Population Growth of the Generalist Mite *Tyrophagus putrescentiae* (Acari: Acaridida) Following Adaptation to High- or Low-Fat and High- or Low-Protein Diets and the Effect of Dietary Switch

TOMAS ERBAN,[1,2] DAGMAR RYBANSKA,[1,3] AND JAN HUBERT[1]

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ABSTRACT *Tyrophagus putrescentiae* (Schrank, 1781) is a cosmopolitan generalist feeder that prefers foodstuffs of high-fat and high-protein content. Our aim was to investigate the population growth of *T. putrescentiae* after long-term nutritional adaptation to two distinct diets that are commonly infested in the synanthropic environment. Crushed dry dog food kernels provided a high-fat, high-protein, and low-carbohydrate diet, whereas wholemeal spelt flour provided a low-protein, low-fat, and high-carbohydrate diet. After >6 mo of nutritional adaptation, each of the two populations were used in two 28-d population growth tests: one that mites remained on their adaptation diet (homogenous diet treatment) and one that mites underwent a dietary switch (dietary switch treatment). Dietary treatment, nutritional adaptation, and their interaction all significantly influenced population growth. The homogenous diet treatment showed 7.5 times higher growth on the dog food diet than on flour. In the dietary switch, flour-adapted mites switching to dog food experienced five times greater population growth than the flour-adapted mites remained on flour, whereas the dog food-adapted population showed a 2.8-fold decrease in population growth when transferred to the flour. A comparison of means between the two dietary switch treatments showed a 1.9-fold higher population growth after flour-adapted mites were shifted to dog food than when the dog food-adapted mites were shifted to flour. We demonstrated that *T. putrescentiae* is able survive and reproduce for many generations on dry dog food and flour with different levels of success. High-fat and -protein food accelerated *T. putrescentiae* population growth compared with the high-carbohydrate diet.

KEY WORDS *Tyrophagus putrescentiae*, nutritional adaptation, dietary switch, dry dog food, adaptive trait

Since the beginning of the Neolithic revolution, various invertebrate species have inhabited synanthropic environments created by humans. One group that has adapted to human dwellings is synanthropic acaridid mites (Acari: Acaridida syn. Astigmata). These mites originally inhabited the soil and migrated into human habitats from the nests of birds and mammals during the Neolithic revolution (OConnor 1979, 1982, 1984). Synanthropic mite species are typically classified into two artificial groups, namely, house dust mites (HDMs) and stored-product mites (SPMs; Hughes 1976, Colloff 2009). Both groups are commonly called "domestic mites," as many SPMs from the families Acaridae, Glycyphagidae, and Chortoglyphydae have also been found in house dust (Colloff and Spieksma 1992). Because humans create diverse habitats that vary in nutrient composition by producing foods for human and animal consumption, these synanthropic environments can host both generalist and specialist species with respect to nutrient preferences. In this context, different mite species preferentially infest different types of foodstuffs (Hughes 1976, Hill 2002).

For example, the dried fruit mite *Carpoglyphus lactis* (L., 1758) specializes in sugar-rich commodities, e.g., dried fruits, jams, honey, and dried milk (Chmielewski 1971; Hubert et al. 2011, 2015). The generalist *Tyrophagus putrescentiae* (Schrank, 1781) appears in diverse habitats, including grain and grain products, flours, oilseeds, bread, cheese, hams, dried milk, dried eggs, dried fish, dried fruits, edible mushrooms, and beehive products (Chmielewski 1999, Duek et al. 2001, Garcia 2004, Kucerova and Horak 2004, Aygun et al. 2007, Palyvos et al. 2008, Mullen and OConnor 2009, Qu et al. 2015). However, *T. putrescentiae* prefers commodities with high-fat and -protein contents (Hughes 1976, Duek et al. 2001, Hill 2002, Aygun et al. 2007, Mullen and OConnor 2009). *T. putrescentiae* is considered the most common pest in dry dog food and, therefore, is of high veterinary importance (Thind 2005, Nayak 2006, Brazis et al. 2008, Canfield and Wrenn 2010, Gill et al. 2011, Hibberson and Vogelnest 2014). It also frequently

[1] Crop Research Institute, Biologically Active Substances in Crop Protection, Drnovska 507/73, Prague 6-Ruzyne, CZ-16106, Czechia.
[2] Corresponding author, e-mail: arachnid@centrum.cz.
[3] Czech University of Life Sciences, Faculty of Agrobiology, Food and Natural Resources, Department of Plant Protection, Prague 6-Suchdol, CZ-16521, Czechia.

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occurs in stored grain (Zakhvatkin 1959, Kucerova and Horak 2004, Palyvos et al. 2008) and primarily damages the fat, oil, and protein-rich grain germ, thereby causing germination loss (Zakhvatkin 1959). Because the germ is separated from the grain during the milling process, flour is relatively poor in protein and fat (Dunford and Zhang 2003). Case studies have uncovered the presence of *T. putrescentiae* in flour that have caused anaphylaxis (Matsumoto et al. 1996, Guerra Bernd et al. 2001, Sanchez-Borges et al. 2009).

Nutritive composition, i.e., the protein–carbohydrate balance, influences animal life history, including reproduction, as shown in studies on insects (Clark et al. 2015, Lee 2015). Nutritional studies on synanthropic acaridid mites including *T. putrescentiae* have shown that protein (Erban and Hubert 2010, Hubert et al. 2014), carbohydrate (Erban et al. 2009), and bacteria cell (Erban and Hubert 2008) additives to the diet influence population growth. However, there is little information on the influence of fat content or fat and protein content on mite population growth. In the present study, dry dog food and flour were used as model diets to evaluate the adaptation of *T. putrescentiae* to two nutritionally distinct synanthropic environments. The results of this study have implications for understanding why *T. putrescentiae* is so common in high-fat and high-protein foods.

Materials and Methods

Experimental Design. We individually reared laboratory strains of *T. putrescentiae* for >6 mo on either a dry dog food diet (DDFd) or a wholemeal spelt flour diet (WSFd). The two nutritionally adapted mite populations were subsequently used in tests of population growth 1) in a homogenous environment, in which the habituated mites were maintained on their adaptation diets (homogenous diet treatment), and 2) in a dietary switch, in which the mites were switched from their adaptation diet to the other diet (dietary switch treatment). An outline of the experimental procedure is shown in Figure 1.

Original Mite Culture. A laboratory strain of *T. putrescentiae* that was collected in 1996 by Eva Zdarkova in Buštěhrad, Central Bohemia, Czechia, was used in this study. The mites used in the present study originated from long-term laboratory colonies that were mass-reared on a wheat-derived rearing diet composed of a mixture of oat flakes, wheat germ, and dried yeast extract (Pangamin, Rapeto, Bezdružice, Czechia) at a weight ratio of 10:10:1, as previously described (Erban and Hubert 2008). The mites were cultivated on an IWAKI 25-cm^2 surface area in 70-ml tissue culture flasks (IWAKI flasks; Cat No. 3100-025; Sterilin, Newport, United Kingdom). A constant 85% relative humidity (RH) was maintained with saturated KCl solutions in Secador desiccator cabinets (Bel-Art Products, Pequannock, NJ), and the air-conditioned dark room was maintained at 25 ± 1°C.

Experimental Diets and Mites. Prior to the experiment, the mites were removed from the standard rearing diet and fed one of two experimental diets for nutritional adaptation, namely, 1) dry dog food (DDFd; Friskies Lifeplus Nutrition Junior, Nestle Purina, Bük, Hungary) that had been crushed by a grinding mortar and pestle and 2) wholemeal spelt flour (WSFd; Bioharmonie, Pro-Bio, Staré Město, Czechia). The declared target food quality characteristics of these two nutritionally distinct diets were 28.0% crude protein and 14.5% fat for the dry dog food and 9.4% protein and 2.5% fat for the wholemeal spelt flour. The mite populations were separately cultivated on the two distinct diets for over 6 mo before the experiment. Each mite population was collected and shifted to a fresh diet at ~2-mo intervals to avoid spoiling the culture. Because *T. putrescentiae* can complete its life cycle at 85% RH from one generation to the next in 2–3 wk (Sanchez-Ramos and Castanera 2005), >10 generations were developed during the adaptation period on these diets. The mites that were adapted on dry dog food (DDFm) and the mites that were adapted on wholemeal spelt flour (WSFm) were further used in the experiment.

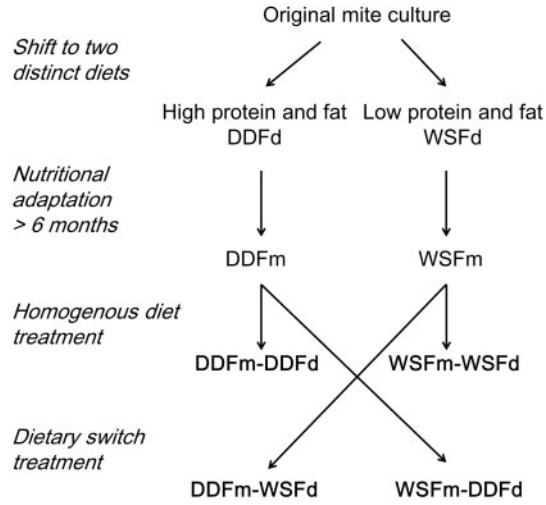

Fig. 1. Experimental design. DDFd, dry dog food diet prepared by crushing dog food kernels; WSFd, wholemeal spelt flour diet; DDFm, mites adapted on dry dog food diet; WSFm, mite population adapted on wholemeal spelt flour.

Experimental Procedure. The experiment was begun by placing 100 mite individuals of good condition and similar size from each of the DDFd or the WSFd adaptation diets into 70-ml IWAKI flasks along with 50 mg of the test diet. The flasks were incubated for 28 d in Secador desiccator cabinets under constant environmental conditions, as described in section Original Mite Culture. The contents of the flasks were examined for the presence of microfungi with a dissection microscope (Carl Zeiss, Jena, Germany), and all the flasks were evaluated as negative. The experiment was terminated by the addition of 10 ml of 80% ethanol to the flasks. The mites were then counted using a dissection microscope. The experiment was conducted over three runs with 6, 6, and 10 replicates per treatment, with the four different treatments initiated within 3 d of each other each run. The runs were started at 1-mo intervals,

and the entire experiment was conducted within 4 mo from the first run. Because the results did not show a difference between the three runs, we present the sum of replicates within each treatment. The experimental design included 22 replicates per treatment.

Data Analyses. The final numbers of mites (*N*) displayed a normal distribution. A two-way analysis of variance (ANOVA) was applied to test for the effects of two factors, i.e., nutritional adaptation and dietary treatment, and their interaction with the final mite count. Tukey's honestly significant difference (HSD) test was used to compare the contribution of the factors. The data were analyzed using XLSTAT 2015 (Addinsoft, New York, NY).

Results

Two populations of nutritionally adapted mites, DDFm and WSFm, were obtained. The final mite count depended significantly ($F_{(3,84)} = 297$; $P < 0.001$) on both nutritional adaptation ($F = 158$; $P < 0.001$) and dietary treatment ($F = 728$; $P < 0.001$), and the interaction of both factors was significant ($F = 6.8$; $P = 0.011$). Comparisons of mite counts in each test and the statistical details are shown in Fig. 2.

The population growth of *T. putrescentiae* in the homogenous diet treatment was 7.5 times higher in the DDFd than in the WSFd. The mites that had been adapted on flour experienced a fivefold increase in population growth when they were transferred to the DDFd in the WSFm-DDFd dietary switch treatment. When the population that had been adapted on the DDFd was transferred to the flour in the DDFm–WSFd dietary switch treatment, the mite population growth decreased by a factor of 2.8. A comparison of means between the two dietary switch treatments showed a 1.9 times higher population growth in WSFm–DDFd compared with DDFm–WSFd. Overall, the growth of both nutritionally adapted populations, the DDFm and WSFm *T. putrescentiae*, was higher on the DDFd diet than on the WSFd diet in both the homogenous diet and dietary switch treatments.

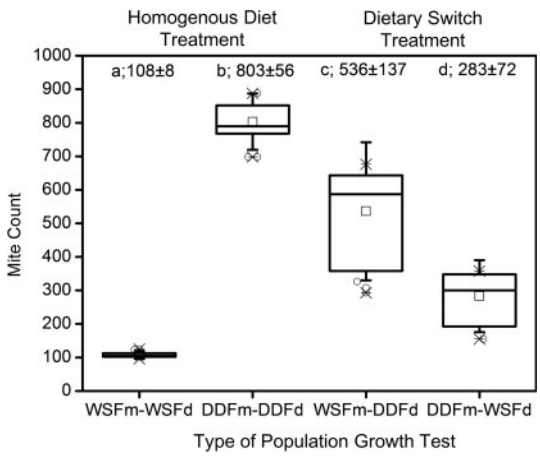

Fig. 2. Boxplot of results of population growth tests of *T. putrescentiae* mites adapted to either a DDFd or a WSFd diet in either a homogenous diet treatment or after dietary switch. DDFd, dry dog food diet prepared by crushing dog food kernels; WSFd, wholemeal spelt flour diet; DDFm, mites adapted to the dry dog food diet; WSFm, mite population adapted to the wholemeal spelt flour diet; letters a–d indicate Tukey's HSD at the 0.05 level; *N*, final mite count ± SD.

Discussion

This study shows the nutritional adaptive traits of the SPM *T. putrescentiae* on model human food and animal feed found in homes. Rearing the mites for over 6 mo on each of two distinct diets that were prepared from dry dog food or wholemeal spelt flour prior to the experiments produced two nutritionally adapted populations. We demonstrated that *T. putrescentiae* is able survive and reproduce for many generations on dry dog food and flour. Analysis of the homogenous diet treatment showed highly accelerated population growth of *T. putrescentiae* on the high-fat, high-protein diet compared with the low-fat, low-protein diet. Analysis of the dietary switch treatment demonstrated that food enrichment of fat and protein highly accelerates reproduction of *T. putrescentiae*, whereas deprivation of these nutriments suppresses mite population growth. Analysis of both the homogenous diet and dietary switch treatments suggests that *T. putrescentiae* is adapted to fast population growth in environments that are rich in protein and fat, represented here by the DDFd. Therefore, this study confirms that dry dog food is a suitable substrate for rapid *T. putrescentiae* reproduction. Indeed, *T. putrescentiae* is the most common pest in this commodity (Thind 2005, Nayak 2006, Brazis et al. 2008, Canfield and Wrenn 2010, Gill et al. 2011, Hibberson and Vogelnest 2014). Accordingly, the rapid population growth of these mites on the DDFd compared with the flour substrate is consistent with the natural occurrence of *T. putrescentiae* as the dominant species in mite communities in pet food factories that process protein-rich materials and the lower prevalence of this species in facilities that process cereals (Thind 2005).

The rapid change in the reproductive rate of mite populations that evolved in a nutritionally homogenous environment after the shift to a different diet in the dietary switch treatment demonstrates that *T. putrescentiae* changes its nutritional habits relatively quickly. Mite population growth rapidly increased after the mites shifted to a high-protein, high-fat environment; in contrast, population growth rapidly decreased after the mites shifted to an environment that was low in fat and protein. These results suggest that the mite is well-adapted to fluctuating food resources. It is known that organisms may adapt to one or several environments. Moreover, in addition to adapting to their environment, organisms can also adapt to environmental fluctuation itself (Magalhaes et al. 2014). However, the final mite counts in the dietary switch treatment were still far different than the numbers in the homogenous diet treatment. The implication is that the mite does not change its nutritional habits directly but rather experiences a delayed reproduction process after dietary switch. The

most likely reason for this delay is the need for metabolic adaptation to the immediate change in fat, protein, and carbohydrate contents in the diet. For example, in human nutrition, when the diet composition is changed from low fat to high fat, several days are required before fat oxidation fully adapts to fat intake (Smith et al. 2000). These findings may explain why mite populations in homes will initially multiply at different rates after shifting from infesting dry dog food to infesting flour (or vice versa). This idea should be considered in population prediction models.

In general, the three primary nutritional components of pet food are protein, carbohydrates, and fat (Thompson 2008). Pet food that is designed for carnivores is enriched with protein and fat but also contains cereal components such as carbohydrates and fiber, and thus, the food provides a complete spectrum of basic nutriments (Thompson 2008). The question thus arises as to whether *T. putrescentiae* tends toward carnivore-like feeding similar to that of the dogs for which dry dog food is designed. An affirmative interpretation would be consistent with the suggestion of Walter et al. (1986), who proposed that *Tyrophagus* spp. mites, including *T. putrescentiae*, reproduce on dead and injured mites and on several species of nematodes (Walter et al. 1986).

An explanation for the adaptation of the mites to the two different food sources we tested in the present study can be found in previous studies that revealed the ability of *T. putrescentiae* to feed on protein, carbohydrates, and lipid substrates, and detected the appropriate enzymes enabling their digestion. Previous laboratory experiments showed that adding both 5% casein and 5% albumin to a wheat-derived diet (for composition, please see "Original Mite Culture" in Materials and Methods) accelerated the population growth of *T. putrescentiae* (Erban and Hubert 2010). The proteolytic processes used to digest the proteins in *T. putrescentiae* were revealed by enzyme analyses (Ortego et al. 2000, Erban and Hubert 2010). Thus, it is not surprising that the higher protein content in the dry dog food accelerated *T. putrescentiae* growth. Although lipid substrates also appear to increase *T. putrescentiae* population growth, appropriate nutritional or lipase studies on mites are lacking. The available studies on mite lipases are limited to enzyme activity detection. Alkaline phosphatase and acid phosphatase (Bowman 1984, Stewart et al. 1992) activity have been detected in HDM and SPM species. Lipases were also detected in the spent growth medium of HDMs and are thought to be digestive (Stewart et al. 1991, 1992). The ability of a high protein, high fat combination to boost the reproduction of *T. putrescentiae* was shown by the increased growth of the nutritionally adapted populations of *T. putrescentiae* on the DDFd relative to the WSFd in both the homogenous diet and dietary switch treatments. However, the effect of lipids alone on mite growth should be investigated further. The ability of *Tyrophagus* to digest carbohydrates first was shown in pioneering studies, and amylase activity was also detected in *T. putrescentiae* (Akimov and Barabanova 1978) and *Tyrophagus longitor* (Gervais, 1844) (Bowman and Childs 1982). According to Matsumoto (1965), *Tyrophagus dimidiatus* (Hermann, 1804) is able to utilize a variety of carbohydrates ranging from glucose to starch. A more recent study by Erban et al. (2009) showed that the growth of *T. putrescentiae* was accelerated by the addition of 5% wheat starch and maltose to a wheat germ diet, whereas 5% sucrose suppressed growth. The authors also showed that digestive α-amylase and α-glucosidase activity localized amylolytic activity to the mite gut (Erban et al. 2009). In addition, a study of enzyme analysis, population growth, and inhibitory tests among nine domestic mite species showed that *T. putrescentiae* is relatively poorly adapted to utilize carbohydrate substrates (Erban et al. 2009). The relatively low level of *T. putrescentiae* adaptation to high-carbohydrate substrates supports the observed low population growth on flour and the marked decrease in population growth after the shift to flour from the high-fat, high-protein DDFd in the present study. Moreover, the flour used in the present study was richer in carbohydrates compared with the dry dog food, whereas the dry dog food was richer in fat and protein than was the flour. Therefore, we conclude that the higher protein and fat content of the dog food was able to boost *T. putrescentiae* population growth and that the higher carbohydrate content of the flour could not compensate for a deficiency in fat and protein content.

Among nine species of domestic mites, *T. putrescentiae* was found in a previous study to be the species most sensitive to the addition of the α-amylase and α-glucosidase inhibitor acarbose, and it also showed low relative amylolytic activity compared with the other mite species (Erban et al. 2009). Furthermore, the higher resistance of *T. putrescentiae* to a proteinaceous α-amylase inhibitor than to the nonproteinaceous inhibitor acarbose can be explained by the powerful proteolytic system in the mite gut (Hubert et al. 2014). In conclusion, *T. putrescentiae* is relatively poorly adapted to carbohydrate-type substrates (Erban et al. 2009). This conclusion may appear at odds with the observed high abundance of *T. putrescentiae* in samples of stored grain (Stejskal et al. 2003, Palyvos et al. 2008, Hubert et al. 2009). The likely explanation for the high abundance of *T. putrescentiae* in grain is that the mite uses a different feeding strategy in grain stores than on dry dog food, as the mites can feed on microorganisms, primarily seed-borne fungi (Sinha 1966). This supposition is supported by the presence of fungi in mites that were isolated from grain (Hubert et al. 2003, 2004). Another piece of evidence is that the wheat-derived diet (for composition, please see "Original Mite Culture" in Materials and Methods) used to cultivate *T. putrescentiae* in the laboratory contains yeasts in addition to the wheat germ. The suitability of yeasts for *Tyrophagus* is supported by studies that showed faster development on pure yeasts for *T. dimidiatus* (Matsumoto 1964) and both faster development and higher body size of *Tyrophagus curvipenis* Fain and Fauvel, 1993 on dry yeasts than on rolled oats and wheat flour (Ye and Zhang 2014). The contents of the flasks in our experiment were evaluated as being free of fungi; therefore, fungi did not influence the population growth of mites.

An understanding of *T. putrescentiae* population growth in different synanthropic environments is

relevant to the mites' medical and veterinary potential. *T. putrescentiae* is one potential source of exposure to mite allergens for canines with this allergy (Nayak 2006, Brazis et al. 2008, Canfield and Wrenn 2010, Gill et al. 2011). The antigenic properties of *T. putrescentiae* have been studied, and the allergenic cross-reactivity between *T. putrescentiae* and HDMs has been examined (Arlian et al. 1984, Park et al. 1999, Saridomichelakis et al. 2008, Marsella and Saridomichelakis 2010). In the Pyroglyphidae mites *Dermatophagoides farinae* Hughes, 1961 and *Dermatophagoides pteronyssinus* (Trouessart, 1897), the diet on which the mites are grown dramatically influences their growth rates as well as Grp1 and Grp2 allergen production and accumulation (Avula-Poola et al. 2012). Both Grp1 and Grp2 allergens are gut-derived and feces-rich *Dermatophagoides* allergens (Erban and Hubert 2015). An analogous situation to the diet-dependent changes in gut-derived allergen production in *Dermatophagoides* sp. may be suggested for other species of domestic mites, including *T. putrescentiae*. Because of the large difference in population growth on the DDFd compared with the flour diet, a higher concentration of allergens, arising from the increased number of mites and their feces, would be expected in dry dog food than in flour. Therefore, the results of this study stress the importance of preventing mite contamination of dry dog food, which can serve as a direct source of allergens for dogs and a source for the rapid contamination of home environments, and thus carries risks to human health after cross-contamination. Moreover, because of the different nutritional compositions of the two test diets, different rates of specific protein or allergen production are suggested.

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