5. Development, life histories and population dynamics

Dead men may envy living mites in cheese,
Or good germs even. Microbes have their joys,
And subdivide, and never come to death.

Wilfred Owen, A Terre.
In: Blunden, E. (Ed.) The Poems of Wilfred Owen
Chatto & Windus (1931)

5.1 Introduction

The life history of any animal concerns the various details of its reproduction and development. These include characteristics of the life cycle, known as life history traits, such as size at birth, age and size at maturity, longevity, mortality, fecundity, number and sex ratio of offspring, as well as the responses of these variables to factors such as diet, temperature and humidity. Most of these life history traits represent key variables in demography, or the study of populations. Combined, these traits are expressed in ways that affect evolutionary fitness, with inevitable trade-offs between reproduction and survival. A good introduction to the interaction of these factors in relation to the way certain life histories have evolved is provided by Stearns (1992).

Comparative life history biology of pyroglyphid, acaroid and glycyphagoid mites can give some insights into their biological 'success', and their relative importance as allergen-producing organisms. By 'success', I mean simply their global distribution and abundance and their capacity to persist following changes in environmental conditions. This chapter highlights the differences in life history traits between these major groups of domestic mites, the relationship between these traits and population dynamics, and the likely consequences for allergen exposure, mite control and avoidance. This approach is useful – not least because several of the species considered herein are found within the same habitats, the same homes or the same geographical regions, although there is a paucity of information on the population consequences of their interactions.

We have already seen a simple example of how life history traits may affect the trade-off between reproduction and survival. In Chapter 3, I explored the association between water loss, the size of females and their eggs, and their rates of fecundity. It emerged there were four categories:

1. small mites that lay a few, large eggs (for example *Euroglyphus maynei*);
2. medium-sized mites that lay a few, medium-sized eggs (such as *Dermatophagoides* spp.);
3. large mites that lay moderate numbers of medium-sized eggs (Glycyphagoidea);

4. very large mites that lay large numbers of eggs that are small relative to the size of the female (Acaroidea).

I suggested that a major constraint on the size and number of eggs produced was the amount of water that has to be acquired by the mother, allocated to the eggs and then expelled from the mother's body upon oviposition. Thus small mites with large eggs lay fewer, less often and over a shorter period than large mites with small eggs. As well as water, the egg contains yolk proteins that require energy-expensive synthesis by the mother from the raw materials of digestion. A major determinate of egg size is the proportion of the mother's dietary intake that can be invested in the egg (a process known as 'bestowal' or 'allocation').

Are there trade-offs between egg size and the survival of the offspring? Do mites from bigger eggs that contain more yolk resources have lower mortality? Or do larger eggs take longer to develop and have therefore extended vulnerability to lethal events like desiccation compared with small eggs? These sorts of questions will be examined in this chapter. They deal with trade-offs, the interaction of reproductive traits (numbers of eggs, development time, oviposition period, mortality and so on) and how these characteristics shape the seasonal rises and falls in the size of mite populations which, in turn, influence the amounts of allergens available to which people can become exposed.

5.2 Stages in the life cycle

Pyroglyphid mites have six stages in the life cycle: egg, prelarva, larva, protonymph, tritonymph and adult (see Figure 5.1.). Glycyphagoid and acaroid mites do not have a prelarva but may have an additional nymphal stage, the deutonymph, in the form of a motile or immotile hypopus. The larval and nymphal stages each have periods of activity and feeding followed by quiescent periods prior to moulting.

5.2.1 The egg and the embryo

All the astigmatid mites found in house dust are well under a millimetre in length as adults, which means their eggs are considerably smaller. The eggs tend to be white in colour, oval and elongate. When laid they may be coated in a thin layer of sticky mucus which adheres them to the substratum. The eggs of *Dermatophagoides farinae* are ca. 160–180 μm long, 70–90 μm broad (Walzl, 1988), while those *of D. pteronyssinus* are ca. 150 μm long by 60 μm broad (see Figure 5.2a) and those of *Euroglyphus maynei* ca. 120 μm long by 55 μm broad (Colloff, 1991b).

The eggs of *Tyrophagus* spp. are smooth when they start to develop but then become heavily ornamented with bands of tubercular microsculpture that protrude from the surface of the shell (Hughes, 1976, her Figure 56). This microsculpture is quite unlike that of other domestic mites which tend to have relatively smooth shells. Scanning electron microscopy reveals the shell (or chorion) of *T. putrescentiae* consists of a complex series of domed exochorionic structures with basal openings (Callaini and Mazzini, 1984). These structures appear to be able to retain a moist layer of air near the surface of the egg in order to reduce water loss, and I suggest that in *Tyrophagus* the egg is the stage in the life cycle that is adapted for survival of desiccating conditions. The females of *Lepidoglyphus destructor* habitually cover most of their eggs with fragments of food and debris (Barker, 1983). This too may be a method for reducing water loss during embryonic development.

Embryological investigations of mites are relatively few and fragmentary. The study by Hafiz (1935) for *Cheyletus eruditus* is one of the more detailed. The following account of the development from egg to larva is based on the study by Walzl (1988) of *Dermatophagoides farinae* (shown in Figures 5.2, 5.3). Embryonic development of *D. farinae* at 75% RH, 25°C takes 170–180 hours, with the completion of the blastula about 20 hours after oviposition (see Figures 5.2b, 5.3b). By 36–40 hours differentiation of the blastoderm is evident, with the germ band and prosomal limb buds present on the ventral surface and extra-embryonic ectoderm present dorsally (see Figures 5.2c, 5.3c). By 48 hours the embryo has closed except for an oval region of extra-embryonic ectoderm in the posterior portion of the embryo (see Figure 5.3d). The chelicheral limb buds form first, then those of the palps, followed by the three pairs of legs. By 74–76 hours a pair of median protrusions appear posteriorly behind the buds representing the third pair of legs (see Figure 5.3e). These protrusions represent the terminal prosomal and initial opisthosomal segment.

5.2.2 The prelarval and larval stages

Pyroglyphid mites, but not glycyphagoids or acaroids, have a vestigial prelarval stage, consisting of a thin membrane that develops inside the eggshell. By about 100 hours after the start of blastulation, a pair

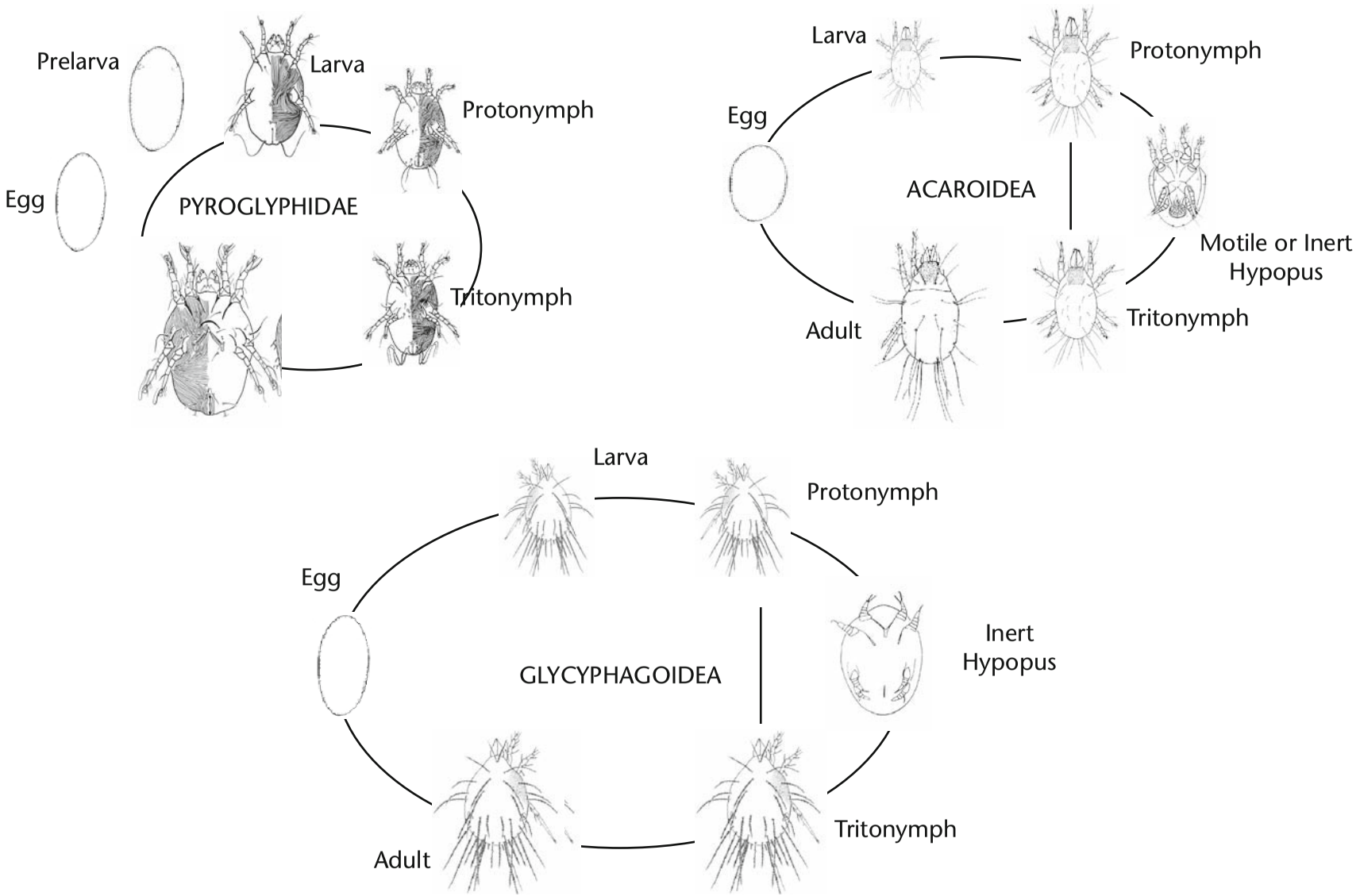

Figure 5.1 Stages in the life cycles of pyroglyphid, acaroid and glycyphagoid mites.

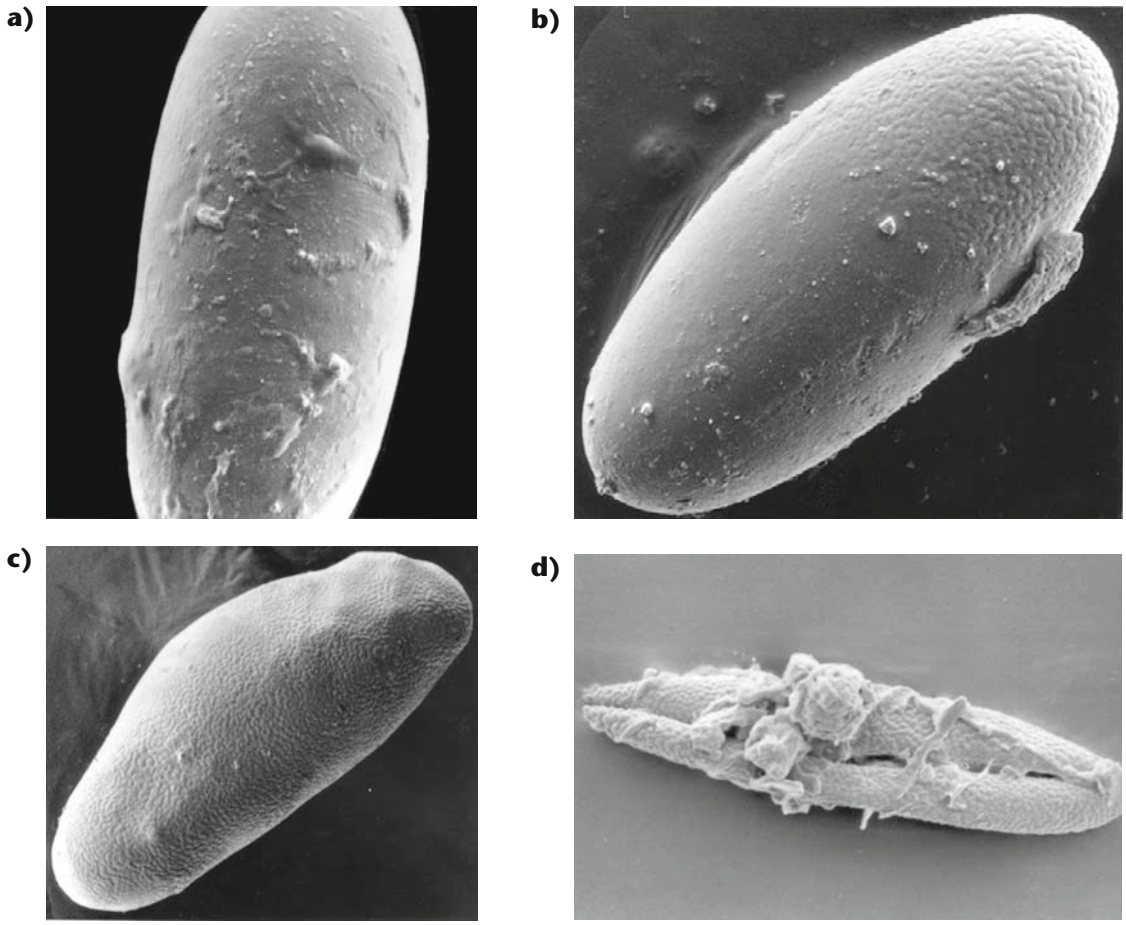

Figure 5.2 Eggs of *Dermatophagoides pteronyssinus*. **a)** Newly laid with layer of mucus; **b)** egg at blastodermal stage with polar change in microsculpture of the cuticle; **c)** at mid/late embryonic stage, with limb buds evident through the cuticle; **d)** cuticle after the larva has hatched, showing dorsoventral line of excision.

of hemispherical egg teeth with pointed tips have developed near where the chelicerae will eventually be, indicating the completed sclerotisation of the prelarval phase (Walzl, 1988). The larva then develops within the prelarval integument. Fain (1977) found females of *Dermatophagoides farinae*, *D. pteronyssinus*, *Euroglyphus maynei* and *Sturnophagoides brasiliensis* that contained eggs in which prelarval or larval development was evident. This suggests these species are ovoviviparous, i.e. the offspring develop within the mother prior to oviposition. However, pyroglyphids are probably normally oviparous (i.e. development occurs after oviposition) but some eggs are not oviposited for some reason, and larval development continues regardless. Fain and Hérin (1978) reported larval development in dead females of *Lepidoglyphus destructor*.

The six-legged larva has a characteristic posture within the egg with its first two pairs of legs folded ventrally and pointing posteriorly and the third pair pointing anteriorly (see Figure 5.3f). The eggshell is split longitudinally (see Figure 5.2d) by the egg teeth and the larva emerges, leaving the prelarval integument, along with the egg teeth, inside the shell (Walzl, 1988).

5.2.3 The nymphal stages

a The protonymph

Protonymphs are obligate stages in the life cycle of astigmatid mites. They have four pairs of legs and one pair of genital papillae. In crowded cultures of *Dermatophagoides farinae* and *D. pteronyssinus*, Ellingsen (1974, 1975) observed immobile (quiescent) protonymphs, which represent a facultative stage that appears in response to high population densities. The stage may have a similar function as the non-phoretic hypopi in the

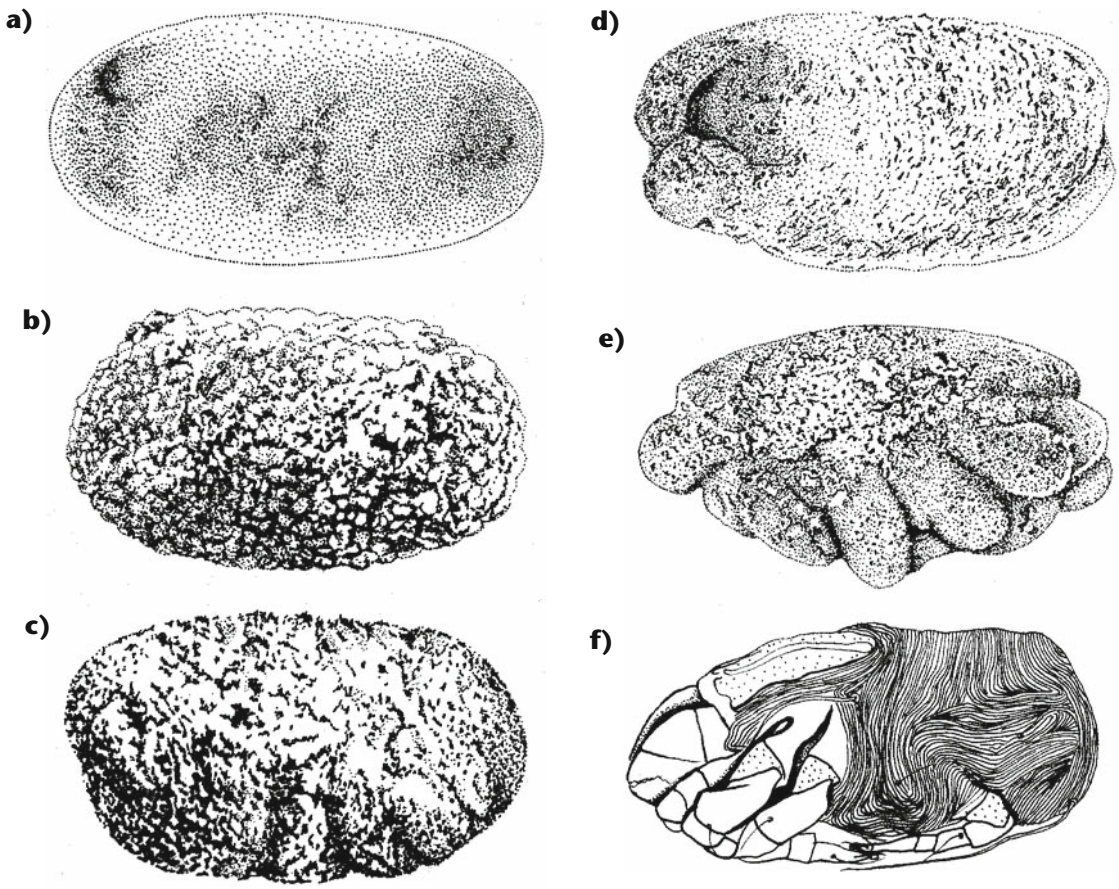

Figure 5.3 The embryonic development of *Dermatophagoides farinae*. **a)** Undifferentiated egg; **b)** uniform blastoderm completed, ca. 20 hours after oviposition; **c)** blastoderm differentiated into germ band and limb buds on ventral side and ectoderm on dorsal side, 36–40 hours; **d)** complete dorsal closure of embryo except for posterior plate of extra-embryonic ectoderm, 48 hours; **e)** limb buds, last prosomal and first opisthosomal segments developed, 74 hours; **f)** hexapod larva fully developed, ca. 100 hours. (Re-drawn from Walzl, 1988.)

Glycyphagidae (Wharton, 1976; see below). Oxygen consumption by quiescent protonymphs is nearly 30 times less than active protonymphs (Ellingsen, 1978) and body water exchange is nearly 140 times slower (Arlian and Wharton, 1974; Ellingsen, 1975), suggesting metabolism is slowed and they represent a survival stage.

b The hypopus

The hypopus (plural: hypopi or hypopodes) is equivalent to the deutonymphal, or second nymphal stage. Its role in the life cycle is the survival of unfavourable conditions and dispersal. In the Pyroglyphidae, the Sarcoptidae (*Sarcoptes* spp. – the scabies mites) and Psoroptidae (*Psoroptes* spp. – the mange mites), the hypopial stage is absent, and protonymphs moult into tritonymphs (see Figure 5.1). In the Acaroidea and Glycyphagoidea, protonymphs may also moult into tritonymphs or they may go through the hypopial stage. Hypopi come in two types: motile forms (see Figures 5.4a–d) which are dispersed on insects (phoretic dispersal), and inert forms which are a survival stage, but are light enough to be dispersed on air currents (Alberti and Coons, 1999; Figures 5.4e–g).

Within the Acaridae, *Acarus siro* has a facultative motile hypopus. This stage attaches to larger arthropods using a set of suckers in the anal region (shown in Figures 5.4c, d). It is dispersed by hitch-hiking on insects, a process known as phoresy (Binns, 1982). Thus motile hypopi are also occasionally known as phoretomorphs. The occurrence of motile hypopi in populations of *Acarus siro* is rare, but frequency and abundance increases in sub-optimum conditions (Hughes, 1976). Non-hypopial-forming strains exist. *Acarus immobilis* and *A. gracilis* have an inert

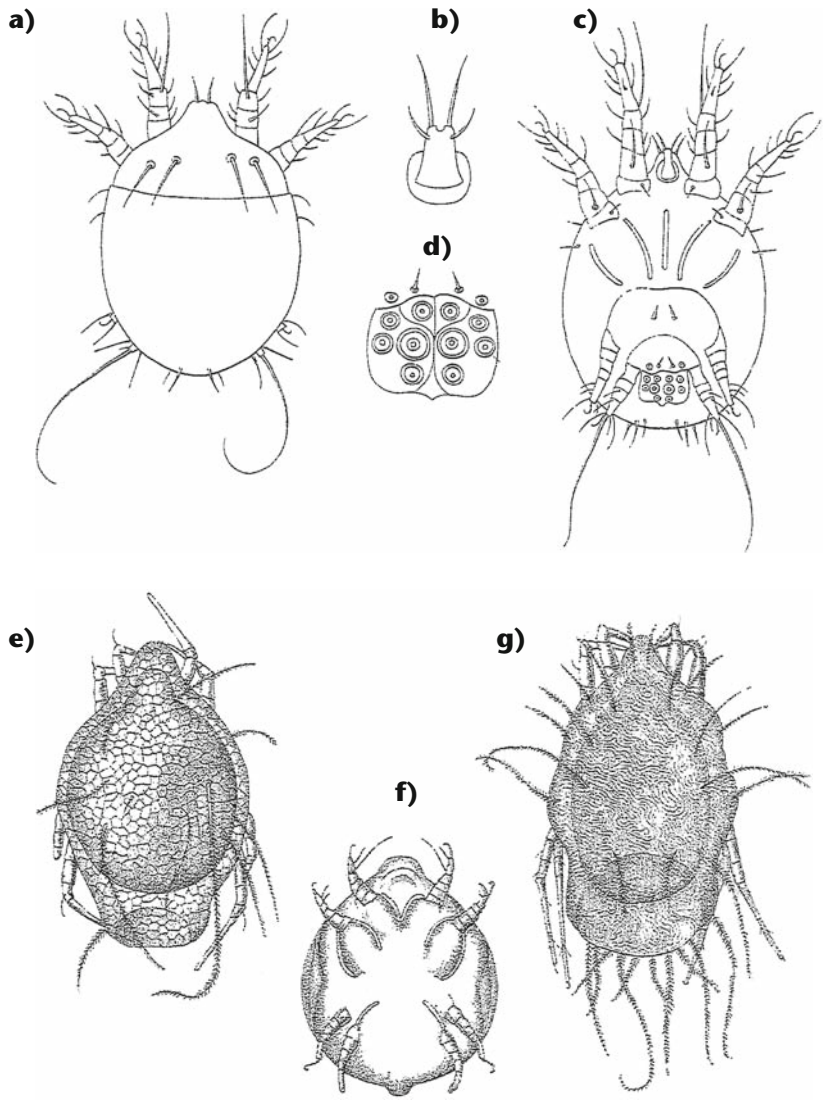

Figure 5.4 a–d) The active hypopus of an acarid mite, *Acarus farris* (from Michael, 1903, pl. 39, Figures 1–4, as *Tyroglyphus longior*, but cf. Griffiths (1964) for details of misidentification). **a)** Dorsal surface; **b)** vestigial gnathosoma; **c)** ventral surface; **d)** anal sucker plate; **e–g)** inert hypopodes of glycyphagid mites (from Michael, 1901, pl. 8, Figures 11, 12, 17); **e)** tessellated protonymphal cuticle of *Lepidoglyphus destructor*; and **g)** striated cuticle of *Glycyphagus domesticus* containing **f)** the inert hypopus, within which the tritonymph develops.

hypopus, which looks like a reduced form of the active hypopus without the anal sucker plate and with fewer setae on the legs and body. Hypopi have been recorded from only one species of *Tyrophagus*. Of the Glycyphagoidea, *Glycyphagus domesticus* and *Lepidoglyphus destructor* have immotile hypopi only. They are different from those of *Acarus* spp., being enclosed within the protonymphal cuticle. In *Lepidoglyphus* and *Glycyphagus* spp. the protonymphal cuticle enclosing the hypopus has a tessellated microsculpture, quite different from that of the normal protonymphal cuticle (shown in Figures 5.4e, g). The tritonymph may develop within the inert hypopus, within the protonymphal exuvium (Alberti and Coons, 1999, their Figure 17). Hypopi have highly reduced, non-functional mouthparts and show varying degrees of regression of the gut. In the immotile hypopi the internal organs degenerate into a mass of undifferentiated cells and tissue. Only the nervous system remains intact (Hora, 1934; Hughes and Hughes, 1939). The processes of moulting and encapsulation of the hypopus

in the protonymphal cuticle of *L. destructor* and *G. domesticus* were studied by Wallace (1960). Hypopi are not known from the genera *Blomia*, *Chortoglyphus* and *Gohieria*.

The existence of the hypopial stage caused considerable confusion for acarologists in the 19th century, so much so that it became known as 'The Hypopus Question' (Michael, 1884). Various theories were advanced (summarised by Michael, 1901), mostly that hypopi were adults of previously unknown taxa. Mégnin (1876), working with what he referred to as *Tyroglyphus mycophagus* (either *Caloglyphus mycophagus or C. berlesei*), surmised that the hypopus is 'the "cuirassed" [that is armoured, sclerotised] heteromorphous, adventitious nymph of *Tyroglyphus* entrusted with the preservation and distribution of the species under adverse circumstances'. Even though Mégnin's conclusion is basically correct, it is not the whole story because there is more than one kind of hypopus. Michael (1884) realised that *Caloglyphus* protonymphs moulted to become hypopi, regardless of whether conditions were adverse or not. The hypopi dispersed by attaching themselves by their anal sucker plates to insects. However, not all protonymphs became hypopi. Some moulted and became tritonymphs.

Michael (1901) was also aware that there were three morphologically distinct forms of hypopus, which he describes: those with posterior sucker plates that disperse on insects; others, which he referred to as the Homopus type, which cling to hairs of mammals by means of a bilobed posterior structure (but without suckers); and the third, the rudimentary, quiescent form of certain *Glycyphagus* spp. He appreciated the economic importance of hypopi, as the dispersive stage of stored products mites:

> *The hypopial stage is biologically far the most interesting portion of the life history of the Tyroglyphidae; it is also of considerable commercial importance, because it is the existence of this remarkable provision that enables many of the most destructive species to spread themselves almost all over the world as they do.*

The evolutionary significance of glycyphagid hypopi (Knülle, 1987, 1991, 1995, 2003; Corente and Knülle, 2003) is that hypopi can survive extreme and prolonged dry conditions, as well as being able to disperse to new habitats. Therefore, hypopi represent an ecologically flexible, risk-reduction strategy against fluctuations in conditions in temporary, patchy habitats in which many of these mites live.

c The tritonymph

Tritonymphs are obligate stages in the life cycle of astigmatid mites. They have four pairs of legs and two pairs of genital papillae, compared with one pair in the protonymphs. More leg and body setae appear in the tritonymphal stage. In pyroglyphid tritonymphs that are ready to moult, the adult cuticle can be observed through the tritonymphal cuticle. I have observed adult males 'guarding' inert tritonymphs. All of them turned out to be females, and the males were waiting for them to moult and emerge in order to mate with them.

5.2.4 The adults

Reproductive morphology and function has been covered in Chapter 2. Female pyroglyphids, acaroids and glycyphagoids tend to be larger than their corresponding males, and tend to live longer.

a Sex ratios

Pyroglyphids, acaroids and glycyphagoids are obligate sexual reproducers. The sex ratio in pyroglyphids is typically close to 1:1 (Hodgson, 1976a), but it can vary considerably in some species. An average of 61% of adults of *Lepidoglyphus destructor* were females (range 14–92%; Chmielewski, 1987), and an average of 56% of adults of *Glycyphagus domesticus* were females (range 20–71%; Chmielewski, 1988).

b Andropolymorphism

Some species in the genera *Dermatophagoides*, *Hughesiella* and *Sturnophagoides* are andropolymorphic (Woodring, 1969). The heteromorphic form of the males has the first or third pair of legs greatly enlarged (refer to Chapter 1 for more detail). The adaptive significance of male polymorphism has been studied in the acaroid mites *Caloglyphus berlesei* and *Rhizoglyphus robinii* (Radwan, 1993, 1994). The thickened third pair of legs is used to attack and kill other males (both homomorphic and heteromorphic forms) by puncturing the cuticle. These 'fighter' males appear to be produced in response to low population densities, a circumstance under which it might be hard to find a mate. Poor diet inhibited the appearance of fighters of both species (Radwan, 1994). The trait is not heritable in *C. berlesei*, but *R. robinii* fighters were more likely to have been sired by fighter fathers (Radwan, 1994). In

small colonies of *C. berlesei*, fighters were more reproductively successful, mainly because they were able to kill all the other males and monopolise the females, but in larger colonies non-fighter males were more reproductively successful because the fighters tended to be killed by rival males more frequently than non-fighters (Radwan, 1993). The occurrence of the fighter phenotype seems to be a response to conditions where there is a good chance of eliminating rivals without being killed, thereby improving mating success and conferring a selective advantage on these individuals.

c *Sperm competition*

The observation by Furumizo (1975a) that males and females of *D. farinae* copulate four or five times with different partners suggests that dust mites may exhibit some form of sperm competition. After intromittent transfer, pyroglyphid sperm remains in the female receptaculum seminis until required to fertilise an egg. Male pyroglyphids are not known to remove the sperm of the previous mate of their partners, but in *Caloglyphus berlesei*, the sperm from the last male to mate with the female fertilises 86% of her eggs (Radwan, 1991a), and does so because he is able to displace the sperm of previous males (Radwan, 1991b). Males of *Rhizoglyphus robinii* that produced larger sperm of even size were more reproductively successful than those that produced smaller sperm more variable in size, and reproductive success was independent of the number of sperm per ejaculate, duration of copulation or male body size (Radwan, 1996).

5.3 Why population dynamics is of practical importance

If asked whether it was more effective to control mites when the population was at its highest or lowest density, most people, including many dust mite researchers, would reply: 'When at its maximum, of course – the more mites you kill, the better!' Intuitively, this answer seems to be rational, practical and correct, but it is flawed because it neglects the fact that dust mites are living, reproducing organisms and their populations tend to increase exponentially. The counter-intuitive approach is that control is more likely to be effective when population density is low, but most effective for mites with populations that fluctuate seasonally, at the time of year just before exponential growth. A female *Dermatophagoides* may lay 30 or more eggs in a month, of which 80% survive to adulthood. Half of these will become females (assuming a 1:1 sex ratio) so by the end of the first month she produces 12 new females (that is 80% of 30 ÷ 2), each capable of generating 12 females. By the end of the second month there would be 144 females. At the end of the third, 1728, and after 6 months, 35.8 million. If a control method achieves a 90% kill of a month-old population there would be one female left. In a 6-month-old population there would be 3.6 million, capable of producing 17.2 million females by the end of the following month. Although the control method seemed to be highly effective at first sight, when put into practice it was a catastrophic failure because the capacity for the dust mite population to regenerate was not taken into account.

This example is both extreme and simplistic (it does not factor in deaths – *Dermatophagoides* spp. only live for about 6 weeks). In nature, a single female dust mite does not give rise to such enormous populations after so few months. Nor do populations continue to grow exponentially. But it serves to emphasise that it is vital to be able to understand the linkage between dust mite control and how populations work in order for dust mite control to be successful. Hitherto, population dynamics have been ignored by most researchers involved in dust mite control. Considering that the control of dust mites effects drastic change on birth and death rates – two of the most basic population parameters – such an omission is remarkable. Furthermore, seasonal fluctuation in mite population density is the underlying cause of seasonal increases in allergen exposure suffered by people with dust mite hypersensitivity. Population dynamics impact directly on allergen exposure, epidemiology and clinical management.

The following sections deal with life tables, the intrinsic rate of natural increase and age structure. These are all elements of classical demographic theory, as developed by Lotka (1922) and extended by Birch (1948): so-called 'stable theory', because it deals with demography of populations that have stable age distributions. I have drawn mainly upon Birch (1948), Andrewartha and Birch (1954), Carey (1993, 2001) and Krebs (2001) as a basis for these sections. The chapter on demography by Stearns (1992) is also useful. Similar accounts can be found in most ecology textbooks.

Carey and Krainacker (1988) point out that many of the concepts and techniques of classical demography are particularly appropriate for the study of mite populations because mites have simple life cycles with overlapping generations, their ages can be estimated from

their morphologically unique life cycle stages, they are easy to rear and their populations grow rapidly. Krebs (2001) observed that these demographic techniques can be used to investigate why organisms evolve one type of life cycle rather than another, and Stearns (1992) referred to demography as the key to life history theory. A great deal of the present book is a tale of eight domestic mite species belonging to three major taxa: *Dermatophagoides farinae*, *D. pteronyssinus* and *Euroglyphus maynei* (the Pyroglyphidae), *Lepidoglyphus destructor*, *Glycyphagus domesticus* and *Blomia tropicalis* (the Glycyphagoidea), *Acarus siro* and *Tyrophagus putrescentiae* (the Acaridae). The comparative demography of these mites allows us to better understand how their different life histories have evolved, as well as their patterns of distribution and abundance.

Populations are complex entities. They change in size as a result of many interacting variables, but the basic parameters that are responsible for changes in population growth centre around the balance between the number of individuals being added to the population (that is being born or migrating into it) and the number leaving the population (that is dying or emigrating). For domestic mites, most of the available data on birth and death rates comes from laboratory studies (shown in Tables 5.1, 5.2). The vast majority of these deal with the effects of two variables – temperature and humidity. A few studies deal with the effects of different diets.

Life history parameters of domestic mites are so plastic over a large range of temperatures, humidities and diets that the laboratory approach has been regarded as the only way of determining them with any degree of accuracy. Typically, this is done by rearing mites at constant conditions. The only variable likely to be considered other than humidity and temperature is diet. Of course in human dwellings conditions of temperature and humidity are anything but constant, and vary diurnally, seasonally and spatially, so laboratory-derived data is quite artificial. For those species that occur in stored products, temperatures and humidities in warehouses and granaries are kept reasonably constant and the data is more applicable. Many of the laboratory studies on population parameters were done in order to determine the physical conditions of storage required to inhibit growth of populations of stored products mites (Solomon, 1962; Cunnington, 1965, 1985) because manipulation of temperature is one of the more straightforward methods of control.

Although there are lots of studies on seasonal fluctuations in population size of dust mites in their natural habitats (see below), they are almost entirely descriptive. There are no published studies that have collected empirical data on seasonal fluctuations in population density and modelled them using demographic techniques. Hence, laboratory-derived data on population growth at constant conditions is virtually all the information that is available for demographic analyses. However, this kind of data is especially useful for comparing population performance of different species.

5.4 Demography

Demography is the mathematics of populations – the statistics of births and deaths. The size of a population (X) at any given time can be expressed as:

$$X = (I + B) - (E + D)$$

where B is the total number of live births, I is the total number of individuals migrating into that population, D is the total number of deaths and E is the number of emigrants.

5.4.1 Migration

For dust mite populations, there is virtually nothing known about the migrant component. Unlike, say, waterbirds on wetlands, where several populations may exist with free migration between them, dust mite populations are geographically isolated from each other. There is almost no continuum of habitable space for dust mites between one home and its neighbours. Periodic events such as bringing in a second-hand sofa are likely to have an effect on the size of the mite population, but otherwise there is little intermingling of populations from one home with those of another. Two situations where that may prove to be an exception are the presence of feral dust mite populations in nests of birds and the presence of mites in clothing. Dust mites are known to inhabit nests of anthropophilic birds such as swallows, swifts, martins, sparrows and pigeons; indeed it is from this source that it has been hypothesised that dust mite populations in homes originated (discussed in Chapter 1). Nests within attics or under eaves could conceivably provide a source of immigrant mites, although this has not been investigated. The evidence that there may be immigration of mites on clothing of visitors to the home is more plausible because of the densities

Table 5.1 Publications containing life history data on domestic mites, based on laboratory studies.

Spp. & reference	RH% range	T°C range	Egg duration (days)	Immatures (days)	Adult female	Total longevity	Pre-oviposition	Oviposition	Mean fecundity	Eggs/female/day	Egg mortality (%)	Juvenile mortality
Dermatophagoides pteronyssinus												
Pike *et al.*, 2005	75	23	+	+	+	+		+	+	+	+	+
Arlian *et al.*, 1990	75–80	16–35	+	+	+	+	+	+	+	+	+	
Matsumoto *et al.*, 1986	61–86	25	+	+	+	+	+	+	+	+	+	+
Blythe, 1976	75–80	25		+								
Colloff, 1987b	75–80	25	+									
Dobson, 1979	60–100	20–35	+	+	+	+						
Gamal-Eddin *et al.*, 1983a–d	75	15–40	+	+	+	+		+	+	+	+	+
Hart & Fain, 1988				+			+	+	+	+		
Ho & Nadchatram, 1984	75	23–37	+	+	+	+					+	+
Saleh *et al.*, 1991	75	25	+	+	+	+	+	+	+	+	+	
Spieksma, 1967	75–80	25	+	+	+	+		+	+	+		
Dermatophagoides farinae												
Arlian & Dippold, 1996	75	16–35	+	+	+	+		+	+	+		+
Matsumoto *et al.*, 1986	61–86	25	+	+	+	+	+	+	+	+	+	+
Furumizo, 1975a	75	16–32	+	+	+	+		+	+	+	+	
Hart & Fain, 1988	75	25		+			+	+	+	+		
Gamal-Eddin *et al.*, 1983a–d	75	15–40	+	+	+	+	+	+	+	+	+	+
Euroglyphus maynei												
Taylor, 1975	60–80	25–30	+	+	+	+	+	+	+	+	+	
Colloff, 1992a	60–80	25–30	+	+	+	+	+	+	+	+	+	+
Hart & Fain, 1988	75	25		+			+	+	+	+		
Tyrophagus putrescentiae												
Boczek, 1974	85	20					+	+	+			
Czajkowska & Kropczynska, 1991	85	25		+								+
Eraky, 1995a, b	80–90	18–26	+	+	+	+	+	+	+	+	+	+
Hart, 1990	75–100	12.5	+	+			+	+	+	+	+	+
Liu *et al.*, 2006	73–87	13–30	+	+			+					
Rivard, 1961a, b	70–100	20–30	+	+	+	+	+	+	+	+	+	+
Sanchez-Ramos & Castanera, 2001, 2005	90	19–34	+	+	+	+	+	+	+	+	+	+
Acarus siro												
Davis & Brown, 1969	70, 90	15	+	+	+	+	+	+	+	+	+	+
Chmielewski, 1995	85	20	+	+	+	+	+	+	+	+	+	+
Cunnington, 1985	65–90	5–30	+		+			+	+	+	+	
Davis & Brown, 1969	70–90	15–20	+	+								
Emekçi & Toros, 1989	70–90	10–25	+	+	+	+	+	+	+	+	+	
Fejt & Zdarkova, 2001	70–90	18–20	+	+	+	+		+	+	+		
Glycyphagus domesticus												
Barker, 1968	70–100	12–24	+	+			+	+	+		+	+
Chmielewski, 1988	65–95	5–25	+	+	+	+	+	+	+	+	+	+
Hart, 1990	75	25		+			+	+	+	+		
Hora, 1934	90	25	+	+								
Lepidoglyphus destructor												
Barker, 1983	75	14–25	+	+			+	+	+	+	+	+
Chmielewski, 1987	65–95	5–25	+	+	+	+	+	+	+	+	+	+
Blomia tropicalis												
Mariana *et al.*, 1996	75	25	+	+	+		+	+	+	+	+	+

Table 5.2 Comparison of some basic life history parameters of domestic mites at or near optimum temperature and humidity for population growth.

Spp.	Optimum temperature	Optimum RH%	Egg duration (days)	Immatures (days)	Adult female	Pre-oviposition period (days)	Oviposition period (days)	Mean fecundity (no. eggs)	Eggs/female/day	Egg mortality (%)	Total juvenile mortality (%)	Reference
Pyroglyphidae												
Dermatophagoides farinae	27	75	7.1	15.8	24.2	ND	19.8	50	2.5	14	ND	Furumizo, 1975a
D. pteronyssinus	23	75	8.1	25.9	31.2	4.3	23.3	68	2.8	14	ND	Arlian *et al.*, 1990
Euroglyphus maynei	25	75	5.0	21.0	19.0	3.1	13.8	15	1.1	17	61	Taylor, 1975
Glycyphagoidea												
Glycyphagus domesticus	25	85	4.4	17.4	12.6	3.1	9.2	26	2.8	68	68	Chmielewski, 1988
Lepidoglyphus destructor	25	85	4.1	12.2	17.5	3.2	28.8	141	4.9	49	69	Chmielewski, 1987
Blomia tropicalis	25	75	5.7	14.0	57.5	2.8	16.5	28	1.7	19	40	Mariana *et al.*, 1996
Acaroidea												
Acarus siro	25	90	4.3	4.6	25.5	1.1	18.3	315	17.2	14	ND	Emekçi & Toros, 1989
Tyrophagus putrescentiae	25	90	3.8	5.6	40.0	1.6	21.5	502	24.0	1	5	Sanchez-Ramos & Castanera, 2001, 2005

involved. Bischoff *et al.* (1992a) found between 800 and 4000 mites per garment on pullovers, sweatshirts and trousers.

In any event, the direction and magnitude of migration events have not been quantified, so the basis of dust mite population dynamics currently rests solely on the analysis and quantification of births and deaths.

5.4.2 Mortality and natality

a Mortality and the life table

Mortality in the demographic sense means the rate of death per unit time of a group of organisms, the cohort. Mortality may be highest among young individuals or older ones, or it may be constant throughout life. The rates of mortality are expressed as a series of terms, presented in a life table, which summarises the pattern of mortality of the cohort. Table 5.3 is the life table for *Euroglyphus maynei*, then smallest of our species in the water-loss versus size-of-females example (see Figure 3.6), and *Tyrophagus putrescentiae*, the largest. The temperature and humidity combinations used for comparison are at, or close to, those representing optima for population growth. We do not have to set up a table with every day of the life listed as a row. If we know the duration and the mortality of each stage in the life cycle – the type of data available from the literature (Table 5.1) – we can group rows according to stages. This is called an abridged life table. It is also a single-decrement table, meaning death is treated as a single category and not split into multiple decrements based on cause of death. The components and how they are calculated in Table 5.3 are as follows (see Carey, 1993, p. 19; Carey, 2001, his Table 1):

Column A in Table 5.3 is the stage in the life cycle;
n is the average duration of the stage, in days (column B);

x is the age interval of each stage (column C), e.g. the larva of *E. maynei*, which lasts 7 days,

Table 5.3 Abridged cohort single-decrement life table based on mean development times and survivorship of *Euroglyphus maynei* at 25°C, 75% RH (from Colloff, 1992a, based on data of Taylor, 1975) and *Tyrophagus putrescentiae* at 25°C, 90% RH (data from Rivard, 1961a, b).

		B	C	D	E	F	G	H	I	J	K
Row	**Column A**	**Duration in days, n**	**Age interval, x to $x + n$ (days)**	**Number alive, N_x**	**Proportion surviving, l_x**	**Period survival, p_x**	**Period mortality, q_x**	**Frequency of deaths, d_x**	**Proportion of days lived in the age interval, L_x**	**Total number of days lived beyond age x, T_x**	**Expectation of life (days), e_x**
	Euroglyphus maynei										
1	Egg	5	0–5	85	1.000	0.753	0.247	0.247	4.382	18.587	18.587
2	Larva	7	5–12	64	0.753	0.688	0.313	0.235	4.447	14.205	18.866
3	Protonymph	6	12–18	44	0.518	0.795	0.205	0.106	2.788	9.758	18.850
4	Tritonymph	8	18–26	35	0.412	0.743	0.257	0.106	2.871	6.969	16.926
5	Pre-reproductive period	3	26–29	26	0.306	0.923	0.077	0.024	0.882	4.099	13.400
6	Reproductive period	14	29–43	24	0.282	0.549	0.451	0.127	3.061	3.216	11.392
7	Post-reproductive period	2	43–45	13	0.155	0.000	1.000	0.155	0.155	0.155	1.000
	Final value:	45			0.000			1.000	18.587		
	Tyrophagus putrescentiae										
8	Egg	6	0–6	200	1.000	0.670	0.330	0.330	5.010	10.900	10.900
9	Larva	3	6–9	134	0.670	0.843	0.157	0.105	1.853	5.890	8.791
10	Protonymph	2	9–11	113	0.565	1.000	0.000	0.000	1.130	4.038	7.146
11	Tritonymph	2	11–13	113	0.565	0.903	0.097	0.055	1.075	2.908	5.146
12	Pre-reproductive period	2	13–15	102	0.510	0.108	0.892	0.455	0.565	1.833	3.593
13	Reproductive period	24	15–39	11	0.055	0.818	0.182	0.010	1.200	1.268	23.045
14	Post-reproductive period	3	39–42	9	0.045	0.000	1.000	0.045	0.068	0.068	1.500
	Final value:	42			0			1.000	10.900		

starts being a larva at the end of day $x = 5$ and finishes at the end of day $x + n = 12$;

N_x is the number alive at age x, the beginning of each age interval, based on the size of the cohort (column D);

l_x is the proportion of the cohort still alive at age x (column E); cell D4 divided by D2 = 44/85 = 0.518 (cell E4):

$$l_x = \frac{N_x}{N_0}$$

p_x is the proportion of the cohort still alive at age x (column F) that survive through the period $x + n$; E4/E3 = F3 = 0.688:

$$p_x = \frac{l_{x+n}}{l_x}$$

q_x is the per capita rate of mortality within the period x to $x + n$ (column G); 1 – F3 = 0.205 (G4):

$$q_x = 1 - \frac{l_{x+n}}{l_x}$$

d_x is the proportion of the original cohort that die in the period x to $x + n$ (column H); E3 – E4 = 0.106 (H4):

$$d_x = l_x - l_{x+n}$$

L_x is the per capita proportion of life lived in the period x to $x + n$, assuming that individuals that die in that period do so at its mid-point (Column H); B4 × (E4 − (1/2 × H4) = 2.788 (I4):

$$L_x = \frac{1}{2}(l_x + l_{x+n})$$

T_x is the total number of days lived beyond age x (Column J); I4 + I5 + I6 + I7 + I8 = 13.176 (J4) and I5 + I6 + I7 + I8 = 10.388 (J5):

$$T_x = \sum_{y=x}^{\omega} L_x$$

e_x is the expected number of additional days an individual aged x will live (column K); J4/E4 = 25.454 (K4):

$$e_x = \frac{1}{2} + \frac{l_{x+1} + l_{x+2} + \cdots + l_\omega}{l_x}$$

Table 5.3 provides some useful points of comparison between the two species. Both have highest mortality as immatures (see Figure 5.5) – only a third of all newborns of *E. maynei* survive to adulthood, compared with half of those of *T. putrescentiae* – but mortality during the reproductive period exacts a massive toll on *T. putrescentiae* with over 80% of the females dying during this period, compared with only half of the females of *E. maynei*. The highest probability of death for *T. putrescentiae* occurs during the egg and larval stages, whereas for *E. maynei* it is as a larva or a tritonymph.

b Natality, net reproductive rate and generation time

Natality, or fertility, is the birth rate, the number of eggs produced per female per unit time. By including natality data in the life table (which now becomes a life and fertility table) we can derive the balance between deaths and births. Only the reproductive period needs to be included. The relevant statistic is m_x, the number of female eggs produced per surviving adult female per day at time x. It is half the total number of eggs laid per female per day, assuming an equal sex ratio. By multiplying l_x by m_x and summing the product we get the total number of female offspring for the cohort. This is the net reproductive rate, R_0, which is the multiplication rate per generation (i.e. the period between the birth of parents and the birth of their offspring).

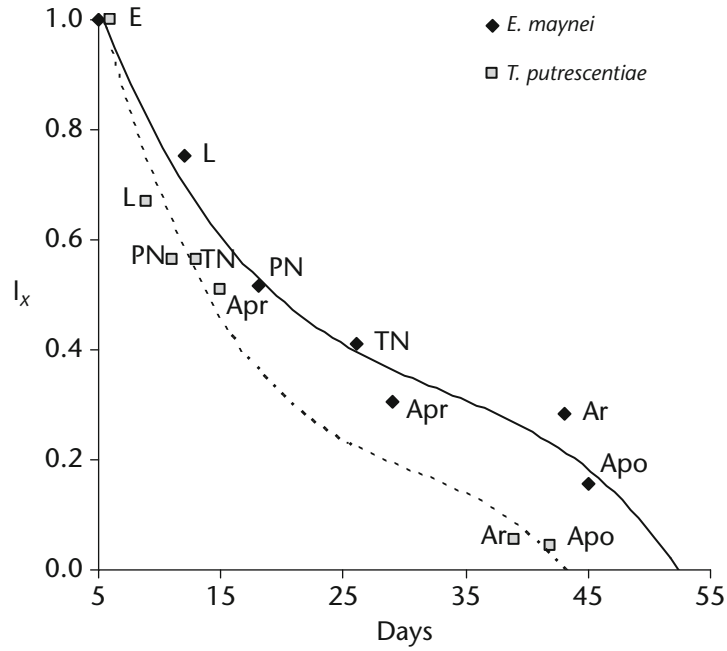

Figure 5.5 Survivorship curves of *Euroglyphus maynei* at 25°C, 75% RH and *Tyrophagus putrescentiae* at 25°C, 90% RH, based on data in Table 5.3. E = egg; L = larva; PN = protonymph; TN = tritonymph; Apr = adult, pre-reproductive period; Ar = adult, reproductive period; Apo = adult, post-reproductive period.

Table 5.4 is the life and fertility table for *E. maynei* at 25°C, 75% RH, and $R_0 = 2.298$, so the population of *Euroglyphus maynei* at 25°C, 75% RH will multiply 2.298 times in each generation. R_0 is not a particularly useful comparative statistic on its own because one also needs to know the generation time for the population concerned. Generation time (T) is the average age of parenthood or, put another way, the average period between birth of parents and birth of offspring and can be estimated approximately from

$$T = \frac{\Sigma x l_x m_x}{R_0}$$

For the data in Table 5.4,

$$T = \frac{75.84}{2.298} = 33 \text{ days}$$

So at 25°C, 75% RH the population of *Euroglyphus maynei* will multiply 2.3 times in 33 days.

5.4.3 The intrinsic and finite rates of natural increase

For the calculation of r we need to know the duration of the immature stages and their survival. Ideally we also need the life and fertility table of the adult female. Putting together such a table is not a trivial task. Davis and Brown (1969) derived empirical measurements of adult survival and age-specific fertility of *Acarus siro* which required making lots of rigorous observations every two days for up to five weeks. Are there any short cuts here? Can we use any estimates based on total adult mortality and fertility?

It seems obvious from the life and fertility data in Table 5.4 that in order to calculate the rate of increase in the population we need to know the age distribution (age structure), the age-specific mortality rates (l_x) and age-specific fertility rates (m_x) because the survival and natality vary so much with age. For example, all the females that have started laying eggs within the first two days contribute over a third of the total value of $l_x m_x$, whereas those in the last two days of the reproductive period contribute less than a tenth. In fact, we do not need to know the age structure of the population because if a population is subject to a constant schedule of mortality and natality rates, Lotka (1922) showed it will approach a stable age distribution and increase according to the equation

$$dN/dt = rN, \text{ or } N_t = N_0 e^{rt}$$

Table 5.4 Cohort life and fertility table based on mean development times, survivorship and fecundity of *Euroglyphus maynei* at 25°C, 75% RH, used to calculate value of r (from Colloff (1992a) based on data of Taylor (1975)).

Age in days (x)	Proportion surviving (l_x)	No. ♀ offspring per female aged x per day (m_x)	$l_x m_x$	$x l_x m_x$	$e^{-0.0253x}$	$e^{-0.0253x} l_x m_x$
29	0.28	1.65	0.462	13.398	0.4801	0.2218
30	0.27	1.35	0.365	10.935	0.4681	0.1706
31	0.26	1.00	0.260	8.060	0.4564	0.1187
32	0.25	0.75	0.188	6.000	0.4450	0.0834
33	0.24	0.70	0.168	5.544	0.4339	0.0729
34	0.24	0.60	0.144	4.896	0.4231	0.0609
35	0.23	0.60	0.138	4.830	0.4125	0.0569
36	0.22	0.50	0.110	3.960	0.4022	0.0442
37	0.21	0.45	0.095	3.497	0.3922	0.0371
38	0.20	0.45	0.090	3.420	0.3824	0.0344
39	0.19	0.40	0.076	2.964	0.3728	0.0283
40	0.18	0.40	0.072	2.880	0.3635	0.0262
41	0.18	0.40	0.072	2.952	0.3544	0.0255
42	0.17	0.35	0.060	2.499	0.3456	0.0206
Final value:		9.60	R_0 2.298	75.835		1.0016

where N_0 = the number of individuals at time zero, N_t = number of individuals at time t and r = the intrinsic rate of increase.

The intrinsic rate of natural increase refers to a population with a stable age distribution and describes its innate capacity to increase given its schedule of mortality and fertility. We can calculate the finite rate of increase, that is the number of times that the population multiplies per unit time. In a population that is increasing exponentially, if there are N_t individuals at time t, then at $t + 1$ there are:

$$\frac{N_{t+1}}{N_t} = e^r$$

and

$$\text{antilog}_e r = \lambda$$

So the finite rate of natural increase (λ) is the natural antilog of the intrinsic rate of natural increase, r.

Birch (1948) pointed out that when $t = T$ = mean generation time, from the definition of net reproductive rate, $N_T / N_0 = R_0$, then:

$$R_0 = e^{rT}$$

and

$$T = \frac{\log_e R_0}{r}$$

This means one cannot get an accurate value of T without knowing the value of r, and the value of 33 days for *E. maynei* above, based on summing xl_xm_x in Table 5.4 is only an estimate. It follows that if it were an accurate value of T, we could then calculate r because, re-arranging the last equation:

$$r = \frac{\log_e R_0}{T}$$

For the *E. maynei* data we get:

$$r = \frac{\log_e 2.298}{33} = 0.0252$$

And the finite rate of natural increase (or daily growth rate), λ, is the natural antilog of r, i.e. antilog_e 0.0252 = 1.0255 per individual per day: for every individual present today, there will be 1.0255 present tomorrow. In other words, if R_0 for *E. maynei* is 2.298 and generation time is 33 days, then the daily growth rate (λ) is the 33rd root of 2.298 = 1.0255. Then $r = \log_e$ 1.0255 = 0.252.

Another useful population statistic is doubling time T_d, which is the time it takes for a population, at a given value of λ, to double in size. It is calculated as:

$$T_d = \frac{1}{\lambda - 1}$$

For the *E. maynei* example it is 39.2 days.

So how do we get a more accurate estimation of r? We do so by solving the following equation by iteratively substituting in values of r. We have to do this because it is not possible to isolate r on one side of the equation.

$$\sum_0^\infty e^{-rx} l_x m_x = 1$$

The next questions are then how do we choose values of r to substitute in, and are there any short cuts to what could be a laborious process? We can start by taking the x and l_xm_x data in Table 5.4 and fitting our previous estimate for r of 0.0252, to derive the value for e^{-rx}, which becomes $e^{-0.0252x}$, (see Table 5.4, column 6) and then multiplying this value by l_xm_x to get $e^{-0.0252x}l_xm_x$ (see Table 5.4, column 7). We can ignore the pre- and post-reproductive days because these values of x return zero values for l_xm_x (because there has been no reproduction). So, using $r = 0.0252$,

$$\sum_{29}^{42} e^{-rx} l_x m_x = 1.005$$

If we change r to 0.0253 we get a value of 1.0016. This is quite a good fit. An estimate of r calculated to the second decimal place was deemed adequate by Leslie (1948), and his method, detailed above, is a shortcut of Lotka's original procedure. Even so, Leslie's method still involves trial-and-error and could become tedious if there were many values of r to calculate. Howe (1953) and Wyatt and White (1977) present some simplified methods. Carey (1993) provides further analytical approximations for r. For practical purposes, there is a negligible difference in our example between $r = 0.0252$ calculated from $\log_e R_0/T$ and $r = 0.0253$ calculated by iterative substitution.

Supposing we only have very basic life history data, typical of many studies in Table 5.1. This might consist of mean oviposition rate, duration of the reproductive period, adult female longevity, egg and immature development times and mortality. We need the mean generation time (T) which we can estimate from the mid-point of the reproductive period. For the *Euroglyphus maynei* example (at 25°C, 75% RH) T is 36 days (see Column C

in Table 5.3) compared with 33 days estimated from the life and fecundity table. The average number of female eggs per female produced during the reproductive period is 7.3 (m_x). The only other bit of information we need is R_0. From basic life history data we probably will not have an estimate of the proportion surviving (l_x) for the mid-range of the female reproductive period, but we know the average duration of life is 45 days, that juvenile mortality is 59% and development time of all the immature stages including the egg is 26 days, so if 0.41 of the cohort are alive on day 26 and 0 are alive by day 45, then by day 36 (mid-range of reproduction), at a rough estimate, the daily rate of mortality is 0.41/45 days = 0.009 per day. There are 10 days from day 26 to the mid-age of reproduction, so the (linear) mortality rate over this period is $0.009 \times 10 = 0.09$, so mortality by mid-age of reproduction is $0.41 - 0.09 = 0.32$, and therefore $l_x m_x$ is $0.32 \times 7.3 = 2.34$. This is also R_0 (compared with $R_0 = 2.3$ in Table 5.3). So $r = \log_e 2.34/36 = 0.0236$ (compared with 0.0253 using the long method above), therefore $\lambda = 1.024$ (compared with 1.0255) and doubling time (T_d) = 41.9 days (compared with 39.2 days).

5.4.4 Age structure of populations and the stable age distribution

a Age structure of populations

The age structure of a population refers to the proportion of individuals in each age class for the total age range of the population. In dust mites and other arthropods, the 'stage structure' of the population is of much more use than age structure because stages in the life cycle tend to be morphologically different from one another and can be counted relatively easily. Stage structure refers to the relative numbers of each stage of the life cycle that constitute the population. Thus, dust mite populations are composed of varying proportions of eggs, larvae, protonymphs, tritonymphs and adult males and females. If the proportions of these different stages fluctuate significantly with time, then the age structure of the population is said to be unstable. An unstable age structure is characteristic of a population that is rapidly colonising or declining, or in which there has been some sort of perturbation event that has led to the interruption of population growth. Stable age distribution is typical of established populations where the environmental factors that affect birth, death, immigration and emigration are relatively constant and favourable.

What is the importance of age structure in population dynamics? The risk of death to each stage in the life cycle is different, and the risk to each stage in the life cycle varies between species. In just the same way that an actuary working for a life insurance company calculates the risk of death of humans according to age, it is possible to calculate the age-specific risk of death in dust mite populations. The reason this is useful is because the age of death can have significant knock-on effects for population growth.

b The stable age distribution

Just to recap, age distribution in relation to the intrinsic rate of increase refers to a population growing geometrically and with constant age-specific mortality and fecundity rates, and such a population will approach a stable age distribution, which can be calculated. If c_x is the proportion of the stable population aged between x and $x + dx$ and b is the instantaneous birth rate, then:

$$c_x = be^{-rx}l_x$$

The short-cut method for solving this is that we assume at time t there are N_t individuals, and if during the interval t to $t + 1$ there are B_t female births, then the birth rate (β) is:

$$\beta = B_t/N_t$$

Then the stationary age distribution, L_x, is:

$$L_x = \frac{l_x + l_{x+1}}{2}$$

L_x represents the value of l_x taken at the mid-point of each age group. In the example of *E. maynei* at 25°C and 75% RH, l_x for Day 0 is 1 and for l_{x+1} (that is Day 1) it is 0.98, so L_x for the time interval of Day 0 – 1 is 0.99. Having estimated the values of L_x for each age class, we calculate $e^{-r(x+1)}$, using our earlier estimate for $r = 0.0253$ for our example of *E. maynei* at 25°C and 75% RH (see Table 5.5). We then calculate $1/\beta$ from multiplying each value of L_x by $e^{-r(x+1)}$ and summing it:

$$1/\beta = \sum_{x=0}^{m} L_x e^{-r(x+1)}$$

where $x = m$ to $m + 1$ is the last age group of consideration in the entire life table age distribution. p_x is the proportion of individuals in the population aged between x and $x + 1$, given by:

$$p_x = \beta L_x e^{-r(x+1)}$$

Table 5.5 Calculation of the stable age distribution of *Euroglyphus maynei* at 25°C, 75% RH when $r = 0.0253$.

Life history stage	x	L_x	$e^{-0.0253(x+1)}$	$L_x e^{-0.0253(x+1)}$	$100\alpha L_x e^{-0.0253(x+1)}$	p_x (% per stage)
Egg	0–	0.990	0.9750	0.9653	7.137	
	1–	0.970	0.9507	0.9222	6.819	
	2–	0.930	0.9269	0.8620	6.374	
	3–	0.870	0.9038	0.7863	5.814	
	4–	0.820	0.8812	0.7226	5.343	
	5–	0.780	0.8592	0.6702	4.956	36.443
Larva	6–	0.730	0.8377	0.6115	4.522	
	7–	0.690	0.8168	0.5636	4.167	
	8–	0.660	0.7964	0.5256	3.887	
	9–	0.620	0.7765	0.4814	3.560	
	10–	0.590	0.7571	0.4467	3.303	
	11–	0.570	0.7382	0.4208	3.111	
	12–	0.540	0.7197	0.3886	2.874	25.424
Protonymph	13–	0.510	0.7017	0.3579	2.646	
	14–	0.490	0.6842	0.3353	2.479	
	15–	0.470	0.6671	0.3135	2.318	
	16–	0.450	0.6504	0.2927	2.164	
	17–	0.430	0.6342	0.2727	2.016	
	18–	0.415	0.6184	0.2566	1.898	13.522
Tritonymph	19–	0.405	0.6029	0.2442	1.806	
	20–	0.395	0.5878	0.2322	1.717	
	21–	0.380	0.5732	0.2178	1.611	
	22–	0.360	0.5588	0.2012	1.488	
	23–	0.345	0.5449	0.1880	1.390	
	24–	0.335	0.5313	0.1780	1.316	
	25–	0.325	0.5180	0.1684	1.245	
	26–	0.315	0.5051	0.1591	1.176	11.748
Adult, pre-reproductive period	27–	0.305	0.4924	0.1502	1.110	
	28–	0.295	0.4801	0.1416	1.047	
	29–	0.285	0.4681	0.1334	0.986	
Reproductive period	30–	0.275	0.4564	0.1255	0.928	
	31–	0.265	0.4450	0.1179	0.872	
	32–	0.255	0.4339	0.1106	0.818	
	33–	0.245	0.4231	0.1037	0.766	
	34–	0.240	0.4125	0.0990	0.732	
	35–	0.235	0.4022	0.0945	0.699	
	36–	0.225	0.3922	0.0882	0.653	
	37–	0.215	0.3823	0.0822	0.608	
	38–	0.205	0.3728	0.0764	0.565	
	39–	0.195	0.3635	0.0709	0.524	
	40–	0.185	0.3544	0.0656	0.485	
	41–	0.180	0.3456	0.0622	0.460	
	42–	0.175	0.3369	0.0590	0.436	
Post-reproductive period	43–	0.170	0.3285	0.0558	0.413	
	44–	0.165	0.3203	0.0528	0.391	
	45		0.3123	0.0500	0.369	12.863
Final value:				$1/\beta$ 13.5239	100.000	100.000

We can calculate this as the percentage distribution, $100\beta L_x e^{-r(x+1)}$. In Table 5.5 the value of $1/\beta$ is 13.5239, therefore the birth rate of *E. maynei* $\beta = 1/13.5239 = 0.0739$. This is not the same as the instantaneous birth rate b, which (for *E. maynei* with $r = 0.0253$) is:

$$b = \frac{r\beta}{e^r - 1} = \frac{0.0253 \times 0.0739}{0.0256} = 0.073$$

$b - r$ is the instantaneous death rate (d) = 0.048. The example I give in Table 5.5 represents the entire life table of *E. maynei*. As we start to compute the values we see that the youngest age groups contribute the highest percentage of individuals to the total population. If the values of p_x for each stage in the life cycle are added together we find the eggs contribute 36% of individuals to the total population, the immatures (larvae, protonymphs and tritonymphs) 51% and the adults only 13% (shown in Figure 5.6a). This proportion represents the stable stage distribution. If we compare the distribution with that of *Acarus siro* from the life tables of Davis

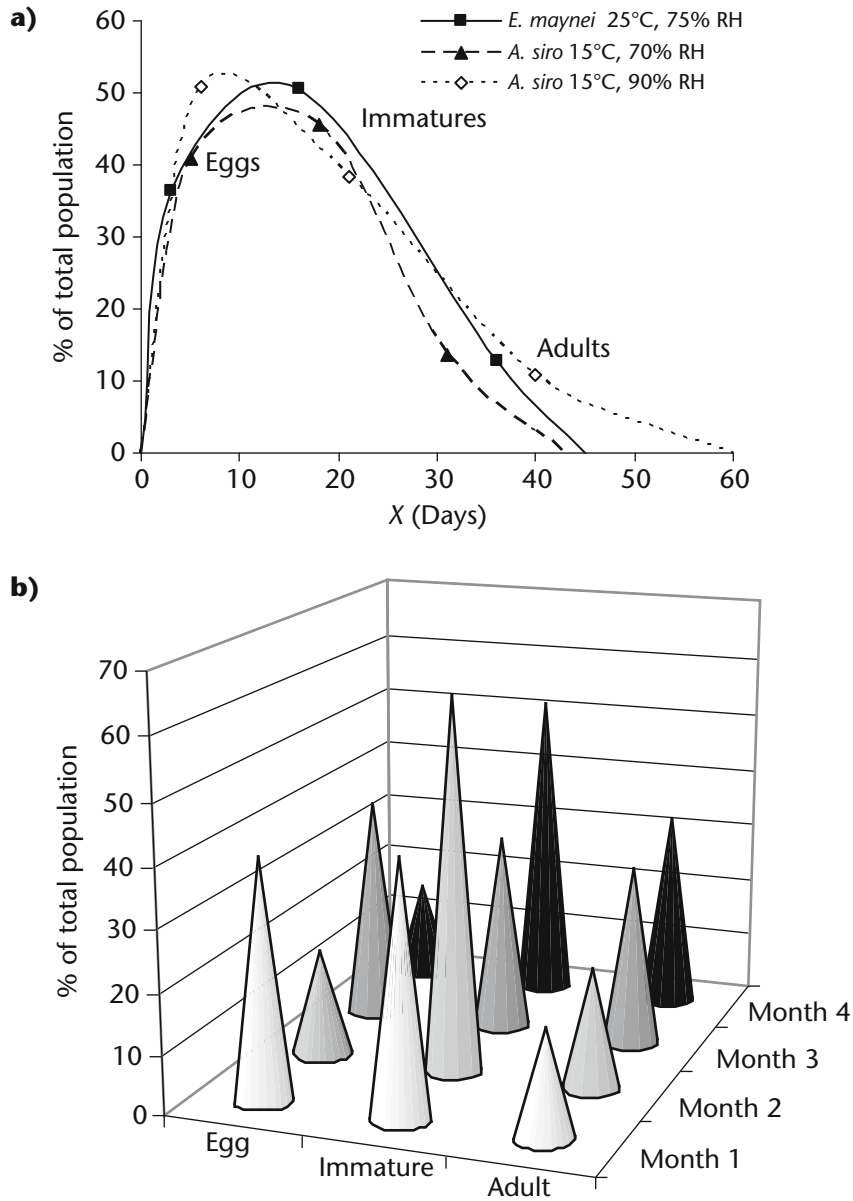

Figure 5.6 **a)** Stable age distribution of *Euroglyphus maynei* at 25°C and 75% RH when $r = 0.0256$, and *Acarus siro* at 15°C and 70% when $r = 0.244$, and 90% RH when $r = 0.225$, showing relative proportions of eggs, immatures and adults, calculated from life and fecundity tables (Colloff, 1992a; Davis and Brown, 1969). Values of x are the means for each stage. **b)** fluctuations in age structure of a field population of *Dermatophagoides pteronyssinus* (data from Colloff, 1992a).

and Brown (1969), they are really quite similar, despite the differences in microclimate and vastly greater growth rates of *A. siro*. At 15°C and 70% RH there are 41% eggs, 46% immatures and 13% adults, and at 15°C and 90% RH there are 51% eggs, 38% immatures and 11% adults.

In a laboratory culture, or in natural populations, it is much more practical to estimate stage structure than age structure. If the average age of each stage is known, then Table 5.5 can be constructed using age intervals that correspond to stages. By classifying individuals by stage rather than age, Lefkovitch (1965) used matrix models to make population projections. Caswell (2001, Chapter 4) gives details on the construction of stage-classified matrix models.

Carey (1982) made the point that stable stage structure of spider mites provides meaningful information on field populations and that field populations are often at, or close to, the stable stage distribution because they are able to increase rapidly and stable stage is approached quickly. For spider mites, stable stage distribution was approximately 66% eggs, 26% immatures and 8% adults. Field data on stable stage distribution of *Dermatophagoides pteronyssinus* showed the most frequent pattern found was immatures dominant, then eggs, then adults; similar to the pattern for *E. maynei* in Figure 5.6a, indicating that *D. pteronyssinus* also tends to be at stable stage distribution in the field (Colloff, 1992a; Figure 5.6b).

5.5 Life history traits and demographic parameters

5.5.1 Age and size at maturity – effects on fecundity and mortality

Life cycles consist of pre-reproductive and reproductive periods. The relative duration of these periods can have a major effect on fitness, because the pressures and trade-offs that operate on immature individuals are different from those for adults. For example, during the life cycle mortality rates tend to be highest for immature mites and they may be more susceptible to dehydration than adults. Intuitively, there should be clear benefits to becoming sexually mature early in the life cycle. Less time spent as juveniles means lower likelihood of mortality and a higher likelihood of reaching sexual maturity and achieving successful reproduction. Individuals that mature early will produce more offspring sooner. The cost of early maturity may be that individuals are smaller than if they matured later, and smaller individuals may be less successful at mating, produce fewer offspring, or the offspring may have a lower chance of survival.

In fact, the relationship between age at maturity and juvenile mortality is not quite as straightforward as this. Although there is a clear positive correlation for *D. farinae* and *D. pteronyssinus* (mites that mature early have lowest mortality; see Figure 5.7c), with the acarid *Tyrophagus putrescentiae* there is a rather loose negative correlation (mites that mature early tend to have higher mortality than ones that mature late; see Figure 5.7a). With the glycyphagids *Glycyphagus domesticus* and *Lepidoglyphus destructor*, there is no relationship at all. Average juvenile mortality is uniformly high (65–80%), regardless of the age at maturity (see Figure 5.7b). The same pattern was found for egg mortality and age at maturity as for juvenile mortality (data not shown). The negative relationship, or lack of relationship, between juvenile and egg mortality and development time in acarids and glycyphagids makes sense for species that live in field habitats (OConnor, 1982a; Table 4.2), where they will encounter a wide range of temperatures and may have to endure cold for extended periods. In general, the lower the temperature the longer the development times. If mortality was highest when age at maturity was greatest, the capacity for populations to survive low temperatures may be less than if mortality were negatively correlated with development time, or independent.

The other side of the mortality story is the relationship between development time and fecundity. In this case, the pattern is the opposite of the mortality one. *T. putrescentiae* shows no relationship (see Figure 5.7d), whereas for *G. domesticus* and *L. destructor* there is a significant negative correlation: mites that mature early have higher fecundity than ones that mature late (shown in Figure 5.7e), as is the case with the two pyroglyphid species (see Figure 5.7f).

Large parts of the juvenile life cycle of astigmatid mites are spent quiescent, waiting to moult (see Figure 5.8). The egg stage is inactive, so are the pre-moult stages of the larva and the two nymphal stages. The duration of the life cycle spent inactive, at any given temperature and humidity, can have some consequences for population dynamics, partly because the risk of mortality is much lower for quiescent than active mites because the main predator, cheyletid mites, are ambush assailants that remain static and attack in response to movement (Wharton and Arlian, 1972b). Also quiescent immatures have

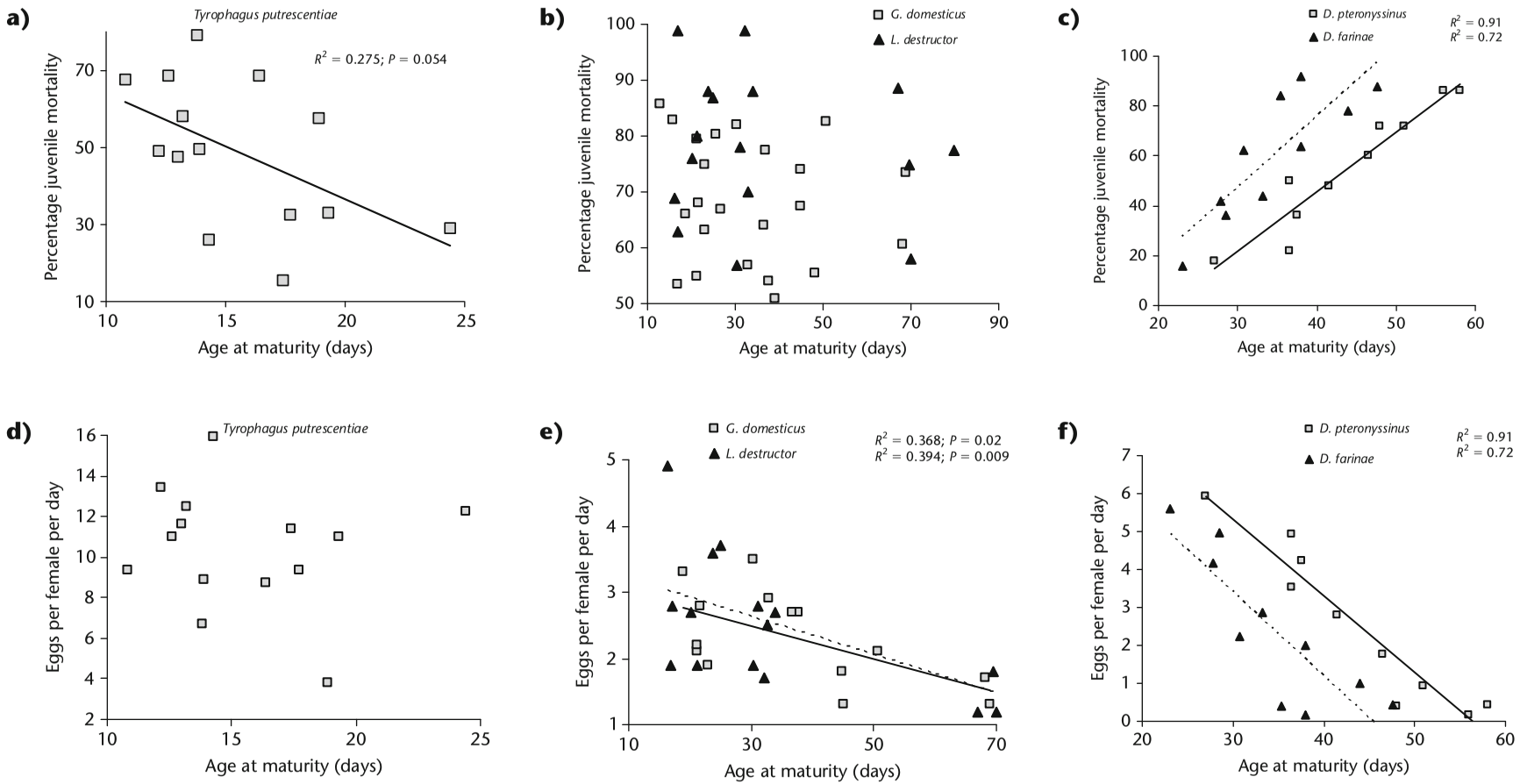

Figure 5.7 Relationship between age at maturity (total mean longevity of all the juvenile stages) and total mean juvenile mortality and fecundity respectively for **a)** and **d)** *Tyrophagus putrescentiae* (data from Rivard *et al.,* 1961a, b); **b)** and **e)** *Glycyphagus domesticus* (data from Chmielewski, 1988); and *Lepidoglyphus destructor* (data from Chmielewski, 1987); **c)** and **f)** *Dermatophagoides farinae* and *D. pteronyssinus* (data from Gamal-Eddin *et al.,* 1983a–d), over a range of temperature and humidity combinations.

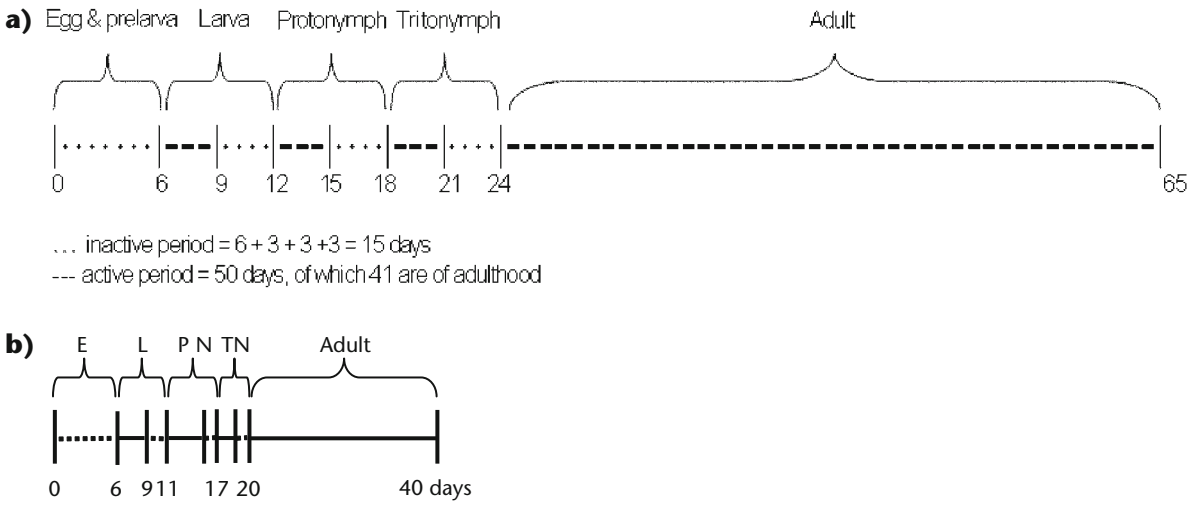

Figure 5.8 Duration of the life cycle of female *Dermatophagoides farinae* at different temperatures and 75% RH, showing proportion of stages spent active (solid lines) and inactive (dotted lines). E = egg; L = larva; PN = Protonymph; TN = Tritonymph. **a)** Mean duration at 21°C; inactive period = 14 + 5 + 5 + 5 = 29 days; **b)** mean duration at 32°C; inactive period = 6 + 2 + 1 + 1 = 10 days. (Data from Furumizo, 1975a.)

behavioural and physiological adaptations to limit water loss and survive desiccation. Figure 5.8 shows the mean duration of each stage of *Dermatophagoides farinae* at 21°C and at 32°C. A quarter of the life cycle is spent inactive, regardless of temperature, but at 32°C the inactive period is three times shorter than it is at 21°C. The period spent immotile has implications for the estimation of population density using the 'Heat Escape Method' (Bischoff and Fischer, 1990; Chapter 6), which depends on the mites being active. If a substantial proportion of the population is immotile, then trapping will be less efficient than it would be otherwise, and estimates of population size are likely to be biased.

Age at maturity (development time) in relation to rearing temperature follows a pattern similar to that for oviposition water loss (Figure 5.9; see also Chapter 3). The mites with the largest females (Acaridae and Glycyphagidae) are fastest to mature and the smallest (Pyroglyphidae) are the slowest. Figure 5.10 shows the inverse power relationship between size of females and age at maturity. Adult female size and population doubling time at comparable temperatures and humidities follow an inverse exponential relationship (Figure 5.11), with the largest mites having the shortest doubling time, the smallest mites the longest, and the medium-sized mites in between. The relationship between female size and finite rate of increase is a positive linear one – big mites have the fastest rate of increase. This is the same pattern as for fecundity and development time (Table 3.3; Figure 5.9) and water loss during oviposition.

5.5.2 Differences in life history traits between dust mites

In summary, big mites lay more eggs and develop more rapidly than small mites. I suggest they are able to do so because they are less constrained by water loss. For *Acarus*, *Glycyphagus* and *Lepidoglyphus* when humidity falls to desiccating conditions, or food resources deteriorate, these mites are able to produce a surviving and dispersing stage, the hypopus. Although production of hypopi by *Tyrophagus* spp. is rare and is known from only one species, members of the genus are extremely fecund, producing between 100 and 700 eggs (Fan and Zhang, 2007). It is the egg that probably represents the survival stage (see section 5.2.1 above), so *Tyrophagus putrescentiae* does not need to produce hypopi. The eggs may also be dispersive – they are smaller than the hypopi of glycyphagids which are thought to be dispersed on air currents. Of the Pyroglyphidae, which do not produce a hypopus, *Dermatophagoides farinae* at least is able to tolerate low humidity as a quiescent protonymph (see section 3.3.4). Furthermore, pyroglyphids tend to have a longer adult life span than the Acaridae and Glycyphagidae, and are better able to withstand low humidity as adults, recovering from desiccation after relatively short exposure to favourable conditions.

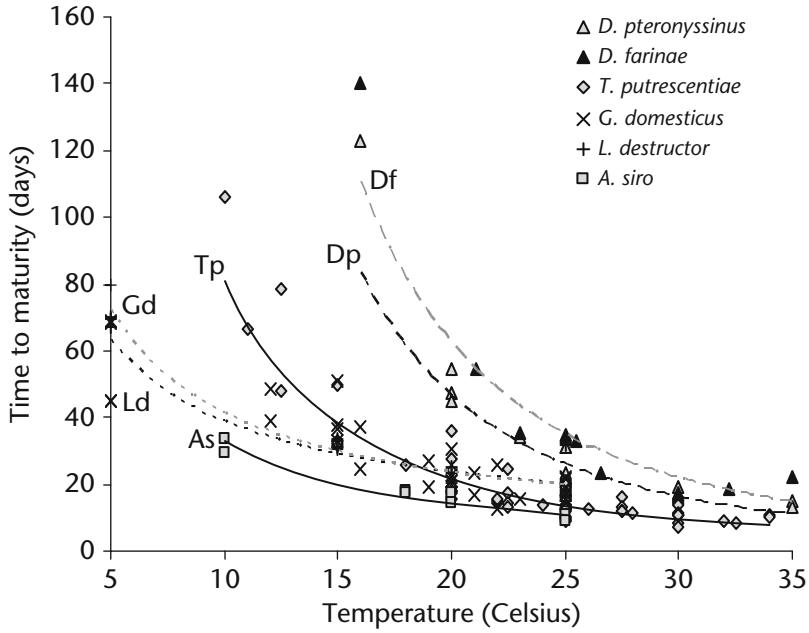

Figure 5.9 Relationship between development time (duration of period, egg to adult) and temperature for six species of domestic mites. Lines of best fit are described by the following power equations: *D. pteronyssinus* (Dp): $y = 114512x^{-2.61}$, $R^2 = 0.782$; *D. farinae* (Df): $y = 141661x^{-2.581}$, $R^2 = 0.888$; *T. putrescentiae* (Tp): $y = 6427x^{-1.902}$, $R^2 = 0.853$; *G. domesticus* (Gd): $y = 201.62x^{-0.717}$, $R^2 = 0.6947$; *L. destructor* (Ld): $y = 267.02x^{-0.81}$, $R^2 = 0.909$; *Acarus siro* (As): $y = 526x^{-1.202}$, $R^2 = 0.925$.

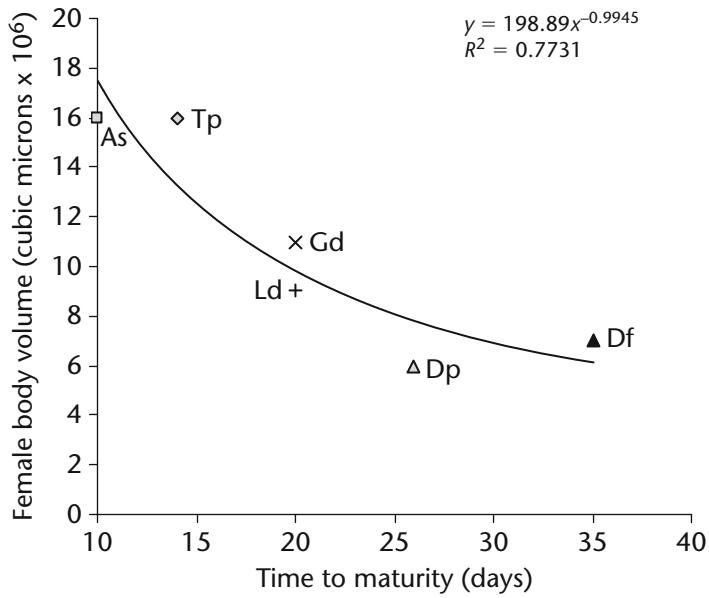

Figure 5.10 The relationship between size of adult females (data from Table 3.3) and mean development time (at 25°C) of six species of domestic mites. Note the clustering of the Acaridae (*A. siro, T. putrescentiae*), Glycyphagidae (*L. destructor, G. domesticus*) and Pyroglyphidae (*Dermatophagoides* spp.). (Legend as for Figure 5.9.)

5.6 Factors affecting population dynamics

This section deals with comparative demography of domestic mites, mostly based on data from laboratory studies at constant conditions of temperature and humidity.

5.6.1 Temperature and humidity

a Effects on stages in the life cycle

We have already seen the effects of temperature on the development time of different species (Figures 5.8, 5.9). The most comprehensive studies of the effects

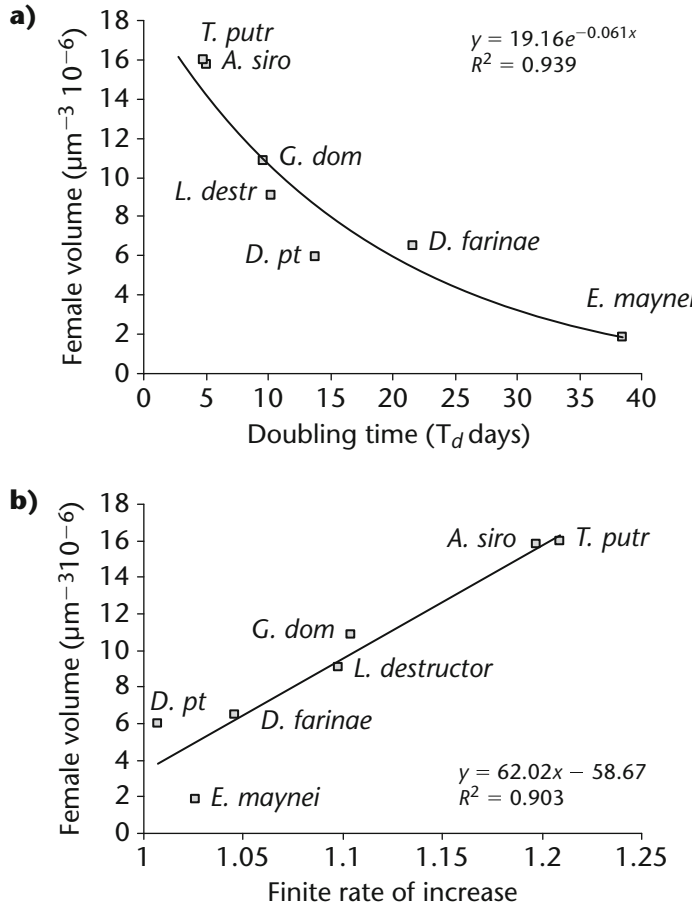

Figure 5.11 Population parameters of domestic mites in relation to size (female volume, Table 3.3). **a)** Doubling time (T_d); **b)** finite rate of increase (λ).

of temperature and humidity on the demographic parameters of dust mites are by Gamal-Eddin *et al.* (1983a–d) and Matsumoto *et al.* (1986) for *D. farinae* and *D. pteronyssinus*. These observations were made at 50–95% RH and 25°C and at 15–40°C and 75% RH, and included six variables relating to longevity, mortality and fecundity. Given so many variables, a single parameter would be of value in order to make sense of the data. R.C. Fisher (1938) developed an Index of Suitability (*I*) (not to be confused with Fisher's Index developed by the statistician R.A. Fisher), where:

$$I = \frac{NV}{L + T}$$

and N = number of eggs laid, V = egg viability (i.e. the inverse of egg mortality), L = duration of the oviposition period and T = duration of the egg stage. This index relates to oviposition and hatching, and the most favourable conditions are those that produce the highest values. It provides a utilitarian comparison of egg laying performance and survival and was used by Cunnington (1985) for determination of the physical limits for complete development of *Acarus siro* at 27 combinations of temperature and humidity. The Index of Suitability is useful because it does not require detailed mortality and longevity data for immatures and adults, which is often missing from laboratory studies on life history parameters. Figure 5.12 shows values of the Index of Suitability (*I*) for two pyroglyphid species, two acarids and two glycyphagids. The data used for the pyroglyphids by Gamal-Eddin *et al.* (1983a–d) was done at temperatures from 15–40°C, but only at 75% RH, and at 50–95% RH, but only at 25°C, rather than the full matrix of 60 combinations, so it is presented differently from the others. It shows the optimum for *D. farinae* is 75% RH, 22°C and for *D. pteronyssinus* is slightly higher at 80% RH, 25°C. Because *I* does not consider mortality data, it tends to be better at predicting the conditions at which populations will not grow, or grow comparatively

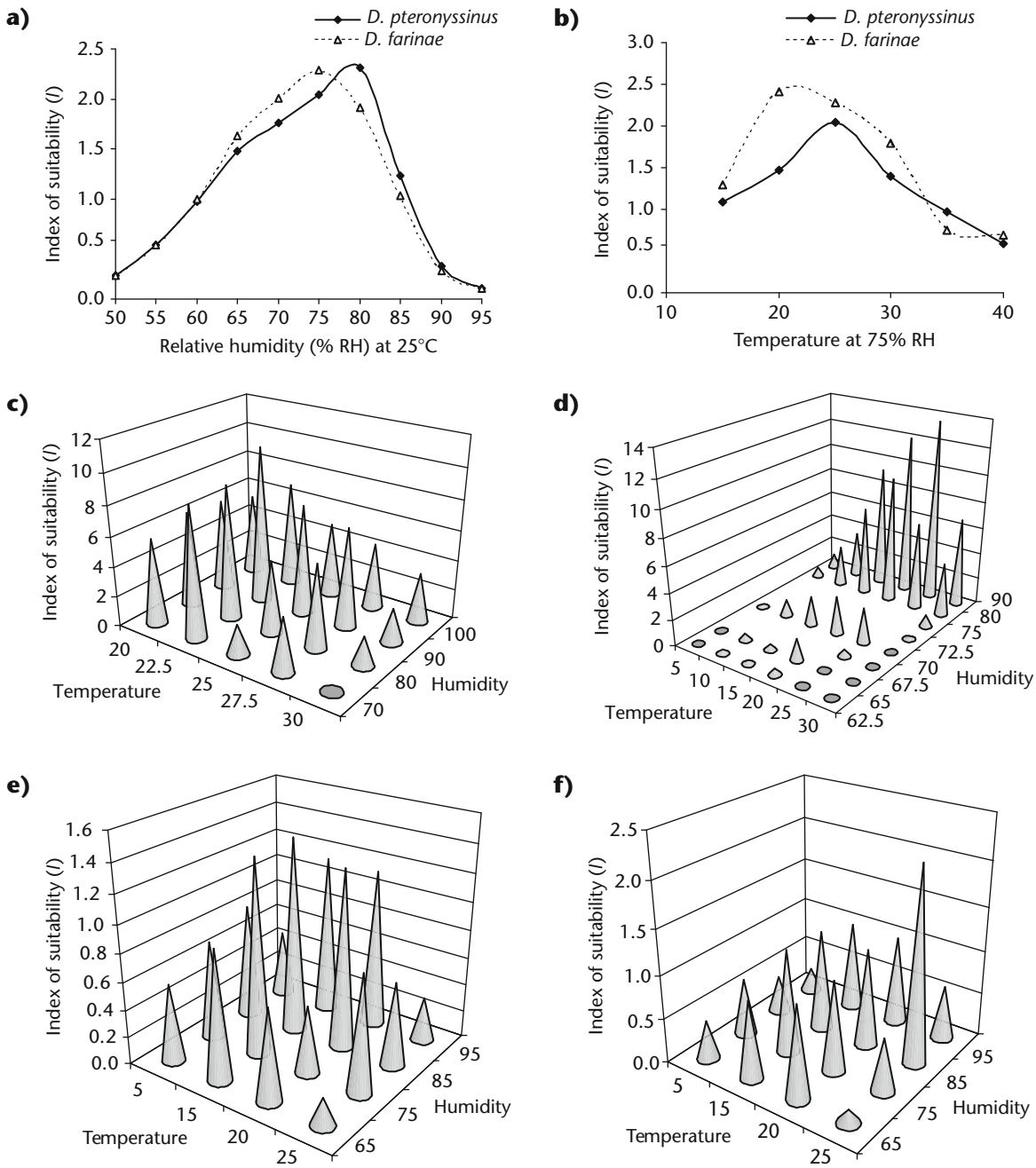

Figure 5.12 The Index of Suitability (*I*) of R.C. Fisher (1938) for egg laying and hatching of *Dermatophagoides farinae* and *D. pteronyssinus* at **a)** a range of humidities and constant temperature (25°C) and **b)** a range of temperatures and constant humidity (75% RH) (data from Gamal-Eddin *et al.*, 1983a–d); **c)** *Tyrophagus putrescentiae* (data from Rivard, 1961a, b); **d)** *Acarus siro* (data from Cunnington, 1985); **e)** *Glycyphagus domesticus* (data from Chmielewski, 1988); and **f)** *Lepidoglyphus destructor* (data from Chmielewski, 1987).

slowly, than the conditions at which growth is optimal. Of the optimum temperatures and humidities for the species in Table 5.6, the highest value of *I* corresponded with the temperature and humidity combination at which λ and T_d would predict most rapid population increase for *Lepidoglyphus destructor*, *Acarus siro* and the pyroglyphids, but not *Glycyphagus domesticus* or *Tyrophagus putrescentiae*. Another suitability index based on immature development times and their mortality was developed by Howe (1971).

Teasing apart the effects of temperature and humidity is not straightforward, and there are many examples of the interaction between the two variables on life history parameters. Colloff (1987b) and Biddulph *et al.* (2007)

Table 5.6 Temperature and humidity optima for population growth of domestic mites based on various life history parameters.

Taxon	T°C	RH%	Reference	Index of suitability (*I*)	Finite rate of increase (κ)	Doubling time (T_d)
Pyroglyphidae						
Euroglyphus maynei	25	75	This chapter	0.6	1.026	39.2
Dermatophagoides farinae	26.5	75	Furumizo, 1975	1.7	1.051	21.6
D. pteronyssinus	25	75	Matsumoto *et al.*, 1986	2.1	1.041	24.3
Glycyphagidae						
Glycyphagus domesticus	25	85	Chmielewski, 1988	0.6	1.123	8.1
Lepidoglyphus destructor	25	85	Chmielewski, 1987	2.2	1.134	7.5
Acaridae						
Acarus siro	28	85	Aspaly *et al.*, 2007	13.6	1.2	5.1
Tyrophagus putrescentiae	30	90	Sanchez-Ramos & Castanera, 2005	10.4	1.9	1.1

provide examples of the interaction for *D. pteronyssinus*. The publication by Stratil *et al.* (1980) on the innate capacity for increase of *L. destructor* represents probably the most comprehensive demographic dataset on the effects of temperature and humidity. The effect of humidity (60–80%) on survivorship (l_x) of *E. maynei* (see Figure 5.13) shows rates of mortality decrease with increasing humidity, especially among immatures, so that at 80% RH mortality is almost constant throughout life, but that low humidities prolong adult life. In essence, temperature is the major driver of population growth because of the thermodynamics of physiological reactions of poikilothermic animals (Frazier *et al.*, 2006). Growth will be slower at lower temperatures, even if humidity is optimal. But humidity acts as a constraining factor on population growth at optimum temperatures (see effects of fluctuating conditions below), especially if an animal is having to expend energy on balancing its body water at the expense of reproduction.

b Effects of fluctuating conditions

Fluctuating conditions of humidity at a given temperature have the effect of prolonging development times (de Boer *et al.*, 1998; Arlian *et al.*, 1998b, 1999b; *Pike et al.*, 2005; see Figure 5.14a). Each stage in the life cycle of *D. farinae* was extended, with the adult and nymphal stages doubling or trebling their duration when exposed to 4 hours per day of 75% RH and 20 hours at 35% RH, though the egg stage was affected least (Arlian *et al.*, 1999b). The most important finding of this study was that *D. farinae* can complete its life cycle, though over a longer time course, even though humidity is sub-optimal for the majority of the time. de Boer *et al.* (1998) found partially dehydrated *D. pteronyssinus* were able to re-hydrate and survive when moist conditions were provided for only 90 min. per day. Oviposition still occurred when dehydrating conditions prevailed most of the time, though fecundity rates were much reduced (shown in Figure 5.14b).

It seems that dust mite populations are capable of surviving cool, dry conditions for prolonged periods, with brief respite periods for rehydration, though de Boer *et al.* (1998) found one culture survived for two and a half months at constant conditions of 44% RH and 16°C, indicating that *D. pteronyssinus* is able to overwinter in an active state and recommence population growth when conditions become more favourable (de Boer and Kuller, 1995c, 1997). Active overwintering by *D. pteronyssinus* contrasts with *D. farinae*, which overwinter as quiescent protonymphs (Suto and Sakaki, 1990; Sakaki and Suto, 1991).

c Effects on laboratory populations

Populations of *D. farinae* in laboratory cultures grew most rapidly to highest density at 25°C and 60% RH (Waki and Matsumoto, 1973a; see Figure 5.15a). At

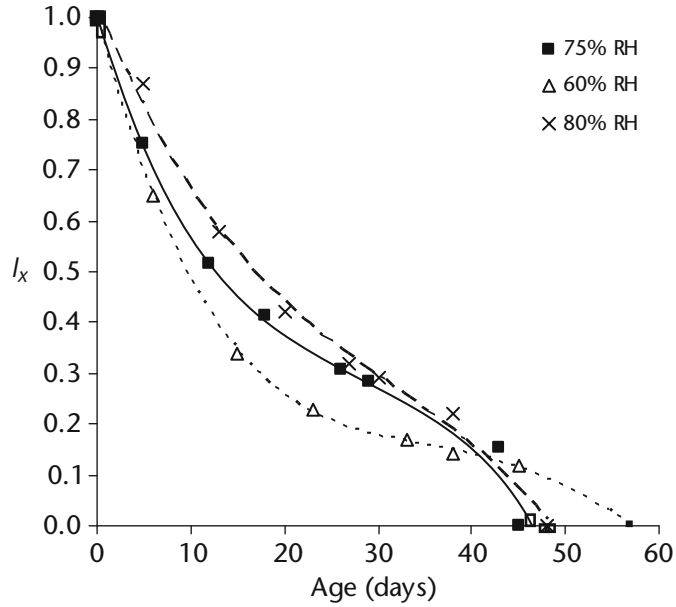

Figure 5.13 Effects of different relative humidities at 25°C on stage-specific survivorship of *Euroglyphus maynei* (from Colloff, 1992a, based on data from Taylor, 1975).

the same temperature and 57% RH, population growth during the exponential phase was similar, but densities tended to be lower, with a higher frequency of fluctuations, and at 75% density was lowest. At 30°C and both 57% and 60% RH, population densities fluctuated at markedly lower levels than at 25°C. The cultures were quite large. They were maintained in conical flasks with 50 g of culture medium, and some would have contained tens or hundreds of thousands of mites. The pattern of growth in these cultures showed a classic exponential growth phase followed by a period of chaotic fluctuation, though with an underlying mean and equilibrium. Equilibrium was reached in 8–10 weeks. When lines of best fit are added to the population growth data in Figure 5.15a (describing 3rd- or 4th-order polynomial models), it can be seen that they follow a basic sigmoid or logistic curve, indicating growth in a limited environment, rather than geometric or exponential growth typical of an unlimited environment (see Figure 5.15b). These patterns suggest that in laboratory cultures, within a relatively short period, dust mite populations exhibit characteristics typical of wild populations (see below).

5.6.2 Diet

Females of *Dermatophagoides pteronyssinus* fed on house dust and freeze-dried human semen produced twice as many eggs as mites fed on house dust alone (Colloff, 1988b). Dried semen is common in mattresses of sexually active people and represents potentially high-quality food for mites, containing substantial amounts of protein, sugar, phospholipids and nucleic acids. However, what this study indicated was not so much the high nutritional quality of dried human semen, but the relatively low quality of the diet of house dust. Most of the laboratory studies listed in Table 5.1 that have been used to derive population growth rates have used high-quality diets rich in lipids, carbohydrates, protein and vitamins such as yeast, dried fish food, powdered bovine liver, dried milk and wheat germ. There are no studies that critically examine differences in population growth of pyroglyphid species on such high quality diets with something approaching their natural diet, though Spieksma (1976) successfully grew dust mites on animal skin scales.

Koren and Eckhard (1995) found that population growth of *D. pteronyssinus* increased with higher protein content of the house dust; the optimal level being at least 11%. Similarly, Matsumoto (1975) and de Saint Georges-Gridelet (1984) found that about 6% fat content of skin scales was optimal for population growth of *D. farinae* (Chapter 2). Furthermore, Koren and Eckhard (1995) found that dust from mattresses had significantly higher protein content (because of the high proportion of keratin-containing skin scales) and, when used as a laboratory

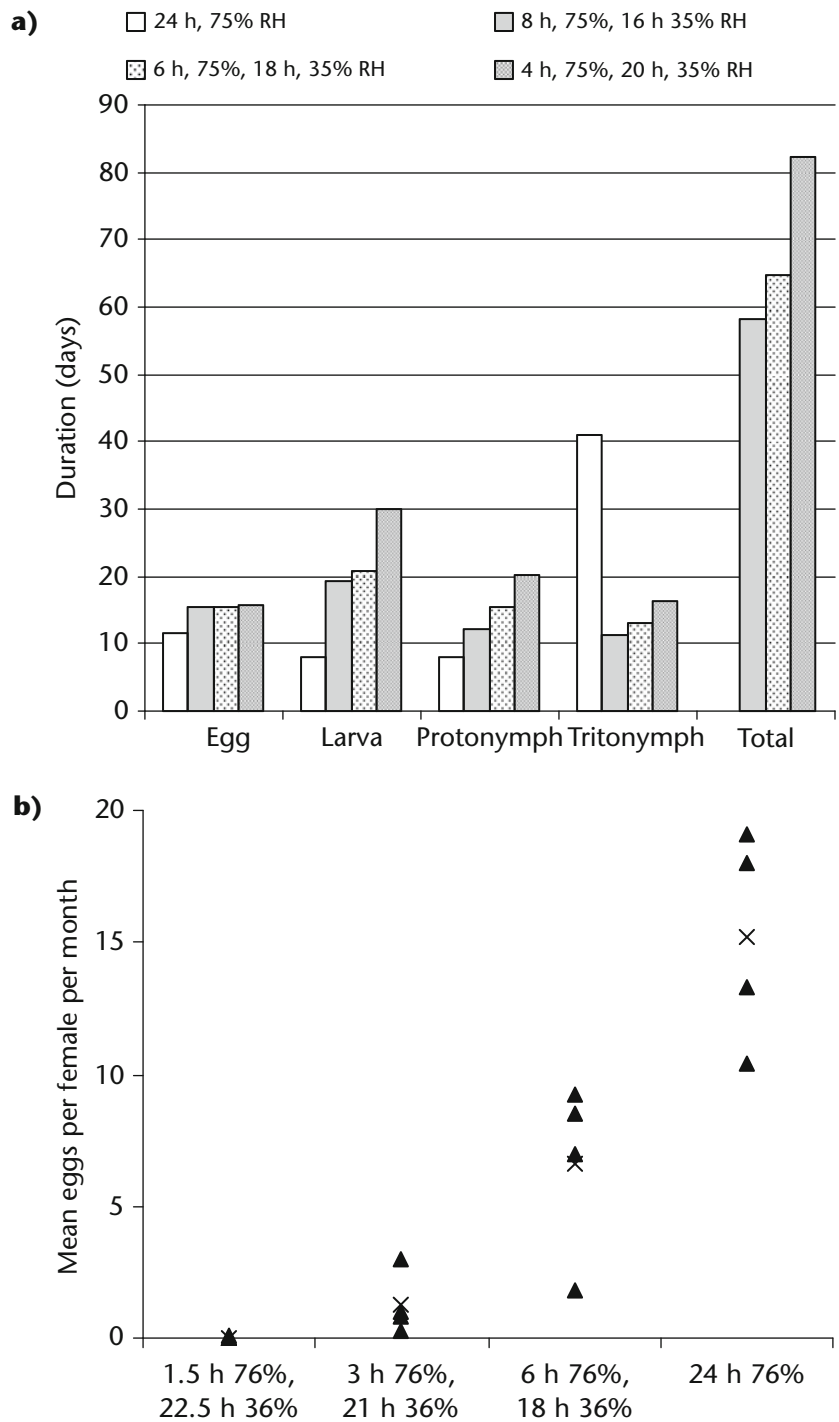

Figure 5.14 **a)** Effect of fluctuating conditions of relative humidity at 21°C on development times of *Dermatophagoides farinae* (data from Arlian *et al.*, 1999b); **b)** fecundity of *D. pteronyssinus* at fluctuating humidities at 16°C (× = mean; data from de Boer *et al.*, 1998).

culture medium at controlled temperature and humidity, supported higher mite populations than dust from carpets which had a low protein content. It seems therefore unlikely that all house dust is of equal nutritional quality and that within a home there is a fair amount of spatial variability. There has been a tendency to assume that food is never a limiting factor to dust mites under natural conditions, that it is always super-abundant and that dust mites never go short. These assumptions may well prove unfounded, and

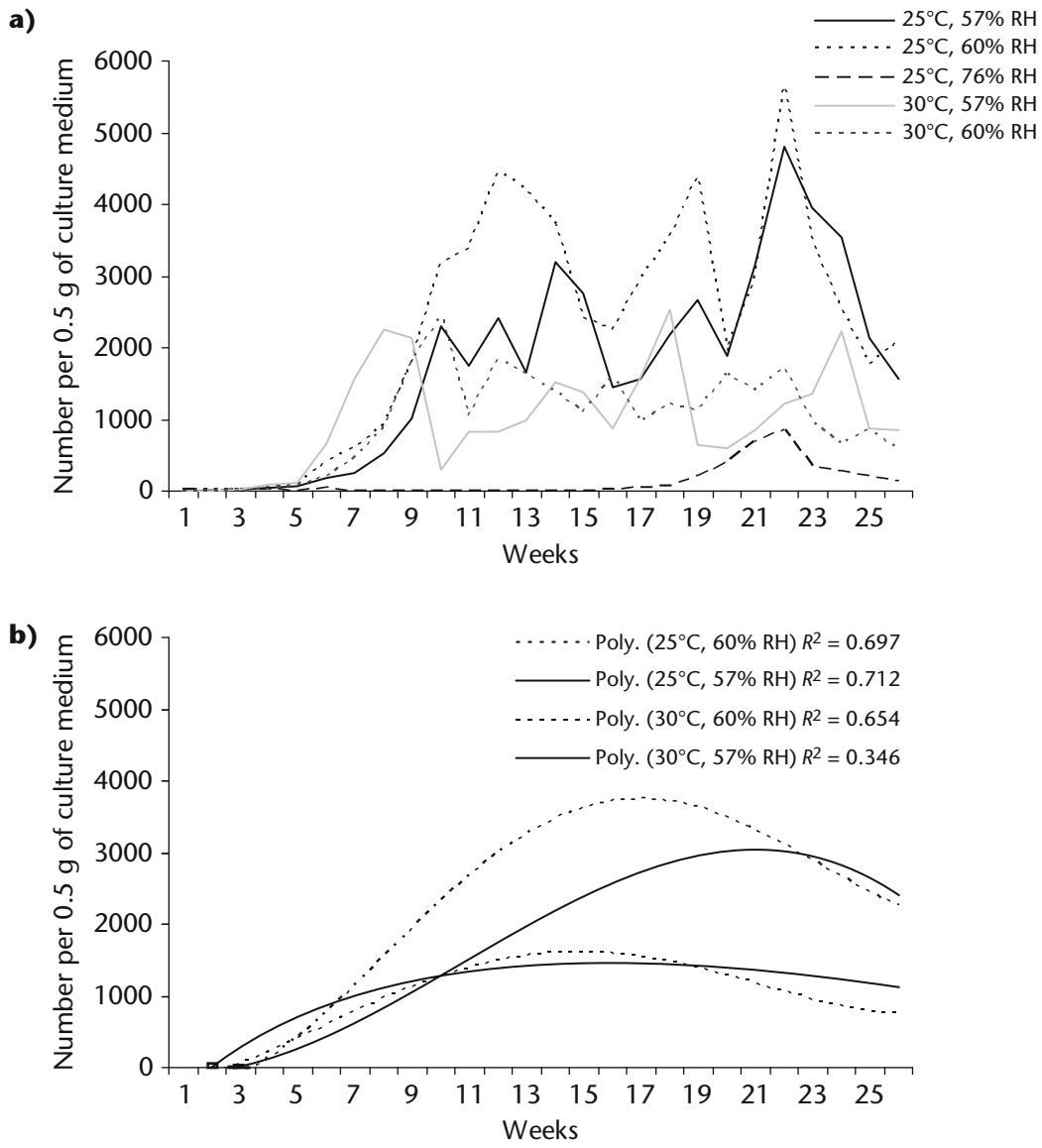

Figure 5.15 **a)** Effects of temperature and humidity on growth of laboratory populations of *Dermatophagoides farinae* reared on dried yeast and fish meal over a period of 31 weeks. No population growth was recorded at 25°C, 40% RH and 30°C, 40% and 75% RH; **b)** the same data (with the values omitted for the 25°C, 76% RH treatment) with lines of best fit to a 3rd- or 4th-order polynomial model, showing logistic growth. (Data from Waki and Matsumoto, 1973a.)

there could well be circumstances under which poor food quality represents a limiting factor for growth of dust mite populations.

Laboratory studies by Ree *et al.* (1997a) showed highest population growth rates by 8 weeks, for both *D. farinae* and *D. pteronyssinus*, on a diet of yeast and fish food, intermediate growth on fish food only, and lowest growth on yeast only (see Figure 5.16). Waki and Matsumoto (1973b) measured population growth of *D. farinae* on diets based on yeast and dried fish to which they added varying amounts and types of lipid and protein. Highest population growth was achieved on diets containing 5% lipid in the form of oil or lard, or protein in the form of bean flour or egg albumin.

5.6.3 Predation, competition and crowding

a Predation

Cheyletus spp. are the only candidate predators for dust mites. These mites are used to control stored products mites in commercial premises (see Pekár and Žďárková, 2004 for many references). Predator–prey interactions of *Cheyletus* spp. have been studied by Gause *et al.*

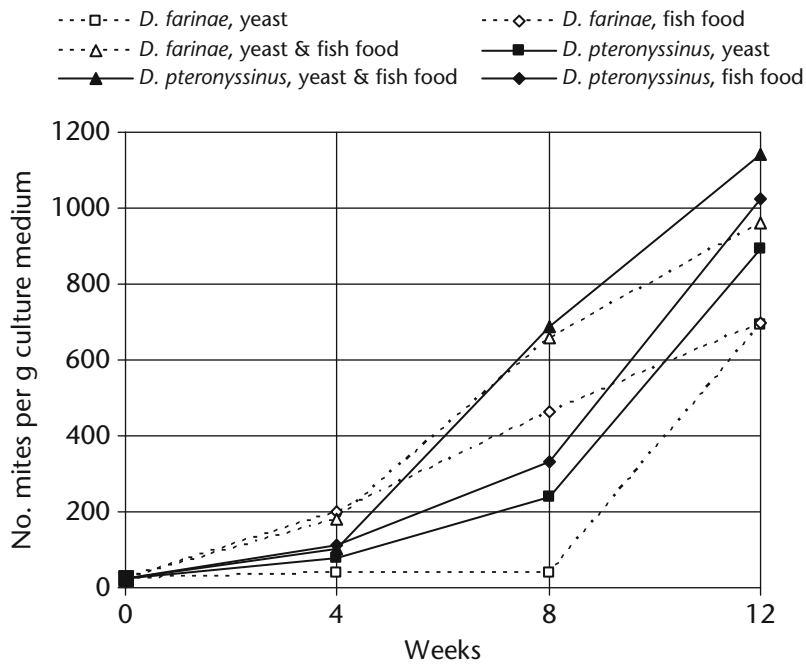

Figure 5.16 Effect of diet on population growth of dust mites. (Data from Ree *et al.*, 1997a.)

(1936), Bereen (1984) and Pekár and Žďárková (2004). Life history parameters were determined by Bereen and Metwally (1984) and Barker (1991).

There is little information to gauge how important *Cheyletus* spp. might be in regulating dust mite populations under natural conditions, except in relation to some general statistics on their distribution and abundance. From the data on global distribution (see Appendix 3) *Cheyletus* spp. occur in about 124 localities (about 17% of the total). Abundance is usually low in relation to abundance of major dust mite species (as is typical of ratios in abundance between predators and their prey), and frequency of occurrence within homes at any particular locality is also well under 20%. So in the majority of homes, in most parts of the world, there is probably no regulatory effect on dust mite populations from predation.

b Competition

Dermatophagoides farinae and *D. pteronyssinus* are often found together in homes in North America and Europe, sometimes with *Euroglyphus maynei* or other species. Where multiple species are present, one is usually numerically dominant, and this has been ascribed to differences in microclimatic requirements; the classic example being the distribution of *D. farinae* and *D. pteronyssinus* in California (Lang and Mulla, 1977a, b, 1978; Chapter 4). Within 3 months *D. farinae* always became the dominant species in cultures that commenced with equal numbers of both species, even though population growth of *D. pteronyssinus* is fastest (Arlian *et al.*, 1998a). This could be due to subtle differences in life history parameters (such as greater longevity of female *D. farinae*), or that 3 months was insufficient for *D. pteronyssinus* to become dominant. Or it could be due to *D. farinae* being able to outcompete *D. pteronyssinus* in some way. When *Euroglyphus maynei* was added to cultures, *D. pteronyssinus* and *D. farinae* showed slower growth rates than in single-species cultures, indicating an inhibiting effect of this species, even though *E. maynei* populations declined. There is lots of scope for clarifying these relationships further.

c Density dependent effects

Anyone who has grown dust mites in the laboratory will be familiar with the necessity to make subcultures on a regular basis in order to stop the cultures becoming too crowded and dying. The processes that regulate birth and death rates in relation to population size are called density dependent effects. They can be negative, whereby deaths exceed births and the population declines, or positive (so-called 'inverse density dependence') whereby the population is up-regulated. McGregor and Peterson (2000) detected inverse density dependence in cultures of mites that were newly inoculated into a 38–75 μm sieved fraction of medium (consisting mostly of

faecal pellets from which eggs had been excluded) taken from a mature culture. Mite populations with higher proportions of faecal pellets in their culture medium grew significantly faster than those with lower proportions or the negative control, and this result was consistent over 10 replications. The mechanism responsible for this effect is not clear, though beneficial effects resulting from coprophagy is one possibility (see Chapter 2). This example serves to demonstrate that population growth can be regulated by modifications that dust mites make to their microhabitat. Extrapolating these results to natural populations suggests that growth will be faster in habitats that previously contained high populations that have died out than in habitats that did not. In natural populations, rapid population growth to high densities occurs in summer and autumn, followed by a crash in late autumn or winter and gradual increase the following late spring/early summer (see below). Could this growth phase be more rapid, all other factors being equal, if the previous population peak was particularly dense?

5.6.4 Differences between laboratory and natural populations

Most of the life history studies in Table 5.1 were done with cultures of mites that have been kept in the laboratory, at constant temperature and humidity on relatively high-quality food, sometimes for many years and countless generations of mites. A laboratory culture might have started with a few hundred or thousand founder individuals, forming the genetic basis for all subsequent generations. It is common practice for researchers in different parts of the world to exchange cultures among themselves and these may get incorporated into other lab cultures over time. By comparison, populations in the wild are subject to diurnal and seasonal fluctuations in microclimate, and food quality may vary in time and space. Wild populations have some limited opportunity for mixing and out-crossing, but considerably more so than for laboratory populations. With species that are globally distributed and exist as metapopulations, it is likely that a population of *Dermatophagoides pteronyssinus* from Belgium will be genotypically and phenotypically different from a population from Brazil. Genetic and phenotypic differences between laboratory and wild populations, and between wild populations from different parts of the world, could potentially manifest themselves as differences in life history parameters and population growth rates, tolerance to extremes of temperature and humidity, and also allergen polymorphisms (discussed further in Chapter 7).

Colloff (1987a) exposed eggs from wild and laboratory populations to diurnal hygrothermic fluctuations to simulate those in a mattress (16 h. at 15°C, 60% RH, 8 h. at 30°C, 75% RH). Wild eggs had more rapid development times and lower mortality due to dehydration than eggs from laboratory cultures. The result suggests that wild eggs are better able to withstand these fluctuations because that is what they normally get exposed to, whereas laboratory cultures have become acclimatised to constant conditions. Colloff (1987b) found that at constant, favourable conditions (30°C, 80% RH) laboratory populations had shorter egg development times and lower egg mortality, but that at cooler, dryer conditions (20°C, 60% RH) wild populations did better. This finding was extended by Hart *et al.* (2007) who found that at favourable conditions (25°C, 75% RH) wild mites were less fecund, with a trend to longer egg development times and pre-oviposition period, than laboratory mites, but at less favourable conditions (25°C, 64% RH) wild mites had better reproductive performance than laboratory mites.

The message is that if life history data based on laboratory populations are used to parameterise population growth models, those models will give inaccurate predictions of growth of natural populations, as was suggested by Pekár and Žďárková (2004) in relation to the effects of laboratory diet. Laboratory studies of life history parameters show a great deal of variation for the same species (*D. pteronyssinus*) kept at the same conditions (23–25°C, 72–76% RH; Table 5.7). Some parameters varied more than others, with oviposition rates and duration of the oviposition period being especially variable in relation to diet. The poorest performance was on wheat bran, the best was on diets containing powdered liver.

5.7 Seasonal dynamics of natural populations and allergens

5.7.1 Mites

Seasonal population dynamics of house dust mites are of importance because they are related to the amounts of allergens that are produced, and when allergen exposure is likely to be highest. This begs the

Table 5.7 Variation in life history parameters of *Dermatophagoides pteronyssinus* from laboratory cultures at 23–25°C, 72–80% RH. (Where stage duration is given based on eventual gender (such as egg duration; males, females) I have quoted data for females.)

Reference	RH%	T°C	Egg development (days)	Larva (days)	Protonymph (days)	Tritonymph (days)	Total immatures (days)	Adult female (days)	Longevity (instars & female, days)	Pre-oviposition period (days)	Oviposition period (days)	Mean total eggs per female	Oviposition per female per day	Egg mortality (%)	Juvenile mortality (%)	Diet
Arlian *et al.*, 1990	75	23	8.1	10.4	6.9	8.3	34.0	31.2	65.2	4.3	23.3	68.4	2.8	14.0		Yeast, animal protein
Ho & Nadchatram, 1984	75	23–37	5.7	8.8	8.0	9.5	33.0	23.0	56.0					19.0		Dried milk, cereal, liver, yeast, vitamin B
Pike *et al.*, 2005	75	23	8.8	11.8			51.1	100.8	151.9							Yeast, wheat germ
Blythe, 1976	70–74	25	7.0	10.0	9.0	9.5	33.0									No data
Colloff, 1987b	75	25	4.7											11.0		Yeast
Hart & Fain, 1988	75	25					14.3			9.0	33.9	58.2	1.8			Fishmeal, yeast, beard shavings
Saleh *et al.*, 1991	75	25	7.5	4.1	3.5	9.6	24.6	32.9	57.5	3.1	16.2	7.4	0.5	10.8		Wheat bran
Saleh *et al.*, 1991	75	25	7.3	6.3	5.7	14.4	37.6	47.1	84.7	4.3	22.3	9.4	0.4	7.5		Wheat bran, yeast
Hart *et al.*, 2007	75	25	3.5				13.3	45.2	58.5	2.2	35.5	100.0	3	0.0	0.0	Liver, yeast
Hart *et al.*, 2007	75	25	3.3				16.4	39.9	56.3	2.6	27.0	79.7	3.2	0.0	0.0	Skin scales, mattress dust
Matsumoto *et al.*, 1986	76	25	6.2	10.7	8.6	10.7	36.3	72.0	108.3	3.5	40.6	76.2	2.1	20.0	35.7	Not known
Spieksma, 1967	75–80	25	6.0	6.0	6.0	6.0	18.0	100.0	118.0		45.0	30.0	0.7			Skin scales, fishmeal
Gamal-Eddin *et al.*, 1983a–d	75–80	25	8.3	3.0			36.5	51.5	88.0		46.0	123.0	2.7	10.0	22.0	Skin scales, bovine liver, yeast
Dobson, 1979	80	25	7.5	10.5	9.4	17.8	45.2	38.7	83.9							Beard shavings, yeast

question as to whether periods of higher risk of allergen exposure can be predicted.

Seasonal rises in house dust mite population density tend to be associated with changing weather conditions, usually an increase in mean monthly humidity and temperature, and many of the studies on seasonal variation include correlations with local climate data (see Table 5.8). Most of these studies lasted up to a year, but it is possible to gauge between-year variation in the timing of population maxima and minima from those studies that ran for about 20 months or longer (Dusbabek, 1975; Dar and Gupta, 1979; Murray and Zuk, 1979; Arlian *et al.,* 1982, 1983; Solarz, 1997). Murray and Zuk (1979) found no consistency in seasonal maxima neither for month nor density. The maximum in their second year (1978) occurred in July and in 1977 it occurred in October. Population density of the 1978 maximum was nearly five times greater than the 1977 one. Arlian *et al.(*1982) recorded population maxima in August in the first and second years and June in the third year with mean maximum density about 3 times that of the second year and 2.5 times that of the first. Murray and Zuk (1979) and Arlian *et al. (*1982) showed the fluctuations in mite density were synchronous with fluctuations in mean indoor relative humidity, coinciding with seasonal use of indoor climate regulation (heating and cooling).

If we plot out the seasonal fluctuations in mite populations from all the studies in Table 5.8, bearing in mind they were done in different years and in different parts of the world (see Figure 5.17), the graph looks fairly chaotic. But on closer inspection, there is usually one major peak per year and one major trough. There are some peaks and troughs from different studies that coincide, and populations are usually on the decline between mid-winter and early spring. If we eliminate the years and line up all the studies according to the month they commenced (correcting by 6 months for the Southern Hemisphere studies, eliminating those studies where n = <3 homes), we can then examine patterns of seasonal fluctuation in more detail. Figure 5.18 shows the result, with mean monthly abundance highest between September and October. If we calculate the ratio of mite abundance for each month to that during the month when abundance was lowest, we get the fold-increase (a crude measure of the maximum rate of population growth during the exponential phase) in abundance. The mean fold-increase shows a similar pattern as mean abundance except for a second peak in August. So although at any particular locality, in any particular year, there may be variation in timing of seasonal population maxima, on average we see a consistent pattern. Populations are lowest during late winter, commence their exponential growth phase during spring, are growing most rapidly during late summer, peak in autumn and then decline sharply during early winter.

So what is the effect of geographical location? When mite numbers during the months of maximum and minimum population densities are plotted against the latitude of the locality there is no obvious trend (see Figure 5.19a). But when mite numbers during the month of maximum population are divided by the numbers in the month prior to the maximum to give a fold-increase, there is a strongly positive correlation (shown in Figure 5.19b). In other words, the higher the latitude, the greater the rate of growth during the exponential phase of population increase, even though there is still a lot of variation in fold-difference between 40° and 50°. The correlation with latitude is more marked when the coefficient of variation of abundance is used (see Figure 5.19c). We calculate the mean and standard deviation of abundance for each month for the sampling period of each study and then divide the standard deviation by the mean to get the coefficient of variation. It is a particularly useful statistic when comparing datasets with broadly different means. What it shows is that there is a likelihood of a consistently greater variation in population size throughout the year with distance from the equator. This accords with greater seasonal variation in temperature at higher latitudes. Putting the data together with that on timing of seasonal maxima, it means that localities at latitudes from about 35–55°N will show relatively greater increases in mite population densities during autumn than localities from 5–35°N.

5.7.2 Allergens

There are not enough studies on seasonal variation of allergen concentrations to examine the association between latitude and seasonal maxima and minima, as for dust mite populations. Much of the data is based on samples taken only every 3 or 6 months from many different homes (for example Kalra *et al.,* 1992; Chang-Yeung *et al.,* 1995a) or localities (Lintner and Brame, 1993), rather than repeat monthly sampling in the same homes as for most studies of mite populations. Of those studies with monthly or bi-monthly data (Platts-Mills *et al.,* 1987; Lau *et al.,* 1990;

Table 5.8 Studies on seasonal variation of dust mite populations, giving locality details, the period during which each study was done, the timing of seasonal population maxima and minima, and whether local climate data (temperature and humidity) were included. *Duration (max. to min.) = the duration (in months) between the timing of the population maximum and the minimum.

Locality	Latitude (decimal)	Years	Duration (months)	Month of maximum population	Month of minimum population	Duration (max. to min.)*	Floors (F) or beds (B)	No. homes	Climate data?	Reference
Leiden	52.15	1964–1965	13	Sep	Mar	6	F	3	✗	Spieksma & Spieksma Boezeman, 1967
Davos	46.8	1967–1968	12	Oct	Feb	4	F	4	✗	Spieksma *et al.*, 1971
Basel	47.58	1967–1968	12	Sep	Nov	2	F	3	✗	Spieksma *et al.*, 1971
Waikiki	21.28	1968–1969	8	Jan	Jul	6	ND	5	✗	Sharp & Haramoto, 1970
Manoa	21.28	1968–1969	8	Oct	Sep	1	ND	5	✗	Sharp & Haramoto, 1970
Groesbeek	51.08	1968–1969	12	Nov	May	6	F	3	✓	Van Bronswijk *et al.*, 1971
Brisbane	27.4	1969–1970	12	Feb	Jun–Jul	4	F	4	✓	Domrow, 1970
Groesbeek	51.78	1970–1971	13	Jul	Jan–Mar	6	B	3	✓	Van Bronswijk, 1973
Knoxville	35.97	1970–1971	12	Sep	Feb	5	F	15	✓	Shamiyeh *et al.*, 1973
Rudgwick	51.1	1970–1971	11	Jun	Mar–Apr	9	B	1	✓	Hughes & Maunsell, 1973
Riverside	34	1971–1972	14	Jun	Feb	8	B	4	✓	Furumizo, 1978
Groesbeek	51.78	1971–1972	8	Jul	Dec	5	F	3	✗	Van Bronswijk, 1974
Prague	50.08	1972–1973	20	Jul	Jan	6	B	1	✓	Dusbabek, 1975
Basel	47.58	1972–1973	12	Sep	Mar	6	BF	32	✓	Mumcuoglu, 1975
Delhi	28.67	1972–1974	24	Aug	Feb–Mar	6	BF	15	✗	Dar & Gupta, 1979
Barcelona	41.35	1972–1974	17	Oct	Mar	5	ND	6	✓	Portus & Blasco, 1977
Prague	50.08	1972–1973	13	Jul	Nov	4	B	1	✓	Dusbabek, 1979
Prague	50.08	1972–1973	13	Jul	Mar	8	B	1	✓	Dusbabek, 1978
Grenoble 200 m	45.18	1973–1974	13	Sep	Dec	3	B	4	✓	Lascaud, 1979
Grenoble 700 m	45.18	1973–1974	13	Mar	Nov	8	B	3	✓	Lascaud, 1978
Grenoble 1200 m	45.18	1973–1974	13	Jun	Nov	5	B	3	✓	Lascaud, 1978
Silistra	44.1	1974–1975	12	Jul	Mar	8	ND	ND	✗	Todorov, 1979
Silistra	44.1	1974–1975	12	Jun	Jan	7	ND	ND	✗	Todorov, 1979
Tokyo	34.75	1974–1976	14	Jul	Jan	6	F	2	✓	Miyamoto & Ouchi, 1976
Brasilia	15.78	1975–1976	12	Mar	Sep	6	B	ND	✓	Cardoso *et al.*, 1979
Bogota	4.37	1975–1976	10	Oct	Dec	2	B	11	✓	Charlet *et al.*, 1978
Reus	41.17	1975–1976	12	Oct	Jul	9	ND	5	✓	Gomez *et al.*, 1981b
Puigcerda	42.43	1975–1976	12	Oct	Mar	4	ND	6	✓	Gomez *et al.*, 1981b
L'Ametlla	41.83	1976–1977	12	Aug	Feb	6	ND	6	✓	Gomez *et al.*, 1981b
Bogota	4.37	1976–1977	7	Sep	Oct	1	B	11	✓	Charlet *et al.*, 1979
Fusagasuga	4.3	1976–1977	7	Oct	Feb	4	B	4	✓	Charlet *et al.*, 1979

(continued)

Table 5.8 (Continued)

Locality	Latitude (decimal)	Years	Duration (months)	Month of maximum population	Month of minimum population	Duration (max. to min.)*	Floors (F) or beds (B)	No. homes	Climate data?	Reference
Girardot	4.3	1976–1977	7	Jan	Sep	8	B	5	✓	Charlet *et al.*, 1979
Groesbeek	51.78	1976–1977	13	Jul	Jan–Mar	7	B	1	✓	Lustgraaf, 1978b
Vancouver	49.33	1977–1979	24	Oct, Jul	Dec, Jan	6	B	3	✓	Murray & Zuk, 1979
Dayton	39.75	1977–1979	27	Jun–Aug	Feb–Mar	7	BF	19	✓	Arlian *et al.*, 1982, 1983
Wakayama	34.21	1977–1979	18	Sep	Mar, Dec	6	BF	55	✓	Uchikoshi *et al.*, 1982
Bangalore	12.97	1978–1980	17	Sep, Dec	Apr	7	B	12	✓	Ranganath & Channa-Basavanna, 1988
Thisted	56.97	1980	12	Oct	May	7	B	1	✓	Hallas & Korsgaard, 1983
Tokyo	34.75	1981–1982	12	Jul	Dec	5	ND	6	✗	Yoshikawa *et al.*, 1982
Tokyo	34.75	1981–1982	12	Jul	Nov	4	ND	6	✗	Yoshikawa *et al.*, 1982
Saitama	36.42	1981–1982	12	Aug	Aug	12	ND	6	✗	Takaoka & Okada, 1984
Sosnowiec	53	1984–1985	24	May, Oct	Dec, Mar	7	B	2	✓	Solarz, 1997
Aurang-abad	19.87	1984–1985	18	Aug–Sep	May	9	B	ND	✓	Tilak & Jogdand, 1989
Shanghai	31.17	1984–1985	12	May	Dec	7	ND	ND	✓	Cai & Wen, 1989
La Paz, Mexico	24.17	1985–1986	13	Dec	Jun	6	BF	17	✓	Servin & Tejas, 1991
Taipei	25.03	1986–1987	12	Oct	Jul	9	B	61	✓	Chang & Hsieh, 1989
Mie Prefecture	32.82	1989–1990	12	Jul	Nov	4	BF	14	✗	Matsuoka *et al.*, 1995
Okinawa	26.53	1990–1991	12	May	Jan	8	ND	11	✓	Toma *et al.*, 1993
Pal-machim	32.00	1995–1996	12	Jun	Apr	10	BF	2	✓	Mumcuoglu *et al.*, 1999
Zova	31.78	1995–1996	12	Jun	Jan	7	BF	2	✓	Mumcuoglu *et al.*, 1999
Taichung	24.09	1998–1999	11	July	Jan	6	BF	8	✓	Sun & Lue, 2000
Dayton	39.75	1998–1999	18	July	Mar	7	F	71	✓	Arlian *et al.*, 2001
Ponteve-dra	42.42	2002	12	May	Jan	4	B	1	✗	Boquete *et al.*, 2006
La Coruña	43.37	2002	12	Jun	Jan	7	B	1	✗	Boquete *et al.*, 2006
Orense	42.33	2002	12	Oct	Jan	9	B	1	✗	Boquete *et al.*, 2006
Lugo	43.00	2002	12	Aug	Mar	5	B	1	✗	Boquete *et al.*, 2006
Mansoura	30.13	2004–2005	12	Spring	Winter	ND	BF	3	✗	El-Shazly *et al.*, 2006

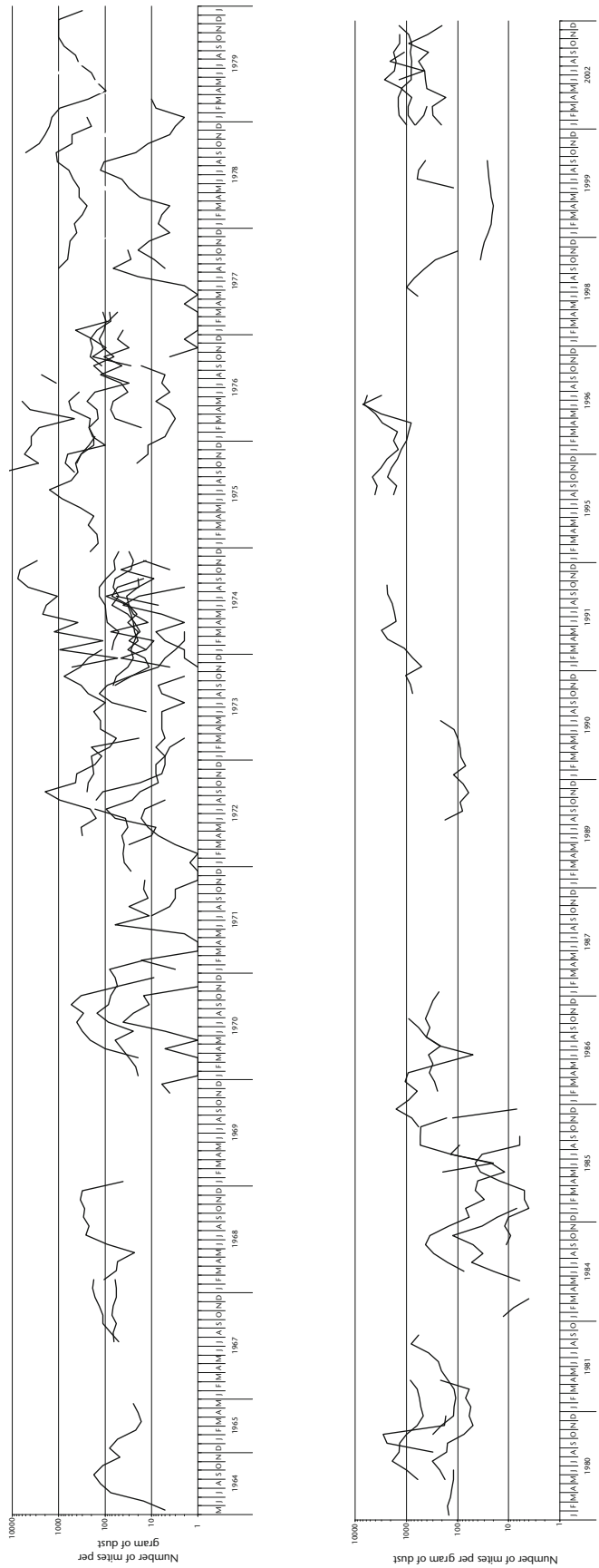

Figure 5.17 Seasonal variation in mite abundance: data from all studies, 1964–2002. The two Southern Hemisphere studies (Domrow, 1970 in Brisbane and Cardoso *et al.*, 1979 in Brasilia) were adjusted by 6 months to match with Northern Hemisphere seasons.

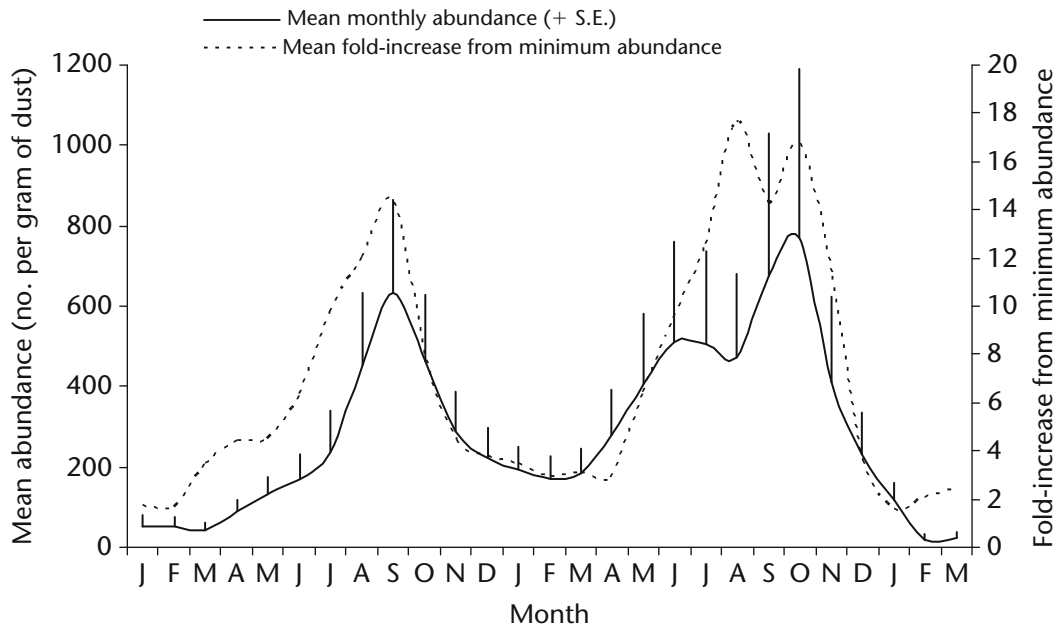

Figure 5.18 Seasonal fluctuations of dust mite populations, based on studies in Table 5.7.

Miyazawa *et al.,* 1996; Garrett *et al.,* 1998; G.L. Chew *et al.,* 1999; Sidenius *et al.,* 2002a), seasonal maxima were between late autumn and early winter. Minima were between late spring and early summer. Of the studies that investigated seasonal variation of both allergen concentrations and population density of mites, Platts-Mills *et al.* (1987) found a slight lag of allergen maxima of up to 8 weeks, whereas Sidenius *et al.* (2002), with observations taken bi-monthly, found mite and allergen fluctuations were more or less synchronous.

Crisafulli *et al.* (2007) analysed seasonal variation of Der p 1 from repeat-sampling of beds of children over a 7-year period (1997–2004) in relation to indoor and outdoor climate in Sydney. This is by far the most comprehensive information available on seasonal fluctuations of allergens. Der p 1 was highest in mid-autumn to winter (May–June) and lowest in mid-summer (January; see Figure 5.20). This pattern is similar to that of van Strien *et al.* (2002), based on a large dataset from the Netherlands, though their minimum falls slightly earlier. Sydney has a temperate climate (mean monthly temperature range ca. 10–23°C) with about 800 mm of rainfall distributed fairly evenly throughout the year. Fluctuations in allergen lagged behind relative humidity (indoors and outdoors) typically by about 2 months. It is likely that increases in humidity and temperature in late summer (February–March) stimulate mite population growth and that allergen levels peak around 8 weeks thereafter. As mite populations decline, stimulated by falling temperatures and humidities, allergen concentrations tend to persist until reduced, presumably, by microbial decomposition.

One of the most striking characteristics of the Sydney Der p 1 data is the mean seasonal maxima are only two-to-three times higher than the minima. Although allergen concentrations fluctuate, they are basically stable between years. The grand mean for the dataset (interpolated from Figure 1 of Crisafulli *et al.,* 2007) is 7.3 μg g^{-1} (range 2.2–17), and for over three-quarters of the time mean allergen levels are between 4 and 9 g^{-1}. For those studies where repeated measurements were done in the same homes, Platts-Mills *et al.* (1987) recorded a difference between seasonal maxima and minima of about eight-fold for Charlottesville, Virginia. The difference for Berlin (Lau *et al.,* 1990) and Tokyo (Miyazawa *et al.,* 1996) was four-fold, and was about two-fold for Cartagena, Colombia (Fernández-Caldas *et al.,* 1996), the La Trobe Valley, Australia (Garrett *et al.,* 1998), Boston (G.L. Chew *et al.,* 1999) and Copenhagen (Sidenius *et al.,* 2002). Markedly higher variation was recorded from Taipei by Li *et al.* (1994), though mean fold-changes per home were not detailed. The fold-difference in seasonal maxima and minima of ca. two to eight for allergens is within the same range as fold-differences

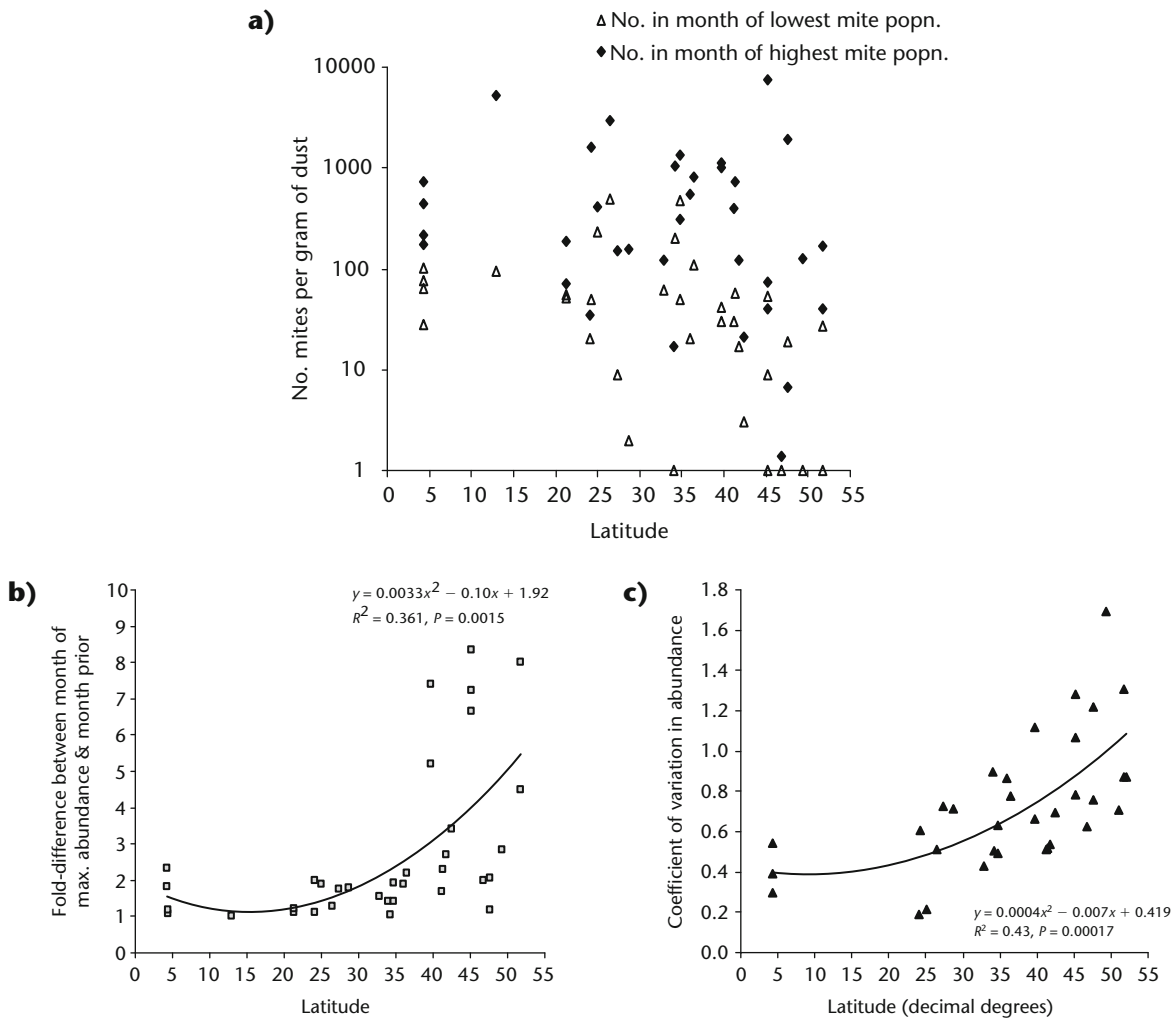

Figure 5.19 **a)** Relationship between latitude and seasonal maxima and minima of mite abundance; **b)** relationship between latitude and the fold-difference between number of mites during month of maximum abundance and number in the month prior; **c)** relationship between latitude and the coefficient of variation in seasonal mite population density from studies of seasonal variation. Lines of best fit for b) and c) are 2nd-order polynomials.

for mite population density during the period of exponential growth (shown in Figure 5.19b).

The data on seasonal variation, together with the regional-scale examples in Chapter 4, start to suggest that, within certain constraints, particular localities may have characteristic (and therefore predictable) mite population densities and allergen concentrations. This issue is explored further in Chapter 8.

5.8 Population models

Any mathematical formula used to describe the behaviour of a population represents a population model, including the equations for stable age distribution and intrinsic rate of natural increase detailed herein. Models represent an explanation for a particular phenomenon or observation that allow a hypothesis to be refined or tested, but they do not represent a test in themselves. Models are particularly useful in helping explain how complex variables might interact, but they are invariably simplifications of reality. For example, Figure 5.5 shows two neat 3rd-order polynomial curves fitted to the empirically derived survivorship data for *Euroglyphus maynei* and *Tyrophagus putrescentiae*. They are models that describe mortality as most rapid early in life and that a greater proportion of the population of *E. maynei* survives longer than *T. putrescentiae*. But because the curves are fitted to the entire dataset for each species, they do a very poor job of detecting the subtle differences of stage-specific mortality: that there is no mortality between the protonymphal and tritonymphal stage and low mortality between the reproductive and post-reproductive stages for *T.*

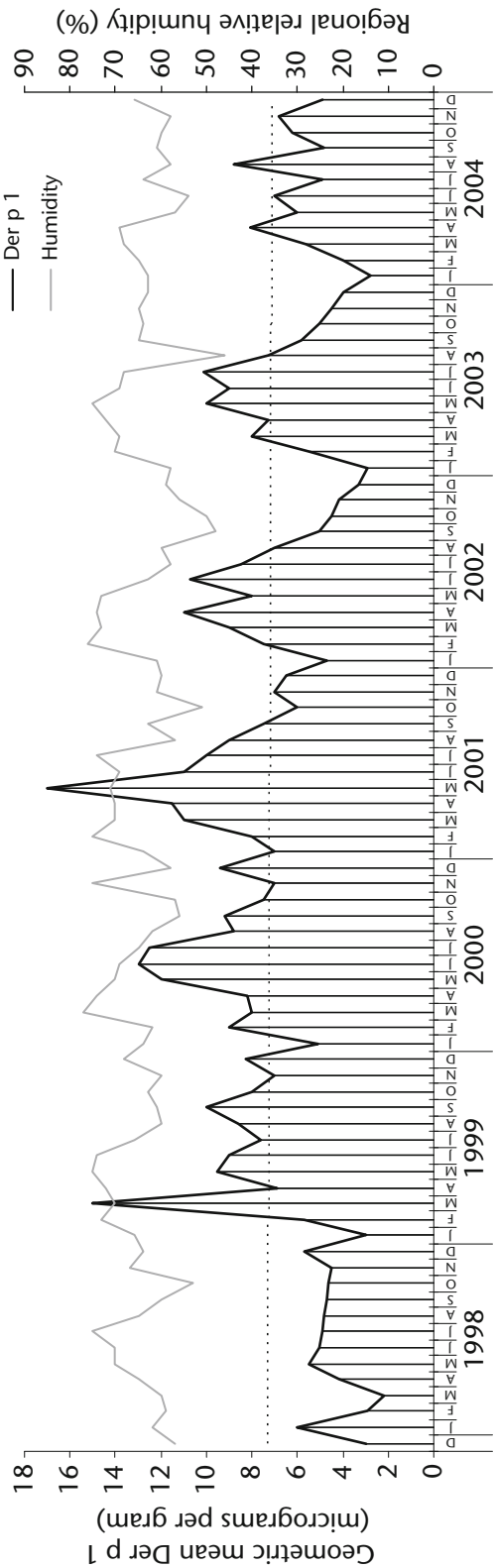

Figure 5.20 Long-term seasonal variation in mite allergen (Der p 1) concentrations in relation to humidity in Sydney, Australia. (Re-drawn from data by Crisafulli *et al.*, 2007.) The dotted line is the geometric mean Der p 1 concentration, 7.3 μg g^{-1}.

putrescentiae, whereas for *E. maynei* the reverse is true, as would be shown more clearly by simply joining the dots rather than fitting a curve. But the curves look nice (whereas the joined dots look raggedy) and, through the seductive complementarity of their shapes, hold the allure of some deeper truth.

Models by Cunningham (2000) and Crowther *et al.* (2006) for *Dermatophagoides pteronyssinus* have used constant rates of increase at any given combination of temperature and humidity, regardless of the size of the population or its age structure, but, as we have seen above, mite populations do not show constant rates of increase. Age structure is a crucial determinant of population increase. Further, both models place considerable emphasis on humidity as *the* major driver of population dynamics. Crowther *et al.* (2006) coin the phrase 'population equilibrium humidity' (that is the humidity at which populations neither grow nor decline). Again, mite population growth is not driven only (or even primarily) by humidity. Populations will decline, even if humidity is optimal, if the diet is inadequate to support reproductive allocation. Populations will increase, even if humidity is sub-optimal for most of the time, if mites are able to regain body water during short periods when humidity is optimal. And we have seen that the effects of temperature and humidity on population growth are hard to separate.

Biddulph *et al.* (2007) improved on these models by factoring in stage-specific mortality and accounting for the interaction of temperature and humidity, and developed contour plots of population growth rates at temperatures from 10–45°C and 30–100% RH. Other population models for domestic mites include those for *Lepidoglyphus destructor* (Danielsen *et al.,* 2004), *Acarus siro* (Pekár and Žďárková, 2004; Aspaly *et al.,* 2007), *Tyrophagus putrescentiae* and *Aleuroglyphus ovatus* (Aspaly *et al.,* 2007). The models by Aspaly *et al.* (2007) and Danielsen *et al.* (2004) were validated based on empirical observations of population growth in laboratory cultures, the latter model also incorporating rates of production of the major allergen Lep d 2, whereas the model by Pekár and Žďárková (2004) was based on statistical interpretation of published life history parameters. These authors made the important point that laboratory studies tend to result in over-estimations of life history parameters, leading to unfeasibly rapid population growth projections when used in models, because mites in cultures are given higher quality food than they are likely to encounter in natural conditions.

The models considered here are all deterministic, that is they project a particular outcome given a set of constant conditions. Because they are deterministic, they have no true predictive capacity. For the difference between a population projection and a population prediction, see Krebs (2001, p. 143). The interaction of several major variables that affect population growth means that models that more closely reflect behaviour of populations in the wild need to be probabilistic, or stochastic; that is they need to account for the probabilities of each variable, and their interactions, that influence population growth. Leslie matrices can be used to generate probabilistic models based on age structure of populations (Caswell, 2001), but this topic is well beyond the scope of the present chapter. Future developments in population modelling may well focus less on life history parameters from laboratory cultures and more on the wealth of untapped data from studies of seasonal population dynamics of mites in their natural habitats (Figure 5.17).

There is a tendency to regard population models as important (or even crucial) to developing more successful methods of mite control. In fact, this is probably not their greatest utility. Models become useful if they can be applied to a particular question and this application leads to an advance, but more successful methods of mite control have been developed over the last 30 years in the absence of population models (see Chapter 9). I suspect that one of the more important uses of models has been in developing a better comparative basis for understanding how the populations of different species behave and how that behaviour relates to differences in life history parameters. The future application of this comparative approach rests in the fact that populations in homes consist of several species (Chapter 4, Figure 4.13), such as *Blomia tropicalis* and *Dermatophagoides* spp. in the tropics and sub-tropics, or *D. pteronyssinus* and *D. farinae* in Europe and North America. We know very little about the behaviour of mixed populations under natural conditions, or the implications for allergen production, sensitisation and exposure.

5.9 Summary

There is a large gap in our knowledge about how domestic mite populations behave in laboratory monocultures on good quality diets and constant conditions, and what happens in mixed populations

in fluctuating conditions and with poorer quality diets in their natural environment. Bridging that gap is likely to be quite a challenge, but would be of considerable benefit in developing a better understanding of the link between mites, allergens and disease.

The combination of life history traits, physiological adaptations of life cycle stages and demographic parameters of the Acaridae, Glycyphagidae and Pyroglyphidae result in two major groups of life history tactics:

1. Large, rapidly growing and reproducing mites which can form extremely large populations very quickly by virtue of their high fecundity and short development times. When conditions are poor, mortality may be very high, but because of the huge populations, enough individuals are able to survive and disperse via a specialised stage in the life cycle adapted for these purposes. These mites are well adapted to exploit a wide range of patchy or ephemeral food resources which they may consume relatively quickly before moving on and colonising new habitats. This group includes the acaroids and glycyphagoids.
2. Small, slow-maturing species with modest fecundity and long generation times which can form quite large populations if conditions are favourable, and survive unfavourable conditions as adults or nymphs rather than as specialised stages. They are well adapted to exploit spatially and temporally contiguous food resources which are consistently renewed. These mites tend to be more restricted than the first group to particular types of food and habitat, and may form lasting associations with mammals and birds on which they depend for dispersal. This group includes the pyroglyphids.

This all sounds like the classic characteristics of *r*- and *K*-selected species (see section 1.4.4), with the first group being the *r*-selected and the second *K*-selected (but see Stearns (1992) for a summary of arguments for the rejection of *r* and *K*-selection). However, there are lots of assumptions and exceptions in these generalised statements. Nevertheless, they serve as a starting point for considering how the life histories and population dynamics of these groups of domestic mites impact on human health and well-being.