examining the vent region and scoring the infestation level on a semilogarithmic scale ranging from 0 (no mites) to 7 (>10,000 mites) (Arthur and Axtell 1983). The current study required rather large numbers of mites from an individual hen (to be divided into the different temperature and humidity treatments); thus, obtaining mites from hens very early or very late in infestation was not feasible. Thus, early infestation was characterized by moderate mite populations that were still increasing on their host (mite score 5; 500–1,000 mites). Peak infestation was characterized by mite populations that had reached their highest population levels (mite score: 6–7; 1,000 to >10,000 mites). Late mite infestation was obtained from hens on which mites were on the decline (mite score 5). Although the general trajectories of mite populations on the donor hens were known due to weekly scoring, mites used in the tests were from different individual hens.

When hens were at the designated infestation level, mites were aspirated in a group into glass Pasteur pipettes (14.5 cm in length, 0.5 cm i.d.) and brought back to the laboratory. Ten adult female mites were aspirated into each of a series of individual glass Pasteur pipettes, sealed with clay on one end and cotton on the other end. For each trial (mites from a single hen), five pipettes (50 mites total) were placed in each of the temperature-humidity combinations. Mites were observed under a dissecting microscope, and mortality was recorded every 24 h until all mites were dead (lack of movement even when gently disturbed). Two trials were conducted for mites from early infestation hens, two from peak hens, and two from later infestation hens, i.e., there were six mite populations total.

Protonymphs are the first blood-feeding stage of the northern fowl mite; they and adult mites are the stages that might persist off-host. To obtain protonymphs, adult females were collected from hens with nearpeak infestation levels (score 6-7) and were held in glass Pasteur pipettes and incubated at 30°C and 75% RH for 24 h. Eggs $(n \approx 10)$ laid in that period were transferred using a fine camel's-hair brush from the Pasteur pipettes to each of a series of straight-sided glass vials (12 mm in diameter by 35 mm in length). A double-layer of Kimwipe tissue sealed the plastic top of each vial to prevent mite escape but allow air exchange and easy mite viewing (J. P. Owen, personal communication). Vials were incubated another 24 h at 30°C and 75% RH. The vials were checked for hatch and molt from larva to protonymph (1–2 d; Sikes and Chamberlain 1954). Protonymph ages thus were equivalent and accurate within ≈12–18 h for all treatments. Five vials (50 mites total) were then placed into each of the temperature–humidity combinations, as described above. Vials were checked every 24 h under a dissecting microscope and mortality was recorded until all mites were dead. The process was then repeated using mites from a second hen.

Lice of all life stages, adults and nymphs, were collected by aspiration from hens with heavy infestations of lice from the aforementioned chicken farm. Unlike the mites, a single hen (single louse population) could not vield the numbers of lice needed for all treatment combinations, so lice from multiple hens (usually three to four) were pooled before placement into the treatments. The lice were separated into individual glass Pasteur pipettes (10 cm in length and 0.5 cm in diameter). The long, narrow tip of each pipette was removed, because lice would pack into the tip, preventing adequate observation. The tubes were sealed on one end with clay and with a cotton plug on the other. Two tubes with adults (n = 10 per tube) and two tubes with third instars (n = 10 per tube) were placed in each of the temperature-humidity combinations. At each time checkpoint, lice held at 15°C were allowed to sit at room temperature for 30 min before observation under the dissecting microscope, because they needed to warm up slightly to show movement. The tubes were checked every 2-6 h and mortality (lack of movement) was observed under a dissecting microscope. This process was repeated until all lice were dead. This process was then repeated on a second group of lice.

Statistical Analysis. Using MINITAB release 14 (Ryan et al. 2004), probit analysis was conducted to obtain time until 50 and 95% mortality (LT_{50} and LT_{95}), along with 95% fiducial limits for each treatment. Survival analysis was applied to calculate the estimated median time of survival, by fitting the data to an assumed distribution. The regression with life data analysis models survival as a function of known factors (in this case temperature and humidity and their interaction) and is documented online (http:// www.minitab.com/support/docs/rel14/14helpfiles/ ReliabilityandSurvival/RegressionwithLifeData.pdf). A separate Friedman test (nonparametric equivalent of a two-way analysis of variance) was applied to the six adult mite populations to determine the differences, if any, between the three infestation ages (early, peak, and late). The 12 combinations of temperature and humidity served as blocks. This was followed by pairwise Mann–Whitney U tests to compare median values among populations.

Results

Adult Female Northern Fowl Mites. There was a trend toward longer survival times at lower temperatures and higher relative humidity. The main effects of temperature (humidities pooled) and humidity (temperatures pooled) are presented for all trials pooled in Fig. 1A and B. Within the context of the comprehensive survival analysis, median survival overall at each level of temperature or humidity differed significantly from the others ($F_{\text{temp}} = 257.67$; df = 3, 3,526; P < 0.001; $F_{\text{humidity}} = 82.60$; df = 2, 3526; P < 0.001). The differences between 15 and 21°C, and between 65 and 85% RH, were less substantial than more extreme temperature or humidity differences such as 15 versus 33°C, or 31 versus 85% RH.

In most treatments, a relatively small proportion of adult individuals survived longer, creating a "tail" on each survival curve. This was most evident at 15°C, as shown for late infestation stage populations 5 and 6 (Fig. 2). Ranges of calculated LT_{50} values for the six adult populations were 3.1-8.3 d at 15°C, 3.8-6.8 d at 21°C, 2.3-4.6 d at 27°C, and 1.8-3.8 d at 33°C. The LT₉₅ values were generally 2–3 times the LT_{50} values for each treatment, reflecting the tails of the distributions. The LT₉₅ values were 6.9-25.5 d at 15°C, 6.8-15.4 d at 21°C, 3.6-13.4 d at 27°C, and 3.1-8.2 d at 33°C. The lowest relative humidity (31%) had the lowest LT_{50} and LT_{95} in every population and for every temperature, although differences were not always significant based on overlap of 95% confidence levels (CL). Based on overlap of the 95% CL, LT_{50} and LT_{95} values for the 65 and 85% RH frequently did not differ significantly within a temperature.

Maximum survival at each temperature and humidity combination is listed in Table 1. Maximum survival times for adult mites ranged from 35 d at 15°C and 85% RH to 7 d at 33°C and 31% RH. In the survival analyses, there generally was no significant interaction between temperature and humidity for the adult mites; four of six populations had interaction coefficients <0.031 (P > 0.17).

Data for survival of adult mites from hens that were early, peak or late infestation are presented in Table 2 for 85% RH at the four temperatures; trends were very similar for the other humidities (Chen 2006). When matched pairwise for individual mite populations, the LT_{50} values for the early mite populations were generally higher than corresponding values (the same temperature-humidity combination) for the peak or late populations, but the 95% fiducial limits for individual values did sometimes overlap with those of peak or late populations. The LT_{50} values for early mite populations were higher than those of peak or late populations in 88 of 96 comparisons. This trend was similar for the LT₉₅ values for early mite populations, which were higher than peak or late populations in 89 of 96 comparisons. Trends for maximum survival were similar, but maximum survival particularly of late mite population 6 (Fig. 2) was as high or higher than early infestation mites for some temperature-humidity combinations.

Survival analysis comparisons of the six adult mite populations by infestation level (early, peak, or late) revealed that survival of the two early infestation populations was significantly greater ($Z \ge 9.55$, P = 0.001) than survival of mites from peak and late infestation stages. However, there was no significant difference (Z = 0.19, P = 0.847) between peak and late infestation populations. A Friedman rank test was applied to the LT₅₀, LT₉₅, and maximum survival of each population. Early infestation populations consistently

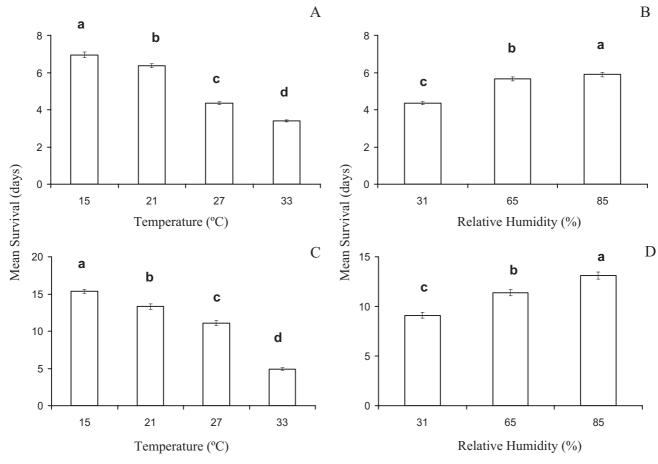


Fig. 1. Main effects of temperature and humidity (trials pooled) on off-host survival of northern fowl mite adult females (A and B) and northern fowl mite protonymphs (C and D). Means and standard errors shown. Within a stage, histograms marked with the same letter are not significantly different (P > 0.05) based on analysis of median survival times (see text).

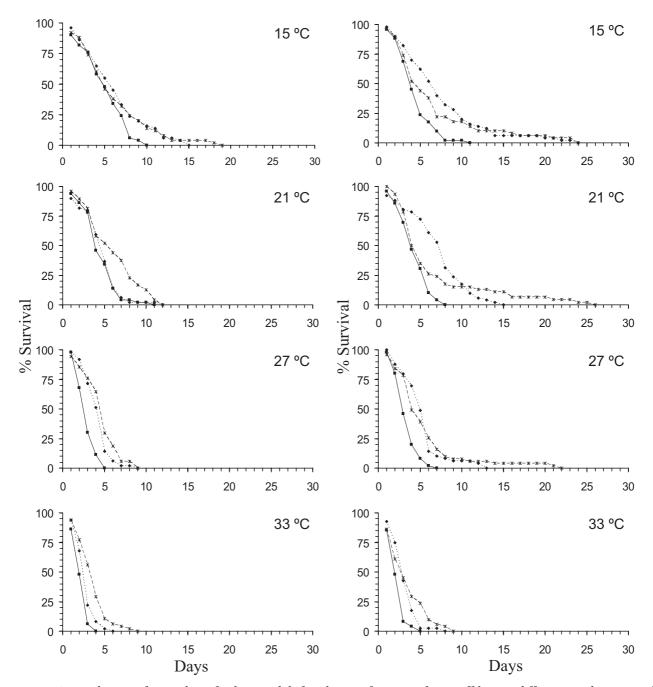
ranked higher, and overall differences among the six populations were evident (adjusted for ties, the LT₅₀ S = 37.64, df = 5, P < 0.001; LT₉₅ S = 42.25, df = 5, P < 0.001; maximum survival S = 35.46, df = 5, P < 0.001). Median survival values of the six mite populations then were compared using the LT₅₀, LT₉₅, or maximum survival in a pairwise manner (Mann–Whitney Utest). Differences were found only for comparisons between populations 1 or 2 (early infestations) versus 3–6 (peak or late populations) (W> 179, P < 0.1). Population 1 differed at the LT₅₀ level from population 3 and from population 5 at the LT₉₅ level. Population 2 differed from populations 3 (W = 187, P = 0.035), 5, and 6 at the LT₅₀ level and from population 5 at the LT₉₅ level.

Protonymph Northern Fowl Mites. As shown in Fig. 1C and D, trends in main effects of temperature and humidity for protonymphs were similar to those seen in adults, except that protonymphs survived about twice as long as adults at the same temperature or humidity. From the comprehensive survival analysis, each median value from the main effect of temperature or humidity was significantly different from the other values in that category ($F_{\text{temp}} = 366.91$; df = 3, 1,119; P = 0.001; $F_{\text{humidity}} = 104.35$; df = 2, 1,119; P = 0.001).

Survival curves for the two groups of protonymphs are presented in Fig. 3. For the protonymph survival analyses, interactions between temperature and humidity were significant for both populations 1 and 2 (coefficient >0.48, P < 0.01). The effect was most easily seen in the relative position of the mortality curve for 65% RH at the different temperatures. At the lowest temperature of 15°C, 65% RH survival was relatively close to survival at 85% RH, whereas at 33°C the difference between 85% and 65% RH was more substantial. Depending on humidity, ranges of calculated LT₅₀ values were 9.3–18.1 d at 15°C, 8.4–17.4 d at 21°C, 4.5–13.6 d at 27°C, and 2.0–8.1 d at 33°C. Ranges of calculated LT₉₅ values were 16.2–29.3 d at 15°C, 12.6–28.5 d at 21°C, 6.6–21.2 d at 27°C, and 3.2–11.7 d at 33°C.

Maximum survival of protonymphs at each temperature and humidity combination is also listed in Table 1. Maximum survival times were 22–29 d at 15°C, 14–28 d at 21°C, 8–28 d at 27°C, and 7–12 d at 33°C.

Adult Chicken Body Louse. Survival of adult lice was substantially less than that of either adult mites or protonymphs for equivalent treatments; mean main effect values for temperature and humidity are shown in Fig. 4A and 4B. As with mites, there was a general trend of higher survival of lice with lower temperature, and the LT_{95} values more clearly distinguished this difference of survival at different temperatures. Ranges of calculated LT_{95} values were 2.1–3.2 d at



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Fig. 2. Survival curves for northern fowl mite adult females as a function of time off-host at different combinations of temperature and relative humidity. Population 5 on left; population 6 on right (each a "late" infestation population from a single hen). Symbols reflect relative humidity as follows: 31% RH (\blacksquare), 65% RH (\blacklozenge), 85% RH (\ast).

Table 1. Maximum survival (days) of northern fowl mites (NFM) and chicken body lice at different temperature-humidity combinations (all trials)

Temp (°C)	RH	NFM adults	NFM protonymphs	Lice adults	Lice nymphs
15	85	35	29	2.6	5.3
	65	26	26	3.3	5.3
	31	20	22	2.6	4.8
21	85	26	28	2.5	5.3
	65	18	25	2.8	5.3
	31	16	14	2.6	5.8
27	85	22	28	2.1	4.8
	65	13	17	2.1	3.3
	31	8	8	2.3	3.6
33	85	10	12	1.8	2.6
	65	8	8	1.8	2.3
	31	7	7	1.1	2.3

15°C, 1.9–2.5 d at 21°C, 1.7–2.2 d at 27°C, and 0.8–1.3 d at 33°C. The LT₉₅ values were generally 1.5–2 times the LT₅₀ values in each treatment. The LT₅₀ values were 1.3–1.7 d at 15°C, 1.0–1.6 d at 21°C, 0.9–1.3 d at 27°C, and 0.6–0.7 d at 33°C. From the comprehensive survival analysis, median survival varied significantly for all temperatures ($F_{\text{temp}} = 85.25$; df = 3, 465; P = 0.001), but median adult louse survival did not vary significantly with humidity ($F_{\text{humidity}} = 0.60$; df = 2, 465; P = 0.547). There was no interaction between temperature and humidity in one trial (coefficient = 0.019, P > 0.55); in the other trial, there was a significant interaction, although the coefficient was small (coefficient = 0.064, P < 0.05). Maximum survival

Table 2. Off-host survival (days) of six groups of adult northern fowl mites at four constant temperatures (all 85% RH) when removed from hens before (early), at (peak), and after (late) maximum mite population density was attained on those hosts

Temp (°C)	Removal time (pop)	LT_{50} (95% CI)	LT ₉₅ (95% CI)
15	Early (1)	8.3 (7.7-8.8)	18.4 (17.4–19.7)
	Early (2)	7.9(7.2-8.5)	25.5 (23.8-27.4)
	Peak (3)	4.8 (4.2-5.4)	16.7 (15.2–18.7)
	Peak (4)	5.9(5.4-6.4)	16.6 (15.5–18.1)
	Late (5)	5.0(4.4-5.4)	13.8 (12.8–15.2)
	Late (6)	4.8 (4.2-5.3)	17.5 (16.0–19.3)
21	Early (1)	5.7(5.2-6.2)	13.5 (12.5–14.8)
	Early (2)	6.8(6.3-7.2)	15.3 (14.2–16.7)
	Peak (3)	4.8 (4.3-5.3)	12.1 (10.8–13.9)
	Peak (4)	6.0(5.6-6.3)	12.2 (11.5–13.2)
	Late (5)	5.3(4.8-5.7)	11.4 (10.4–12.8)
	Late (6)	4.1 (3.6-4.6)	13.4 (12.4–14.7)
27	Early(1)	4.3 (3.9-4.7)	9.2 (8.5–10.3)
	Early (2)	4.6 (4.2-5.0)	9.9 (9.0-11.1)
	Peak (3)	3.4(3.1-3.8)	7.2 (6.6-8.1)
	Peak (4)	3.8(3.4-4.2)	10.1 (9.3–11.1)
	Late (5)	4.1(3.8-4.4)	7.6 (7.1-8.4)
	Late (6)	4.1 (3.6-4.6)	13.4 (12.4–14.7)
33	Early(1)	3.8(3.4-4.2)	8.2 (7.5–9.2)
	Early (2)	3.3 (2.9-3.6)	7.3 (6.6-8.2)
	Peak (3)	2.6(2.2-3.0)	7.0 (6.2-8.1)
	Peak (4)	3.2(2.8-3.5)	6.9(6.3-7.7)
	Late (5)	3.1(2.8-3.4)	6.3(5.8-7.1)
	Late (6)	2.7 (2.3-3.1)	7.3 (6.5–8.4)

times of adult lice are shown in Table 1. No adult lice lived longer than 3.3 d off a host.

Nymphal Chicken Body Lice. Survival of louse nymphs consistently was higher (\approx 1.5–2 times) than adult survival when comparing the corresponding LT₅₀ and LT₉₅ values for the same temperature-humidity combinations. The LT₅₀ values were 1.5–2.8 d at 15°C, 1.7–3.3 d at 21°C, 1.5–2.0 d at 27°C, and 1.2–1.4 d at 33°C. The LT₉₅ values were generally 1.5–2 times as long as the LT₅₀ values, a reflection of the shorter overall off-host survival of lice relative to mites. Ranges of calculated LT₉₅ values were 3.0–6.9 d at 15°C, 3.7–6.0 d at 21°C, 2.7–4.2 d at 27°C, and 1.5–2.7 d at 33°C.

Main effects of temperature and humidity on median nymphal louse survival are shown in Fig. 4C and D. Survival differed significantly for each temperature; it was highest at 21°C, followed by 15, 27, and 33°C (F = 30.41; df = 3, 402; P < 0.001). In contrast, relative humidity did not significantly affect louse nymph survival (F = 0.23; df = 2, 402; P = 0.795). In the survival analysis, there was no interaction between temperature and humidity (coefficient <0.04, P >0.38). Maximum survival of the nymphs was also higher at each treatment level than survival of the adult lice. Maximum survival ranges were 3.3–5.3 d at 15°C, 4.3–5.8 d at 21°C, 3.0–4.8 d at 27°C, and 1.8–2.6 d at 33°C (Table 1).

Discussion

The representative data here reflect the more detailed data in Chen (2006). Both temperature and humidity played an important role in the off-host survival of the northern fowl mite, but only temperature affected the survival of the chicken body louse. The calculated LT_{50} values for both the adult and protonymph stages of *O. sylviarum* were drastically lower than the values presented by DeVaney and Beerwinkle (1980). The ranges of LT_{50} values given in that study were 29–31 d at 15°C, 24–27 d at 21°C, 17–21 d at 26°C, and 6–10 d at 33°C. These values generally are at least 3 times, and up to 10 times, greater than the calculated LT_{50} values for adult *O. sylviarum* for corresponding temperature treatments in the current study. The data of DeVaney and Beerwinkle (1980) compare slightly better to the results calculated for protonymphs, in which their estimates are $1.4-3 \times$ greater than the data presented here.

The large discrepancies between DeVaney and Beerwinkle (1980) and this study may be a result of several things. First, the mite populations (Texas versus California) may have had intrinsic survival differences. Second, DeVaney and Beerwinkle (1980) placed a large number (≈ 200) of mites of various (mixed) physiological stages into a vial and observed and counted mortality. As the current study shows, the adults and protonymphs differ dramatically in survival, and the relative proportions of the stages, if they differed, would greatly affect overall estimates of mortality. Usually entire feathers (perhaps with variable numbers of eggs that hatched at variable times) were held. It is possible that the presence of feathers may have enhanced mite survival in some way, but counting or scoring mites for survival is impossible to do accurately under these conditions. There might have been a tendency to see the moving mites and overestimate their numbers compared with dead mites tucked in among feather barbules. Third, the time intervals at which the mites were observed were not stated, and variation in this aspect obviously would affect accuracy of survival estimates and influence attempts to analyze the data statistically. Fourth, as shown in the current study, different mite populations may vary with stage of infestation or for unknown reasons, and this aspect was not treated in the earlier study.

Off-host survival for *O. sylviarum* has been reported to range from 13 d at 25°C, 75.5–80% RH (Abasa 1969) for adults to 2–3 wk for mixed physiological stage mites maintained at assumed laboratory temperatures (21–26°) (Cameron 1938, Kirkwood 1963).

Mite survival, for both stages, was greater at 15°C than at the other three temperature treatments, especially notable with the LT_{95} values. At 33°C, the mites had a considerably lower LT_{50} (≈3 d for adults and 4 d for protonymphs). Populations of *O. sylviarum* decline in the summer (Combs and Lancaster 1965). Data in Combs and Lancaster (1965) suggest that mite resting sites, also used for oviposition, were on feathers in a zone ≈28–30°C. Indeed, when infested hens are first exposed to hot temperatures (≈30–35°C), we have observed more mites out on distal feather regions, and producers frequently report the sudden appearance of large numbers of mites on hen eggs at that time (B.A.M., unpublished data). Although the

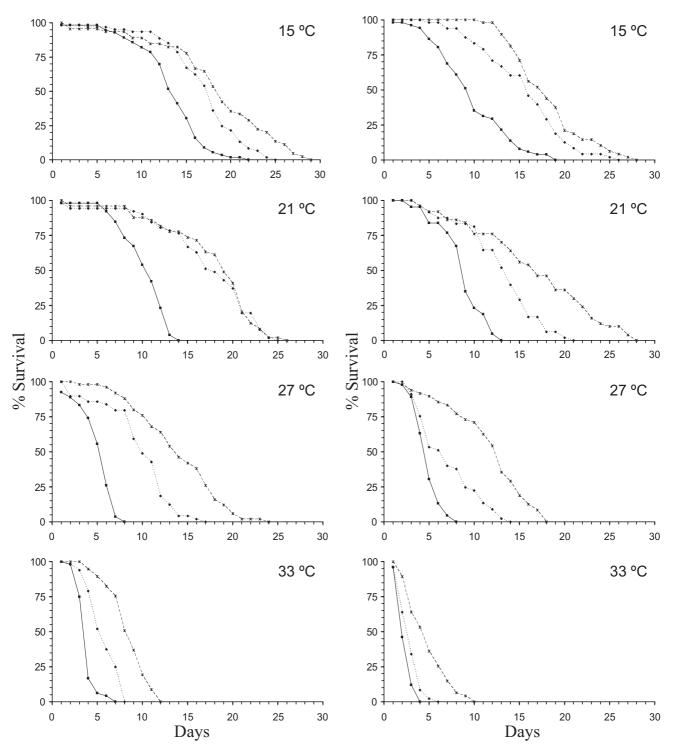


Fig. 3. Survival curves for northern fowl mite protonymphs as a function of time off-host at different combinations of temperature and relative humidity. Population one on left; population two on right (each population reflects protonymphs hatched from eggs of mites from a single hen). Symbols reflect relative humidity as follows: 31% RH (\blacksquare), 65% RH (\blacklozenge), 85% RH (\ast).

details of high-temperature effects on mite distribution and fitness require more study, ambient temperatures in the range of 33°C or higher seemed to be more stressful for northern fowl mites.

Survival of both adult and protonymph northern fowl mites also was influenced by relative humidity. *O. sylviarum* did not survive well at low humidity (31%RH), but they were capable of surviving for up to 26 and 35 d at 65% and 85%RH, respectively. Although a statistical difference in survival was detected for adult mites kept at 65% RH as opposed to 85% RH, these differences were not marked in the survival curves, where 65% RH survival often was comparable to that at 85% RH. In contrast, the differences between protonymph survival at 65 and 85% RH were more substantial, especially at higher temperatures. Abasa (1969) studied adult mite survival at 25°C over a large range of humidities for a 13-d period; sometimes less

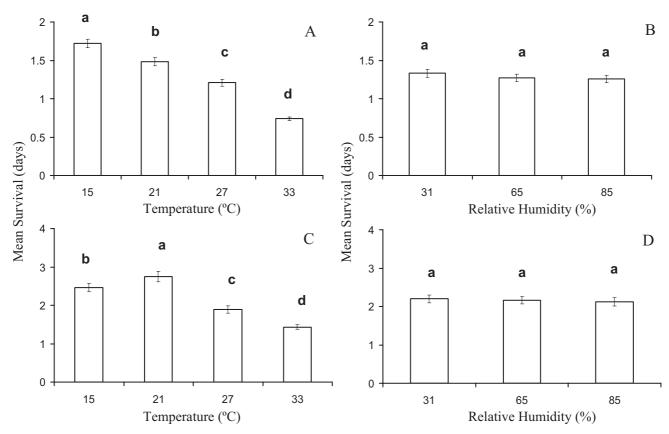


Fig. 4. Main effects of temperature and humidity (trials pooled) on off-host survival of chicken body louse adults (A and B), and chicken body louse third instars (C and D). Means and standard errors shown. Within a stage, histograms marked with the same letter are not significantly different (P > 0.05) based on analysis of median survival times (see text).

than required for complete mortality. Although no analysis was done by Abasa (1969), our probit analysis of the data (Abasa 1969; Fig. 1) for 33%, 53%, and 80% RH generated approximate LT_{50} values of 6.7, 7.8, and 11.5 d, respectively. These estimates are generally somewhat longer than the LT₅₀ values in the current study, but they are in the same approximate range. The inability of the protonymph to survive well at the lowest humidity (31%) also agrees with observations that mite eggs fail to hatch at that humidity (B.L.C., unpublished data). The greater surface-to-volume ratio should contribute to a greater risk of protonymph desiccation, and the lighter cuticle (versus the adult) also might contribute, but this would require more study. Better survival at higher humidities may be a factor in the distribution of *O. sylviarum* on the host (vent region).

The other primary mite pest of poultry is the chicken mite, *Dermanyssus gallinae* (De Geer). Unlike *O. sylviarum, D. gallinae* spends most of its time offhost, but its survival also is affected by temperature and humidity (Nordenfors et al. 1999). In general, *D. gallinae* survives much longer off-host than *O. sylviarum*. Protonymphs and adult female *D. gallinae* survived up to 9 mo off-host (5°C) and up to 5 mo at 20°C and 70% RH, but survival, especially of protonymphs, was very reduced at low humidities (Nordenfors et al. 1999).

Although *M. stramineus* leaves the host less often than does *O. sylviarum*, it is common for workers near

heavily infested hens to have lice thrown onto their bodies as hens move in cages. Once it is away from the host, the chicken body louse fares much worse than does the northern fowl mite, living no more than ≈ 6 d under any tested combination of temperature and humidity. The effects of temperature on the off-host survival of *M. stramineus*, although significant, were not as dramatic as with *O. sylviarum*, probably due to the far greater rate of mortality observed for *M. stramineus*. The LT₅₀ value for *M. stramineus* adults did not exceed 2 d compared with almost 8.5 d (15°C) for adult *O. sylviarum*. Nymphs of *M. stramineus* lived slightly longer, with an LT₅₀ up to 3.3 d at 21°C.

Very limited off-host survival was documented with the chewing louse *B. columbae* surviving 2–3 d off-host at 20–24°C, and two other chewing lice, *C. columbae columbae* and *C. bidentatus compar*, survived for 3–11 d off-host in the same conditions as *B. columbae* (Rem and Zlotorzycka 1981). Much higher survival by the nymphs (up to 29 d), relative to adults, has also been documented with unstarved *Bovicola ovis* (Crawford et al. 2001).

Unlike the northern fowl mite, *M. stramineus* survival was not significantly influenced by the different humidity treatments at any temperature. The high rate of mortality experienced by *M. stramineus* when removed from the host may have masked any subtle effects that humidity would have had on survival. It also may be possible that humidity does not factor into the survival of lice due to their larger size or nature of

the cuticle and risk of water loss. *M. stramineus* is highly motile on the host and occupies more body regions than *O. sylviarum*. The environmental differences in these body regions may have resulted in evolution of less stringent humidity and even temperature requirements for *M. stramineus*.

The experiment provides for a very preliminary examination of relative mite survival versus three time points of O. sylviarum population development on a hen: early, peak, and late infestation. In an early infestation, the adult mites on the hen could be younger overall, as yet less stressed by host immune system pressures, and perhaps would be more capable of surviving off the host. Because significant numbers of mites were needed from one host in the present studies, the "early" and "late" mite populations at this level actually typically are not too far removed in time from "peak" levels (only $\approx 1.5-3$ wk). Still, analyses comparing the six populations (two at each of the three time points of infestation) indicated longer survival for populations 1 and 2 (both early) as compared with the other four populations. Survival for peak and late infestations did not differ significantly. Because only six populations were used (two per time point), more detailed and thorough study on this aspect is needed, ideally including other aspects of mite fitness as well.

Evidence of the variation among mite populations probably reflects host variation and suitability, and it also can be observed with the maximum survival time of *O. sylviarum*. The maximal survival time is a reflection of only a small percentage of *O. sylviarum*, creating the tail in the survivorship plots. The difference in maximum survival for the six adult mite populations at 15°C and 85%RH, for example, was 16 d. Maximum survival at 33°C did not exceed 2 wk for adults or protonymphs, reflecting their poor survival at high temperatures. Unlike *O. sylviarum*, the survival plots for *M. stramineus* did not have the characteristic tail evident in *O. sylviarum* plots, and off-host survival of the *M. stramineus* did not exceed 6 d.

Knowledge of the off-host survival capabilities of O. sylviarum and M. stramineus is very relevant to the control of these two ectoparasites in commercial poultry operations. We did not measure actual ability of off-host mites or lice to survive if placed back on a host. However, this would be expected to be at least slightly less than (at most, equal to) the survival times reported here. Poultry houses are left empty between flocks, and in California laying hens this period often is ≈ 2 wk. Understanding how long and at what temperatures these obligate ectoparasites may survive offhost would allow for prevention of infestation on subsequent flocks by adjusting the vacancy time. Reinfestation by residual lice from a previous laying cycle is relatively unlikely, as no lice survived past 6 d off-host. However, off-host survival of O. sylviarum was as much as 35 d at 15°C and could be even longer at lower temperatures (DeVaney and Beerwinkle 1980). Poultry operations in California could try to plan to cycle out their old flocks in the summertime when daily average temperatures are highest. A vacancy period of >5 wk in summer or >8 wk in winter

in southern California should allow for mite mortality high enough to eradicate residual populations. The data presented should be useful in similar efforts in other areas with somewhat different temperature and humidity regimes as well.

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