Reproduction and Development of Laboratory and Wild House Dust Mites (Acari: Pyroglyphidae) and Their Relationship to the Natural Dust Ecosystem

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ABSTRACT Life histories of "wild" house dust mites, *Dermatophagoides pteronyssinus* (Trouessart) (Acari: Pyroglyphidae), were compared with laboratory cultures by using a diet consisting of skin and dust or a laboratory diet consisting of dried liver and yeast. Under constant conditions of 25°C and 75% RH, fecundity and rate of reproduction were higher in laboratory cultures on both diets compared with wild mites. There were also trends for a shorter prereproductive period and more rapid egg development of laboratory mites compared with wild mites. Overall, there was little effect of diet on either strain of mites at 75% RH. At low RH (64%), fecundity was significantly lower (for both strains on both diets), and there were also trends for longer prereproductive period, reduced rate of reproduction, reduced adult survival, prolonged egg and juvenile development, or a combination compared with 75% RH. Additionally egg and juvenile mortality were significantly higher on the liver and yeast diet. Overall, the skin and dust diet favored both strains of mites at 64% RH. On the liver and yeast diet at 64% RH, wild mite adults performed significantly better than laboratory mites, and egg mortality was lower. These results suggest that laboratory mites have stronger reproduction and development than wild mites, except when under environmental stress and that diet is a significant factor, particularly in suboptimal conditions. This could have important implications for predictive models of house dust mite populations in their natural habitat. Ideally, such models should be developed using data from wild dust mite populations reared on a natural diet.

KEY WORDS *Dermatophagoides pteronyssinus*, wild populations, life history

Population models to predict house dust mite, *Dermatophagoides pteronyssinus* (Trouessart) (Acari: Pyroglyphidae), populations in the home are currently under development (Pretlove et al. 2001, 2005; Crowther et al. 2006, Biddulph et al. 2007). Their aim is to assist in the effective control of mites by manipulating the temperature and relative humidity in their habitats, psychrometric conditions known to play a crucial role in their survival (Cunningham 1999, Pretlove et al. 2002). The models set out to simulate, first, psychrometric conditions in mite habitats (given climate and building characteristics), and, second, the effect of these conditions on house dust mite populations. In this way the most successful and feasible strategies for achieving psychrometric control can be determined, whether by improving ventilation or by a combination of modifications to building design, building operation, and occupant behavior (e.g., with respect to moisture production, window opening habits). However, the population models upon which these simulations depend require mite physiology data inputs that relate to the house dust ecosystem.

Data on house dust mite reproduction and development have, until now, predominantly been obtained from mite cultures that have been reared for many years under laboratory conditions (Spieksma 1967; Blythe 1976; Dobson 1979; Gamal-Eddin et al. 1983a, 1983b, 1983c; Ho and Nadchatram 1984; Andersen 1988; Hart and Fain 1988; Arlian et al. 1990). However, in 1987, Colloff (1987a, 1987b) studied eggs from wild populations of house dust mites and suggested that they differed from eggs from laboratory populations with respect to their developmental time, mortality, and water loss. There have been no subsequent studies on wild populations of house dust mites, and no data are available on juvenile or adult physiology from wild cultures.

The principal aims of this study were therefore to obtain more detailed information on the physiology of wild house dust mite populations compared with lab-

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oratory populations and to determine the importance of wild mite data for predictive mite population models compared with existing data from long-term laboratory populations.

Materials and Methods

Mite Cultures. The laboratory strain of *D. pteronyssinus* had been reared for at least 10 yr under constant laboratory conditions of 25°C temperature and 75% RH. Before experiments, they were reared under these constant hygrothermal conditions on a typical optimized liver and yeast diet of ground dried porcine liver (Oxoid, Basingstoke, UK) and brewers yeast (Holland and Barrett, Nuneaton, UK) at a 1:1 (wt:wt) ratio.

A "wild" strain of *D. pteronyssinus* was collected from carpet dust from a UK home in September 2004. From the time of collection, this culture was reared under fluctuating hygrothermal conditions, that is, fluctuating room temperatures and a diurnal relative humidity fluctuation of 8 h at 64% RH and 16 h at 75% RH. Wild cultures were reared on a mixture of 1:0.1 (wt:wt) house dust and nondegreased (fresh) skin scales, with no addition of yeast. Experiments using these wild cultures were started in July 2005.

Mite Physiology Studies. Glass microculture vials 12 mm in diameter by 10 mm in depth were used to hold individual couples (males attached to tritonymphs) isolated from the laboratory or wild cultures for determination of adult survival and reproduction. Glue was applied around the rim of the vials to prevent escape of the mites and an equal quantity of food was added to each vial. Ten couples were used for each assay, and initially observations were made daily to determine prereproductive period and then two to three times weekly for further egg production and adult survival.

The liver and yeast diet (described above) and a skin and dust diet were used in separate experiments to determine the influence of diet on mite performance. To standardize the skin and dust diet, a stock of mattress dust was collected from the beds of a total of 20 nonsmokers, and the dust was pooled. It was then frozen at −20°C for a minimum of 1 wk to kill any mites, sieved through a 500-μm mesh, and then kept at room temperature for at least 1 mo before use in experiments. The aim of the latter step was to enable recovery of house dust fungi after the freezing step. A pooled stock of skin scales was obtained using beard shavings collected from electric razors of eight volunteers, and these scales were left untreated at room temperature before adding to the dust stock at the start of each experiment to provide a 1:1 (wt:wt) mixture. No yeast was added to this "natural" skin and dust diet.

To obtain eggs for developmental studies, 30 adult females were added to glass microculture vials as described above that contained either the liver and yeast diet or the pooled skin and dust diet. They were left at 25°C and 75% RH until 50 eggs were laid. The females were then removed, and the eggs placed into the relevant hygrothermal conditions for the experiment. Observations were made daily for egg hatch and two to three times weekly for juvenile mortality and development.

Constant hygrothermal conditions of 25°C and 75 or 64% RH were used in separate experiments to represent optimal laboratory rearing conditions and the lower relative humidity typical of a domestic environment, respectively. Relative humidity was controlled inside airtight plastic boxes by using saturated inorganic salt solution (Winston and Bates 1960), and it was verified periodically throughout experiments by using a relative humidity meter.

Principal components analysis (PCA; Legendre and Legendre, 1998) was implemented to assess correlations between response variables and to test for significant effects of predictor variables on the principal components, thereby avoiding inflation of type 1 errors. Provided the PCA showed a response variable was significantly affected by the treatment, it was assessed individually using analysis of variance (ANOVA) (Sokal and Rohlf, 1995). Data were log transformed to meet the assumptions of parametric tests: examination of residuals and fitted values showed that transformation was adequate to remove heteroscedasticity and non-normality of error variance. Significance was assumed at the 5% level ($P = 0.05$), and a Gaussian error distribution was used.

Results

Adults. In the PCA, the first two principal components had eigenvalues greater than 1 and together captured 72% of the total variation in the response variables. Principal component 1 (PC1) was positively correlated with reproductive period, female survival, fecundity, and male survival, whereas PC2 was positively correlated with prereproductive period and negatively correlated with reproductive rate. The pattern of high factor loadings on the same components suggests that the dependent variables are highly intercorrelated and that they are likely to show similar patterns among the ANOVAs.

In a multiple ANOVA using PC1 as the dependent variable, the three-way interaction between strain, diet, and relative humidity was significant ($F = 68.1$; df = 7, 71; $P < 0.001$). All three manipulated variables were significant predictors of PC2, and the interaction between strain and RH was also significant ($F = 19.8$; df = 4, 74; $P < 0.001$). This suggests that the effects detected within each life history trait below were real and not artifacts of accepting random patterns as significant due to the number of separate tests done.

Fecundity. The three-way interaction between strain, diet, and relative humidity was significant ($F = 130.9$; df = 7, 72; $P < 0.001$). Fecundity was always higher at 75% compared with 64% RH for all strain and diet combinations (Tables 1 and 2). This difference was particularly striking on the liver and yeast diet at 64% RH, where fecundity was up to 25 times lower than at 75% RH and up to 10 times lower than on the skin and dust diet at 64% RH.

Table 1. Life history parameters of laboratory and wild populations of *D. pteronyssinus* (DP) reared on liver and yeast (lab) and skin and dust (dust) diets at 25°C and 75% RH

	Lab DP lab diet	Wild DP lab diet	Lab DP dust diet	Wild DP dust diet
Adults (*n* = 10)				
Total fecundity per female	100 ± 33.4	66.9 ± 15.9	79.7 ± 12.6	60.9 ± 15.9
Prereproductive period (d)	2.2 ± 0.6	2.9 ± 1.1	2.6 ± 0.9	8.3 ± 3.4
Reproductive period (d)	35.5 ± 12.9	43.1 ± 22.9	27.0 ± 8.2	35.9 ± 18.9
Rate of reproduction (eggs/female/d)	3.0 ± 1.1	1.7 ± 0.5	3.2 ± 1.0	1.9 ± 0.8
Female survival (d)	45.2 ± 13.8	52.8 ± 22.1	39.9 ± 17.5	48.6 ± 20.2
Male survival (d)	34.8 ± 14.4	31.2 ± 5.9	33.9 ± 21.1	45.4 ± 16.1
Immatures (*n* = 50)				
% egg mortality	0	0	0	0
Egg developmental time (d)	3.5 ± 0.9	4.5 ± 0.8	3.3 ± 0.5	5.4 ± 2.8
% juvenile mortality	0	0	0	0
Juvenile developmental time (d)	9.8 ± 1.2	10.9 ± 1.7	13.1 ± 0.7	10.1 ± 3.5
Total egg–adult developmental time (d)	13.3 ± 1.4	15.4 ± 2.4	16.4 ± 0.7	15.4 ± 4.4

Results show mean ± SD.

At 75% RH (Table 1), there was no effect of diet on fecundity. The laboratory strain of mites, however, had significantly higher fecundity than the wild strain on both diets ($F = 15.6$; df = 1, 38; $P < 0.001$).

At 64% RH (Table 2), the interaction between strain and diet was significant ($F = 86.0$; df = 3, 36; $P < 0.001$). Both mite strains had higher fecundity on the skin and dust diet than on the liver and yeast diet, but on the skin and dust diet the laboratory strain had the highest fecundity, whereas on the liver and yeast diet the wild strain had higher fecundity.

Prereproductive Period. The three-way interaction between strain, diet, and relative humidity was significant ($F = 27.9$; df = 7, 72; $P < 0.001$). Prereproductive period (defined here as the period between mating of female tritonymphs with males and production of first eggs) was shorter at 75% RH than at 64% RH for every combination of strain and diet (Tables 1 and 2). High relative humidity shortened prereproductive period to less than any group at low relative humidity, except for wild mites on the skin and dust diet.

At 75% RH (Table 1), there was a significant interaction between strain and diet ($F = 27.2$; df = 3, 36; $P < 0.001$). On both diets, the laboratory mites had a shorter prereproductive period than the wild mites.

Wild mites had a significantly longer prereproductive period on the skin and dust diet compared with the liver and yeast diet ($F = 32.0$; df = 1, 18; $P < 0.001$), but no effect of diet was seen in laboratory mites.

At 64% RH (Table 2), there were no significant differences between strains. In both strains, the skin and dust diet resulted in significantly longer prereproductive periods compared with the liver and yeast diet ($F = 18.9$; df = 1, 18; $P < 0.001$).

Reproductive Period. The three-way interaction between strain, diet, and relative humidity was significant ($F = 33.9$; df = 7, 72; $P = 0.008$). On the liver and yeast diet, both strains of mites showed markedly shorter reproductive periods at 64% RH compared with 75% ($F = 68.4$; df = 2, 36; $P < 0.001$). There was no significant response to relative humidity in wild mites on the skin and dust diet, but in the laboratory strain fed on the skin and dust diet reproductive period was significantly longer at 64% than at 75% RH ($F = 5.9$; df = 1, 18; $P = 0.026$) (Tables 1 and 2).

There was no influence of diet on reproductive period at 75% RH. The only significant difference between strains was seen on the liver and yeast diet on which wild mites had a longer mean reproductive

Table 2. Life history parameters of laboratory and wild populations of *D. pteronyssinus* (DP) reared on liver and yeast (lab) and skin and dust (dust) diets at 25°C and 64% RH

	Lab DP lab diet	Wild DP lab diet	Lab DP dust diet	Wild DP dust diet
Adults (*n* = 10)				
Total fecundity per female	3.8 ± 0.9	6.9 ± 3.2	48.0 ± 10.3	24.4 ± 5.5
Pre-reproductive period (d)	6.2 ± 1.9	6.0 ± 1.6	12.4 ± 6.2	10.1 ± 3.7
Reproductive period (d)	2.8 ± 1.9	6.3 ± 3.5	36.2 ± 8.8	29.4 ± 10.3
Rate of reproduction (eggs/female/d)	2.3 ± 1.7	1.3 ± 0.7	1.4 ± 0.6	0.8 ± 0.4
Female survival (d)	10.2 ± 2.4	18.7 ± 4.8	56.6 ± 13.1	33.1 ± 7.8
Male survival (d)	9.8 ± 2.9	11.6 ± 4.0	44.0 ± 14.1	37.9 ± 12.8
Immatures (*n* = 50)				
% egg mortality	40	0	0	0
Egg development time (d)	4.5 ± 1.1	8.0 ± 0	8.0 ± 0	2.3 ± 1.0
% juvenile mortality	100	100	0	0
Juvenile development time (d)			16.0 ± 3.5	23.9 ± 9.8
Total egg–adult development time (d)			24.0 ± 3.5	26.0 ± 9.9

Results show mean ± SD.

period than laboratory mites ($F = 68.4$; df = 2, 36; $P < 0.001$) (Table 1).

At 64% RH (Table 2), the magnitude of the response to diet differed between the two strains of mites ($F = 35.8$; df = 3, 36; $P = 0.003$). Although both strains of mites showed significantly shorter reproductive periods on the liver and yeast diet compared with the skin and dust diet, the response was greater in the laboratory strain. As found at 75% RH, wild mites had a longer mean reproductive period than laboratory mites on the liver and yeast diet. In contrast, on the skin and dust diet, laboratory mites had a significantly longer reproductive period than wild mites.

Reproductive Rate. Reproductive rate was higher at 75% RH than at 64% in both mite strains and higher in the laboratory strain than in the wild strain at both relative humidity levels ($F = 27.0$; df = 2, 77; $P < 0.001$) (Tables 1 and 2). Diet did not affect reproductive rate.

Female Survival. Female survival (the period from mating of female tritonymphs with males and death) of both mite strains decreased at 64% RH compared with 75% RH on the liver and yeast diet ($F = 57.8$; df = 3, 36; $P < 0.001$), and this decline in survival was more marked in the laboratory mite strain than in the wild strain. On the skin and dust diet, female survival increased with relative humidity in the wild strain, but it decreased with increasing relative humidity in the laboratory strain ($F = 5.0$; df = 3, 37; $P = 0.005$) (Tables 1 and 2).

Diet had no significant effect on female survival at 75% RH, and the only difference between strains at this relative humidity was found on the liver and yeast diet, on which survival of wild females was greater than laboratory-reared females ($F = 57.8$; df = 3, 36; $P < 0.001$) (Table 1).

At 64% RH (Table 2), the two mite strains differed in the magnitude of their response to diet ($F = 71.9$; df = 3, 36; $P < 0.001$). Although female survival of both mite strains was lower on the liver and yeast diet compared with the skin and dust diet, the laboratory strain demonstrated a much greater increase in survival on the skin and dust diet than did the wild mites. Wild females on the liver and yeast diet had greater survival than laboratory mites on this diet, whereas the laboratory strain had much greater survival than the wild strain on the skin and dust diet.

Male Survival. The three-way interaction between mite strain, diet, and relative humidity was significant ($F = 20.8$; df = 7, 71; $P < 0.001$). Survival of males (survival time of males of unknown age during experiments) of both mite strains decreased at 64% RH compared with 75% RH on the liver and yeast diet ($F = 125.3$; df = 1, 37; $P < 0.001$). On the skin and dust diet, this effect was seen only in the wild mite strain ($F = 29.5$; df = 3, 35; $P < 0.001$), and it was less marked than that seen on the liver and yeast diet (Tables 1 and 2).

At 75% RH (Table 1), there was no effect of mite strain on male survival; however, wild males on the skin and dust diet had greater survival than those on the liver and yeast diet at this relative humidity ($F = 29.5$; df = 3, 35; $P < 0.001$). At 64% RH (Table 2), again diet was the only significant predictor of male survival,

with males of both strains on the skin and dust diet living longer than those on the liver and yeast diet ($F = 125.3$; df = 1, 37; $P < 0.001$).

Immature Development. Only PC1 had an eigenvalue greater than 1, and it explained 78.8% of the variation in egg, juvenile, and total development. PC1 was positively correlated with all of these factors, and it had high factor loadings of all, suggesting that the dependent variables are highly intercorrelated and likely to show similar patterns among the ANOVAs.

The significant interactions between strain and relative humidity and strain and diet in predicting PC1 ($F = 85.6$; df = 5, 255; $P < 0.001$) indicate that the effects of strain on immature development are different at different levels of relative humidity and on different diets. These findings suggest that effects detected within each developmental trait were real and not artifacts of accepting random patterns as significant due to the number of separate tests done.

Egg Development. The three-way interaction between mite strain, diet, and relative humidity was significant ($F = 91.1$; df = 7, 333; $P < 0.001$). Compared with 75% RH, egg mortality at 64% was 40% higher in laboratory mites on the liver and yeast diet. On this diet, eggs of both strains of mites developed faster at 75% RH compared with 64% ($F = 111.6$; df = 7, 333; $P < 0.001$). However, on the skin and dust diet, although the laboratory strain showed more rapid egg development at 75% compared with 64%, egg development in the wild strain was inhibited at 75% RH ($F = 100.6$; df = 7, 333; $P < 0.001$) (Tables 1 and 2).

At 75% RH (Table 1), there was no effect of diet on egg development. Eggs from the laboratory strain, however, developed more quickly than those laid by the wild strain on both diets ($F = 52.7$; df = 1, 198; $P < 0.001$).

At 64% RH, both mite strain and diet influenced egg development (Table 2). Developmental times were quicker when the laboratory mite strain was on its accustomed diet (liver and yeast) compared with the skin and dust diet and also when the wild mites were on their accustomed diet (skin and dust) compared with the liver and yeast diet ($F = 194.3$; df = 1, 198; $P < 0.001$). Strain effects were seen on the liver and yeast diet where wild mite eggs had much slower development than eggs from the laboratory strain ($F = 111.6$; df = 7, 333; $P < 0.001$), whereas the reverse was true on the skin and dust diet.

Juvenile Development. No juveniles of either strain of mites completed development on the liver and yeast diet at 64% RH; thus, comparisons could be made between strain and relative humidity on the skin and dust diet only. At 75% RH, both strains had faster juvenile development than at 64% ($F = 70.4$; df = 5, 294; $P < 0.001$) (Tables 1 and 2).

At 75% RH, juvenile development responded differently to diet between strains ($F = 24.3$; df = 3, 196; $P < 0.001$). Each strain had faster development on the diet to which they were accustomed compared with the alternative diet (Table 1). At 64% RH on the skin and dust diet, the wild mites had slower juvenile de-

velopment than the laboratory strain on this diet (F = 60.6; df = 3, 196; P < 0.001) (Table 2).

Total Development. Again, because no juveniles of either strain of mites completed development on the liver and yeast diet at 64% RH, comparisons were made between strain and relative humidity on the skin and dust diet only. On this diet, total development was faster at 75% RH than at 64% RH in both strains (F = 72.3; df = 4, 295; P < 0.001) (Tables 1 and 2).

At 75% RH in the laboratory mite strain, the skin and dust diet markedly delayed total development compared with the liver and yeast diet, but no significant effect of diet was detected in the wild strain (F = 12.0; df = 1, 198; P < 0.001) (Table 1). At 64% RH there were no significant differences in total development of the two mite strains on the skin/dust diet (Table 2).

Discussion

This study has provided life history parameters of laboratory-reared *D. pteronyssinus* on a laboratory diet at 25°C and 75% RH. The mites tested seemed to have higher reproductive parameters and faster development than those from previous reports (Spieksma 1967; Blythe 1976; Dobson 1979; Gamal-Eddin et al. 1983a, 1983b, 1983c; Ho and Nadchatram 1984; Colloff 1987a, 1987b; Andersen, 1988; Hart and Fain 1988; Arlian et al. 1990). Differences between these results are likely to be due to differences in strain of mites, diet, or both. We have demonstrated the importance of diet in this study, and we are also currently investigating the extent to which different strains of wild mites may vary in their life history parameters.

There have been few published studies on life history parameters of laboratory-reared *D. pteronyssinus* at 25°C and 64% RH. However, our laboratory mites seemed to perform less well at low relative humidity than those from previous reports (Gamal-Eddin et al. 1983a, 1983b, 1983c; Colloff 1987a, 1987b). This may be due to the diet of desiccated liver and yeast, which seemed to be unsuitable for mite reproduction and development at low relative humidity compared with the skin and dust diet (see below).

This study also has provided the first comprehensive data set of adult reproduction and immature survival and development of wild *D. pteronyssinus* in optimal and suboptimal rearing conditions. Previously, only egg survival and development have been reported by Colloff (1987a, 1987b), who suggested that eggs of wild mites survive better and develop more quickly than those of laboratory mites when reared in cool, dry conditions of temperature and relative humidity, whereas in warm, humid conditions the reverse is true. Our results also suggest that laboratory mites perform better (higher fecundity and rate of reproduction, shorter prereproductive period, and faster egg development) than wild mites in optimum rearing conditions (75% RH), but in suboptimum conditions (64% RH), laboratory-reared mites perform less well (lower fecundity, shorter reproductive period, reduced female survival, and higher egg mortality) on the liver and yeast diet than wild mites. In contrast, on the skin

and dust diet at low relative humidity, fecundity, rate of reproduction, reproductive period, and female survival of laboratory mites were higher than found in wild mites, but rearing the laboratory mites before the experiment on an optimized liver and yeast diet is likely to have had an influence on their subsequent egg production and survival on the skin and dust diet.

In some arthropods, specific traits can be selected after as little as five generations (Navarro et al. 1985, Yano and Takafuji 2002, Young et al. 2003). Therefore, during the period between collection and the start of experiments, it is possible that our wild mite cultures may have, in part, adapted to laboratory culture conditions and thus represent an intermediate stage between wild and fully adapted long-term laboratory cultures. However, this seems unlikely, because our wild cultures were reared in conditions relating very closely to those found in the home (diurnally fluctuating hygrothermal conditions) and on a natural diet consisting of only skin scales and house dust.

The poor performance of adults and immatures on the liver and yeast diet compared with the skin and dust diet at low relative humidity was particularly striking. Most existing data on reproduction and development of house dust mites have been obtained from mites reared on laboratory diets that are highly nutritious and that provide good population development in optimum hygrothermal conditions, but such diets may not provide an ideal substrate for mite survival at low relative humidity. This could explain the sparse data on survival, reproduction, and development of house dust mites reared at relative humidities below 75%. However, de Saint Georges-Gridelet (1984) previously reported high population growth of *D. pteronyssinus* at 64% RH on diets high in lipids. In this study, lipids present in skin scales in the house dust substrate could explain the survival of mites in their natural habitat where hygrometric conditions are often below the critical equilibrium activity (Arlian 1975, Arlian and Veselica 1981) of the mites. Our results seem to agree with this hypothesis, and they suggest that data on mite performance on laboratory yeast-based diets, particularly in suboptimal conditions, are unlikely to represent performance on a skin-based diet in their natural dust habitat.

Population models to predict dust mite populations in homes are currently under development by using previously published data primarily from laboratory populations of mites reared on laboratory diets (Pretlove et al. 2001, 2005; Crowther et al. 2006; Biddulph et al. 2007). The current study has highlighted the requirement for a more comprehensive data set from wild mite populations reared on a natural diet for use in these models. Work is underway by the current authors to provide these data.

Another critical factor likely to have an influence on the life history parameters of house dust mites is fluctuating temperature and relative humidity. De Boer et al. (1998) have shown that *D. pteronyssinus* can survive and produce eggs when held at low relative humidity and given as little as 3 h of moist air per day. Arlian et al. (1999) suggested that the development of

Dermatophagoides farinae (Hughes) was slower in fluctuating relative humidity compared with constant high relative humidity. More recently, Pike et al. (2005) found that the population dynamics for *D. pteronyssinus* were similar in both fluctuating and constant conditions of temperature and relative humidity. However, Colloff (1987a) proposed that laboratory mite populations were less able to withstand diurnal fluctuations in microclimate than wild populations of mites. This is also the subject of a subsequent article by us using wild mites reared on a natural diet.

Acknowledgments

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