

Short life cycles in insects and mites¹

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Abstract—Under favourable conditions some species of insects and mites complete development very quickly. This paper considers species with a mean minimum generation time of 15 days or less and tabulates developmental data for many sample species. Such species belong chiefly to a limited number of taxa of small size, notably aphids and several families of mites and parasitoid Hymenoptera. Characteristics of these taxa are reviewed. Even in families containing many species with rapid life cycles, normally many other species lack such rapid development. Very short life cycles depend on phylogeny, strain, rapid development in all stages, small size, rich food, and other habitat features including high temperatures. Within this framework, life cycles are accelerated by reducing elements requiring the investment of resources (size, fecundity, longevity, structural complexity), eliminating instars and even life stages, accelerating development (through lower requirements especially of heat, heat gain by adaptations such as basking, and rapid reproduction), and choosing the most suitable habitats and microhabitats from those available. Mean minimum generation times in insects and mites with coincident adaptations of this sort can be as short as 4 days. Notwithstanding the advantages of rapid development in maximizing the intrinsic rate of natural increase (and hence fitness), most species cannot achieve the highest rates of development. They are constrained not only by resources and intrinsic physiological or phylogenetic patterns but also by variability of conditions and seasonality that can be survived only by interpolating delays or resistant stages.

Résumé—Sous des conditions favorables, certains insectes et acariens complètent leur développement très rapidement. Il est question ici d'espèces qui ont une durée de génération minimale moyenne de 15 jours ou moins et on y trouve des compilations des données de développement pour plusieurs espèces choisies. La plupart de ces espèces appartiennent à un nombre réduit de taxons de petite taille corporelle, particulièrement des pucerons et plusieurs familles d'acariens et d'hyménoptères parasitoïdes. Les caractéristiques de ces taxons sont passés en revue. Même dans les familles qui contiennent plusieurs espèces à cycle biologique rapide, il y a normalement beaucoup d'autres espèces qui n'ont pas ce développement rapide. Les cycles biologiques très courts dépendent de la phylogénie, de la race, d'un développement rapide à tous les stades, d'une taille réduite, d'une nourriture riche et d'autres caractéristiques du milieu, dont des températures élevées. Dans ce cadre, l'accélération du cycle se fait par la réduction des éléments qui requièrent un investissement de ressources (taille, fécondité, longévité, complexité structurelle), l'élimination de stades ou mêmes d'étapes du cycle, l'accélération du développement (par des exigences réduites particulièrement de chaleur, l'acquisition de chaleur par des comportements tels que l'exposition au soleil et la reproduction rapide) et le choix des habitats et des microhabitats les plus appropriés parmi ceux qui sont disponibles. Les durées de génération minimales moyennes chez les insectes et les acariens qui possèdent des combinaisons d'adaptations de ce type peuvent être aussi courtes que 4 jours. Malgré les avantages du développement rapide pour augmenter le taux intrinsèque d'accroissement naturel (et ainsi la fitness), la plupart des espèces n'arrivent pas à atteindre les taux les plus rapides. Elles en sont empêchées non seulement par le manque de ressources et par leurs taux physiologiques et phylogénétiques intrinsèques, mais aussi par la variabilité des conditions et par les variations saisonnières qui exigent des animaux l'insertion dans leur cycle de délais ou de stades résistants pour assurer leur survie.

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Introduction

Some arthropod species develop rapidly, especially in certain life stages. For example, many entomologists have commented on the fact that in several families of Diptera the larvae ("maggots") grow conspicuously fast (*cf.* Levot *et al.* 1979). However, extremely rapid development in all stages from egg to adult is not especially common, and many earlier studies of life cycles have instead emphasized long life cycles (Danks 1992) and developmental delays such as diapause (*e.g.*, Danks 1987). This paper explores the features of species in which some individuals can complete a whole life cycle in 15 d or less under suitable conditions. Characteristics of such species can be related to intrinsic features and external conditions, providing wider lessons about the nature of habitats and the constraints on development.

Methods

Information on species with short life cycles was obtained by a review of publications on the life cycles of arthropod species in the international entomological and acarological literature; that review included the detailed examination of each volume from 1960 onwards of about 20 journals selected because they commonly contain papers on insect and mite development. Data that document short life cycles, as well as information on intrinsic or environmental correlates and on mechanisms by which these life cycles are achieved, have three major weaknesses. First, many publications present data on only part and not the whole of the life cycle, making it impossible to put the data reported to full use for the current purpose. For example, a majority of publications on insect development give the duration of immature development but provide insufficient information on adults to determine the generation time. In some instances the difficulty is compounded because larval-pupal (or larval) development has been examined in detail, but there is no corresponding information on eggs (or on eggs and pupae). Other publications provide detailed adult reproductive statistics, especially the duration of oviposition, but give insufficient data on preoviposition intervals. Moreover, because strains and food conditions in experiments done at different times usually are not the same, data on the same species in different studies are not equivalent. For example, in different studies cited by

Morgan *et al.* (2001: Table 5), minimum generation time of the aphid *Acyrtosiphon pisum* (Harris) at 20 °C varied between 6.4 and 9.9 d.

Second, there are biases as to the species and conditions examined, so that the relative occurrence of reports on fast development does not fully reflect the real patterns among taxa. For example, an emphasis on plant-feeding pests in the literature somewhat favours species with relatively rapid development in the larval stage because this feature tends to increase the potential for crop damage. Another emphasis is on potential agents for biological control, including predators and parasitoids with relatively rapid development that favours their ability to constrain prey or host populations.

Third, many published data on development suffer from weaknesses of experimental design or analysis (Danks 2000). For example, measures from adults kept under poor conditions (*e.g.*, inadequate food for maintenance or egg development, or inadequate light for activity) give no meaningful measures of preoviposition intervals or patterns of oviposition. Even measuring short life cycles accurately presents several experimental difficulties. Rapid stages are best recorded using intervals for observation of less than a day, because otherwise means will be inaccurate and the variance of the results will be artificially reduced (references in Danks 2000, p. 296). A major difficulty, especially with recent publications, is that instead of basic information, only highly transformed statistics or graphical representations are presented; these may serve the purpose of the individual paper, such as mathematical modelling, but are not more widely useful (Danks 2000).

Consequently, despite the many published studies of insect and mite development, it is not feasible to tabulate a wide range of life-cycle statistics for a diversity of rapidly developing species. Instead, I document the reported values of four informative and relatively widely available measures. (1) **Minimum generation time** (labelled *G*, the commonly used symbol for this statistic, in tables in this paper) is the mean interval from oviposition (or larviposition) to the *first* progeny of the next generation (*cf.* Abou-Setta and Childers 1991). This interval is equivalent to the mean immature development time plus the mean preoviposition interval. (2) **Observed generation time** (*O*) is the recorded interval from oviposition to the *mean* progeny of the next generation. (3) **Calculated generation time** (*T*) is the calculated demographic statistic

for mean generation time (Birch 1948; Carey 1993). It is similar to the observed generation time but may differ somewhat depending on the way in which data are recorded and the method of calculation. (4) **Immature development time (D)** is the mean duration from egg deposition to adult emergence (or larviposition to the adult moult). When available, the duration is that of the development of females, on which the generation time depends. This sort of information is readily available and can supplement information for taxa in which generation time has been reported elsewhere.

Generation times or developmental intervals estimated from published information (rather than cited directly) are shown in parentheses in tabulations here. For example, in some reports relevant information could be estimated from methodological comments, such as the age of adults when the next batch of eggs was obtained, from graphical summaries of the pattern of oviposition, or from other quantitative information.

Developmental and generation times of a given species may depend on the strain and the conditions (temperature, food, humidity, density, and so on). For the main purpose of this paper, only the fastest times given in any report are listed. However, in some species a very short minimum generation time has been reported under conditions that are generally unsuitable (such as high temperatures), giving extremely low survival, fecundity, or rates of natural increase (r_m). For example, egg to adult development of the mosquito *Culex annulirostris* Skuse takes 8.3 d at 35 °C and 12.5 d at 30 °C, but survival at the higher temperature is only 22%, compared with 65% at the lower temperature (Mottram *et al.* 1986). Because the gonotrophic cycle lasts a minimum of 4 d in this species, life cycles of less than 15 d are possible but not optimal. The mean generation time of the aphid *Brachycaudus rumexicolens* (Patch) is only 5.6 d at 30 °C (Scott and Yeoh 1999), compared with 7.2 d at 27.9 °C, but at the higher temperature survival and reproduction are so low that r_m is negative. Such data for very rapid development were rejected if the life cycle was clearly unsuccessful under the given conditions and data were available for less extreme conditions.

Some comparative remarks are made here about species with longer life cycles. These remarks are based on many reports in the literature (consulted whilst compiling data on short

life cycles) but the reports generally have not been cited in order to avoid adding hundreds of additional references peripheral to the main theme.

Taxa with very short life cycles

Taxa characterized by species with very short life cycles are summarized here. Normally other species in the same taxa (not tabulated here) have life cycles that are longer even under the most favourable conditions. Such differences among species are especially noticeable in more diverse taxa (*e.g.*, Tetranychidae, Braconidae). Typically, the differences accord with ecological or other requirements discussed in later sections.

Acari

Most mites are small and in certain families many species, but by no means all, develop relatively rapidly. However, other large groups are characterized by slow development: ticks (Ixodida), in which delays may also be associated with host finding; soil mites (Oribatida), which have unusually slow development (*e.g.*, Woodring and Cook 1962; Jalil 1972; Norton 1994); and many water mites (Hydrachnidia), which have only one generation per year (Proctor and Pritchard 1990).

Mesostigmata

Many species of Phytoseiidae have been reared in the laboratory as potential predators of pest mites and small insects or their eggs. The family is characterized by rapid development without elimination of instars. Many species have minimum generation times of less than 10 d, and even mean generation times of less than 15 d are not uncommon (Table 1; Jeppson *et al.* 1975, p. 79; see also Sabelis 1991; additional data for immature development only, *e.g.*, Takahashi and Chant 1992, are not included in the Table).

Records of rapid development are available for a few other families of mites in the same suborder (Table 2). Most of the species are relatively small and most of them are predatory. Egg to adult development is extremely rapid in some species, for example lasting only 1.5 d in some species of *Macrocheles* (Table 2; Cicolani 1983). Records for species with egg to adult development times of less than 10 d, in addition to those in Table 2, were listed by Walter and Ikonen (1989) for Digamasellidae (8–9 d) and

Table 1. Sample records of short life cycles in Phytoseiidae, listed with the shortest records first.

Species	G	O	T	D	°C	Reference
<i>Neoseiulus womersleyi</i> (Schicha) [<i>Amblyseius</i>]	4.0		6.9	2.0	33	Lee and Ahn 2000
<i>Neoseiulus fallacis</i> (Garman) [<i>Amblyseius</i>]	4.0			3.3	32	Smith and Newsom 1970
	4.4			3.5	26.4	Ball 1980
	6.6	(13)		4.1	26	Boyne and Hain 1983b
				4.6	26	Kramer and Hain 1989
<i>Neoseiulus bibens</i> (Blommers) [<i>Amblyseius</i>]	4.7			(3.7)	31	Blommers 1976
	5.3		9.1	4.1	29	
<i>Mesoseiulus longipes</i> (Evans) [<i>Phytoseiulus</i>]	5.0	7.8		3.9	35	Badii and McMurtry 1984
<i>Euseius citrifolius</i> Denmark and Muma [<i>Amblyseius</i>]	(5.3)	(10.6)		3.6	30	de Moraes and McMurtry 1981
<i>Phytoseiulus macropilis</i> (Banks)	5.4		8.8	4.2	28	Ali 1998
	5.5			4.2	26	Prasad 1967
	7.5			6.0	26.4	Ball 1980
	8.9			6.8	23–25	Kropezyńska <i>et al.</i> 1988
<i>Neoseiulus longispinosus</i> (Evans) [<i>Amblyseius</i>]			9.7	4.1	27	Mallik and ChannaBasavanna 1983
	5.5		10.4	4.4	25	Saitô and Mori 1981
	8.4			4.8	28	Thongtab <i>et al.</i> 2001
	5.5	(10)		4.5	35, 30	Pruszyński and Cone 1973
<i>Galendromus occidentalis</i> (Nesbitt) [<i>Typhlodromus</i> , <i>Metaseiulus</i>]	5.9		10.2		32	Tanigoshi <i>et al.</i> 1975b
	7.6			6.3	23.9	Lee and Davis 1968
	8.1			6.4	25	Badii and McMurtry 1984
	5.5			3.9	26.4	Ball 1980
<i>Galendromus longipilus</i> (Nesbitt)	(5.5)		9.6		26	Abou-Setta and Childers 1989
<i>Euseius mesembrinus</i> (Dean) [<i>Amblyseius</i>]	5.5	17.0		3.8	26	El-Laithy and Fouly 1992
<i>Typhlodromips swirskii</i> (Athias-Henriot) [<i>Amblyseius</i>]	7.5			5.7	27	Momen and El-Saway 1993
	9.2		19.7	8.0	29	Abou-Awad <i>et al.</i> 1999a
	5.8		8	5.0	25	de Moraes and Lima 1983
<i>Euseius concordis</i> (Chant)	(6)				25	Steiner <i>et al.</i> 2003b
<i>Typhlodromalus lailae</i> (Shicha)	(6)		15.9	4.3	32	Broufas and Koveos 2001
<i>Euseius finlandicus</i> Oudemans [<i>Amblyseius</i>]	(7.4)		14.7	6.4	20	Broufas and Koveos 2000
	9.8			7.8	23–25	Kropezyńska <i>et al.</i> 1988

Table 1 (continued).

Species	G	O	T	D	°C	Reference
<i>Euseius stipulatus</i> (Athias-Henriot)	5.8		9.7	5.5	32	Ferragut <i>et al.</i> 1987
<i>Galendromus helveolus</i> (Chant)	6.1		10.2	4.6	30	Caceres and Childers 1991
<i>Euseius alatus</i> DeLeon	6.3		14.1	4.5	25	Reis and Alves 1997
<i>Amblyseius deleoni</i> Muma and Denmark	6.3		11.25	4.9	25	Saitô and Mori 1981
<i>Cydnoseius africanus</i> (Yousef) [<i>Typhlodromus</i>]	6.7			5.2	25	Yousef 1981
<i>Phytoseiulus persimilis</i> Athias-Henriot	6.8			4.0	25	Toyoshima and Amano 1999
	6.9	(15?)		5.1	25	Badii and McMurtry 1984
	7.5	(15)		5.4	25	Takafuji and Chant 1976
	10.4		17.3	6.1	25	Amano and Chant 1977
	7.0		17.0	7.4	~20.3	Laing 1968
<i>Neoseiulus idaeus</i> Denmark and Muma [<i>Amblyseius</i>]	(7)		9.3	4.6	25	Dinh <i>et al.</i> 1988
<i>Typhlodromips montidorensis</i> (Schicha)	7.4		13.6		25	Steiner <i>et al.</i> 2003a
<i>Typhlodromus phialatus</i> Athias-Henriot	7.5			5.3	32	Ferragut <i>et al.</i> 1987
<i>Phytoseiulus plumifer</i> (Canestrini and Fanzago)	7.6		17.8	4.9	29.5	Zaher <i>et al.</i> 1969
<i>Neoseiulus anonymous</i> (Chant and Baker) [<i>Amblyseius</i>]	7.8		14.7	6.1	25	Dinh <i>et al.</i> 1988
<i>Euseius scutalis</i> (Athias-Henriot) [<i>Amblyseius</i>]	8.0		13.5	5.9	26	El-Laithy and Fouly 1992
<i>Neoseiulus paraki</i> (Ehara) [<i>Amblyseius</i>]	8.0	(?19)		5.7	25	Saitô and Mori 1981
<i>Iphiseius degenerans</i> (Berlese) [<i>Amblyseius</i>]	8.1		14.4	6.3	25	Takafuji and Chant 1976
<i>Typhlodromalus peregrinus</i> (Muma) [<i>Typhlodromus</i>]	(8.4)	(16.4)		6	26	Fouly <i>et al.</i> 1995
<i>Neoseiulus umbraticus</i> (Chant) [<i>Amblyseius</i>]	8.5			6.4	25-26	Knisley and Swift 1971
<i>Typhlodromalus limonicus</i> (Garman and McGregor) [<i>Amblyseius</i>]	8.7			6.7	22.2	McMurtry and Scriven 1965
<i>Neoseiulus masiaka</i> (Blommers and Chazeau) [<i>Amblyseius</i>]	8.8	(17)		6.7	25	Blommers 1974
<i>Euseius hibisci</i> (Chant) [<i>Amblyseius</i>]			8.8	6.7	25.5-26.7	Tanigoshi <i>et al.</i> 1983
<i>Amblyseius largoensis</i> (Muma)			9.0	4.6	35	Tanigoshi <i>et al.</i> 1981
<i>Amblyseius badryi</i> Yousef and El-Brolllosy	9.0		17.2	3.2	35	Yue and Tsai 1996
<i>Euseius metwalli</i> Basha, Yousef and Mostafa	9.1			7.4	27	About-Awad <i>et al.</i> 1998
<i>Bawus talbii</i> (Athias-Henriot) [<i>Typhlodromus</i>]	9.2		17.3	7.3	27.1	Basha <i>et al.</i> 2002
<i>Orientiseius rickeri</i> (Chant) [<i>Typhlodromus</i>]	9.4			6.7	27	Camporese and Duso 1995
<i>Amblydromella caudigans</i> (Shuster) [<i>Typhlodromus</i>]	9.5			6.4	22.2	McMurtry and Scriven 1964
				6.7	24.4-25	Putman 1962

Table 1 (concluded).

Species	G	O	T	D	°C	Reference
<i>Amblyseius andersoni</i> (Chant)	9.6	(18)		7.4	25	Amano and Chant 1977
<i>Euseius gossipi</i> (El-badry) [<i>Amblyseius</i>]	9.8			6.5	30.6	Yousef <i>et al.</i> 1982b
<i>Typhlodromus exiltaratus</i> Ragusa	(9.9)			7.4	26	Castagnoli and Liguori 1986
	10.0	16.7		7.5	25	Castagnoli <i>et al.</i> 1989
<i>Typhlodromips sessor</i> (DeLeon)	9.9			7.6	25	Sciarappa and Swift 1977
<i>Paraseiulus soleiger</i> (Ribaga) [<i>Phytoseius</i>]	9.9			7.5	23–25	Kropeczynska <i>et al.</i> 1988
<i>Euseius finlandicus</i> (Oudemans) [<i>Amblyseius</i>]	10.0			7.8	23–25	Kropeczynska <i>et al.</i> 1988
<i>Proprioseiopsis temperellus</i> (Denmark and Muma)	10.4			5.7	26.4	Ball 1980
<i>Kampimodromus aberrans</i> (Oudemans) [<i>Amblyseius</i>]	10.5			8.3	23–25	Kropeczynska <i>et al.</i> 1988
<i>Amblydromella kettanehi</i> (Dosse)	11			5.5	23	Arbabi and Baradaran 2001
<i>Neoseiulus barkeri</i> Hughes [<i>Amblyseius</i>]	11.3			8.45	25	Momen 1995
<i>Phytoseius hawaiiensis</i> Prasad	11.6			6.9	24	Sanderson and McMurtry 1984
<i>Typhlodromus pyri</i> Scheuten	12.4			9.6	24	Kropeczynska <i>et al.</i> 1988
	15			10	18.3	Herbert 1961

Note: G, minimum generation time; O, observed generation time; T, calculated generation time; D, immature development time. All values are mean durations, shown in days; estimated values are shown in parentheses. For further details see Methods. Taxonomy for this family is according to de Moraes *et al.* (1986); other names used in the cited references are shown in brackets.

Table 2. Sample records of short life cycles in other mesostigmatic mites.

Species	G	O	T	D	°C	Reference
Digamasellidae						
<i>Dendrolaelaps neodisetus</i> (Hurlbutt)	9.4			7.9	25	Kinn 1984
Laelapidae						
<i>Haemolaelaps centrocarpus</i> Berlese	14.8			11.8	27	Furman 1966
Macrochelidae						
<i>Macrocheles muscaedomesticae</i> (Scopoli)	4.6 5.1		4.5	1.8 2.3 2.9	30 26.7 30	Filippini <i>et al.</i> 1971a; Cicolani 1979 Wade and Rodriguez 1961 Ho 1989
<i>Macrocheles matrius</i> (Hull)			4.5	2.1 2.2 3.4	34 34 30	Filippini and Cicolani 1974; Cicolani 1979 Cicolani 1978 Soliman <i>et al.</i> 1978
<i>Macrocheles subbadius</i> (Berlese)	4.9		4.9	1.6	31	Cicolani <i>et al.</i> 1977; Cicolani 1979
<i>Macrocheles robustulus</i> (Berlese)			5.2	1.4	3.3	Filippini and Mosna 1968; Cicolani 1979
<i>Macrocheles pergaber</i> Filippini and Peggazano			5.6	1.8	34	Filippini and Petrelli 1969; Cicolani 1979
<i>Macrocheles boudreauxi</i> Krantz	6.3			4.2	20	Kinn and Witcosky 1977
<i>Macrocheles peniculatus</i> Berlese			7.7	3.0	28	Filippini and Passariello 1969; Cicolani 1979
<i>Macrocheles penicilliger</i> (Berlese)			11.6	4.6	22–26	Filippini <i>et al.</i> 1971b; Cicolani 1979
Ascidae						
<i>Rhinozetus richardsoni</i> Hunter	5–7				Field	Colwell 1973
<i>Rhinozetus colwelli</i> Hunter	5–7				Field	Colwell 1973
<i>Blattisocius tarsalis</i> (Berlese) [<i>Melichares</i>]	7.4	(15)		5.9	27	Haines 1981
	8.7			6.9	25	Darst and King 1969
<i>Arctoseius semiscissus</i> (Berlese)	(9)		13.85	7.0	25	Nielsen 2001
<i>Lasioseius athiasae</i> Nawar and Nasr			17.9	7.85	20	Rudzińska 1998
<i>Blattisocius dentriticus</i> (Berlese) [<i>Melichares</i>]	(14)			7.4	27	Abou-Awad <i>et al.</i> 2001
Hypoaspidae						
<i>Hypoaspis miles</i> Berlese	14.2		26.6	10	22.2	Rivard 1960
Pachylaelapidae						
<i>Zygozetus furciger</i> Berlese				10.5	30	Ydergaard <i>et al.</i> 1997
				4.5	25	Walter and Proctor 1999, p. 49

Note: Conventions as in Table 1.

Ascidae (5–9 d) and by Ruf (1996, Appendix) for Eviphidae (9 d), Ascidae (5–9 d), Laelapidae (5–9 d), and Parasitidae (6–8 d). These records suggest that other mesostigmatid mites will prove to have short life cycles.

Prostigmata

Many species of Tetranychidae, small phytophagous species that are pests or potential pests on a wide range of plants, have been reared in the laboratory. A few species have minimum generation times below 10 d, and many more are below 15 d (Table 3).

There are relatively few observations for other families of prostigmatic mites (Table 4). However, rapid development is known in various families. For example, scattered records are available for fungus-feeding mites in the families Pygmephoridae and Tarsonemidae, for some species of tiny phytophagous mites of the family Eriophyidae, for insect egg parasitoids (*sensu* Lindquist 1983) of the families Pyemotidae and Acarophenacidae, for the tarsonemid genus *Iponemus*, and for other families. However, most other species of prostigmatic mites develop more slowly, including species in the subcohort Parasitengona (Wohltmann 2000: Table 5).

Astigmata (Acarididae)

This suborder includes many slow-moving and non-predatory mites, although many others are parasitic on birds and mammals. Acarids normally feed on fungi, and relatively short generation times are known in a range of species (Table 5; OConnor 1994). Some species in the family Histiostomatidae, which appear to be filter-feeders on microorganisms and live in many different habitats, also have rapid development (Table 5).

Insecta

Very short generation times are confined to relatively few taxa of insects, and most species develop more slowly. For example, many species of Odonata are large and take several years to develop. Most Plecoptera live in very cool habitats and few species have more than one generation per year. Cockroaches have a reputation for rapid population growth, but developmental times of most species are not particularly short. Long life cycles are also prevalent in the major orders Coleoptera and Lepidoptera. Most of the species that develop

very rapidly belong to relatively few families of Hemiptera, Diptera, and Hymenoptera.

Hemiptera

Many species of aphids have minimum generation times of 10 d or less under suitable conditions and mean generation times that are only a few days longer (Table 6). Rapid larval development is followed by very short periods between adulthood and larviposition of the next generation. Most members of this family are adapted for rapid reproduction by apterous virginoparae on summer host plants. However, fundatrices, the initial generation in spring, may develop even faster than the virginoparae. For example, the minimum generation time of fundatrices of *Eulachnus agilis* (Kaltenbach) is only 11.5 d, compared with 13.3 d for virginoparae (Bliss and Kearby 1971).

Most other families of small phytophagous Homoptera have slower larval development than aphids and are not larviparous, so that generations normally take slightly more than 15 d even in the smallest and most rapidly developing species of families such as Aleyrodidae, Psyllidae, Cicadellidae, and Delphacidae (but see Patil *et al.* 1994). Many other species take longer.

Development of most Heteroptera is slower still, not only in blood-feeding species in families such as Reduviidae, but also in phytophagous and predatory species (*e.g.*, in the Pentatomidae). A generation can be completed in less than 20 d in a few small species of mirids and anthocorids, and some anthocorids, which are predators of other arthropods, have minimum generation times just below 15 d (Table 7).

Thysanoptera

Most thrips are very small, normally less than 2 mm in length. Different species eat a variety of foods including fungi, plant tissues, pollen, and other invertebrates. Pest species in the largely phytophagous family Thripidae have been the most studied, and generation times of 12 to 15 d are not uncommon (Table 8). However, by no means all species are included, notably because egg development may take longer than larval development.

Coleoptera

Very few beetles have short life cycles, and even in species with rapid immature development the reproductive period normally is prolonged, typically including both a long preoviposition

Table 3. Sample records of short life cycles in Tetranychidae.

Species	G	O	T	D	°C	Reference
<i>Oligonychus pratensis</i> (Banks)						
	5.6		5.9	4.9	36	Perring <i>et al.</i> 1984a
	6.5		10.6	5.2	36	Perring <i>et al.</i> 1984b
	7			6.0	31	Congdon and Logan 1983
	5.7			6	24–41	Tan and Ward 1977
<i>Oligonychus indicus</i> (Hirst)				5.15	30	Gupta <i>et al.</i> 1975
	5.3			4.05	35	
<i>Panonychus citri</i> (McGregor)				4.6	25	Ashihara 1987
<i>Tetranychus urticae</i> Koch	6.8		13.2	6.1	29.4	Carey and Bradley 1982
	7.1			6.1	35	Pruszyński and Cone 1973
	7.3			6.7	26.4	Ball 1980
	(9.6)			7.6	27	Shih <i>et al.</i> 1976
						Feldmann 1981
	10.2			9.9	25	Saitô 1979
	(11.6)			8.0	21	Herbert 1981b
	15.1				25	Krips <i>et al.</i> 1998
	19.0			14.5	24	Grissa-Lebdi <i>et al.</i> 2002
				16.9	~20.3	Laing 1969
						Feldmann 1981
<i>Tetranychus pacificus</i> McGregor	6.3		17.2	7.4	30	Bounfour and Tanigoshi 2001
	7.1		12.5	6.7	30.2	Oi <i>et al.</i> 1989
	12.3	(24?)		10.5	29.4	Carey and Bradley 1982
<i>Tetranychus turkestani</i> (Ugarov and Nikolski)	7.2		12.55	6.4	25	Takafuji and Chant 1976
<i>Tetranychus cinnabarinus</i> (Boisduval)	<8		10.6	7.0	29.4	Carey and Bradley 1982
	<7		8.5	6.0	30	Hazan <i>et al.</i> 1974
<i>Tetranychus mcdanieli</i> McGregor	8.1		10.5		35	
				5.5	35	Tanigoshi <i>et al.</i> 1975a
				10.8	34	Roy <i>et al.</i> 2002
<i>Eotetranychus orientalis</i> Klein	8.2			5.9	25.5	Tanigoshi and Browne 1978
<i>Tetranychus evansi</i> Baker and Pritchard	9.9			9.0	29	Rasmy 1978
					23.3	Qureshi <i>et al.</i> 1969

Table 3 (continued).

Species	G	O	T	D	°C	Reference
<i>Eotetranychus hicoloriae</i> (McGregor)	10	(13.1)		8.5	32.2	Micinski <i>et al.</i> 1979
<i>Oligonychus coffeae</i> (Nietner)	(10.2)		(15.5)	9.5	32	Jackson <i>et al.</i> 1983
	12.3		17.6	11.5	30	Gotoh and Nagata 2001
	10.3			9.4	30	Das and Das 1966
<i>Tetranychus ludeni</i> Zacker	10.3		15.5	9.2	27	Mallik and ChannaBasavanna 1983
<i>Tetranychus kanzawai</i> Kishida	11.0		16.5	9.3	25	Gotoh and Gomi 2003
<i>Schizotetranychus schizopus</i> (Zacher)	11.5		16.1	10.4	25	Gotoh 1983
<i>Tetranychus parakanzawai</i> Ehara	11.6		18.4	9.3	25	Gotoh and Gomi 2003
<i>Oligonychus ununguis</i> (Jacobi)	11.95		18.0	10.4	25	Saitô 1979
	14.3		17.4	12.1	29	Boyne and Hain 1983a
<i>Panonychus citri</i> (McGregor)	12.0			11.3	26	Kramer and Hain 1989
	13.5		19.7	11.0	26	Beavers and Hampton 1971
<i>Eotetranychus uncatus</i> Garman	12.7		18.7	12.0	25	Saitô 1979
<i>Oligonychus ilicis</i> (McGregor)	13.1	(15.5)		11.4	25	Gotoh 1987a
	13.7			12.6	35	Childs <i>et al.</i> 1984
<i>Schizotetranychus leguminosus</i> Ehara	13.1		19.1	12.5	24	Mague and Streu 1980
<i>Panonychus aktitanus</i> Ehara	13.2		22.3	11.75	25	Gotoh 1983
<i>Eotetranychus carpini</i> (Oudemans)	13.4		20.1	11.6	25	Gotoh 1987c
<i>Eotetranychus borealis</i> (Ewing)			21.45	12.0	25	Castalogni <i>et al.</i> 1989
<i>Eotetranychus sudanicus</i> Elbadry	13.5			12	30	Bounfour and Tanigoshi 2001
<i>Tetranychus arabicus</i> Attiah	13.6		21.0	11.2	Greenhouse	Siddig and Elbadry 1971
<i>Eotetranychus tiliarium</i> (Hermann)	13.8			12.4	27	Attiah <i>et al.</i> 1978
	16.5			12.4	25	Gotoh 1987a
<i>Oligonychus milleri</i> (McGregor)	13.8			14.1	23–25	Kropczynska <i>et al.</i> 1988
<i>Tetranychus viennensis</i> Zacher	13.9		22.1	12.8	30	Landwehr and Allen 1982
<i>Aponychus corpuzi</i> Rimando	14.1		22.0	12.1	25	Gotoh 1986
<i>Eotetranychus pruni</i> (Oudemans)	14.2		19.9	12.5	25	Saitô and Ueno 1979
<i>Mononychellus progresivus</i> Doreste			14.4	13.7	24	Grissa-Lebdi <i>et al.</i> 2002
				9.9	26	Bonato <i>et al.</i> 1995

Table 3 (concluded).

Species	G	O	T	D	°C	Reference
<i>Schizotetranychus cercidiphylli</i> Ehara	14.9		20.4	13.8	25	Gotoh 1983
<i>Panonychus ulmi</i> (Koch)	15.0		22.7	13.7	25	Gotoh 1987b
				5.6	25	Osakabe <i>et al.</i> 1990
	17.8		21.3	14.0	21	Herbert 1981a
<i>Oligonychus gossypii</i> (Zacher)			15.1	10.2	26	Bonato <i>et al.</i> 1995

Note: Conventions as in Table 1.

period, usually with feeding, and a long adult life. A minimum generation time of 13 d at 27 °C is known in the small predaceous staphylinid *Atheta coriariae* (Kraatz) (Miller and Williams 1983). A few predaceous coccinellids may have life cycles of just under 15 d, because egg to adult development in some species is as fast as 10.4–13 d at about 30 °C (McMullen 1967; Obrycki and Tauber 1978, 1981, 1982; Miller 1992; Miller and Paustian 1992; Giles *et al.* 2001; Roy *et al.* 2002) and preoviposition intervals in the same or similar species, though commonly prolonged (Phoofolo and Obrycki 2000), are as short as 4.5 or even 3.5 d (*e.g.*, Brown 1972; Francis *et al.* 2001; Stathas *et al.* 2001). Some other beetles have minimum generation times of less than 20 d, as in some chrysomelids with rapid larval development and short preoviposition intervals and, exceptionally, curculionids (Buckingham and Bennett 1981). Although some additional species of beetles might be found with life cycles of less than 15 d under very favourable conditions, in most families and species minimum, and especially mean, generation times are long or very long.

Diptera

Several species of Nematocera develop rapidly (Table 9). Mosquitoes, especially the species of temporary pools, are well known for rapid larval and pupal development. However, in many species of *Aedes* and other genera there is a long interval before the eggs hatch, and some species of *Aedes* characteristic of cool-temperate annual temporary ponds overwinter as eggs and are univoltine. Egg to adult development may take only 7–10 d in some species of *Culex* and *Anopheles*, but in most species reproduction after emergence is delayed by the need for mating, blood feeding, and egg development, which commonly take a week or more (*e.g.*, Cõnsoli and Williams 1978; Okazawa *et al.* 1991). Therefore, although rapid life cycles do occur, they are not especially common.

Most larval chironomid midges are broadly saprophagous. They are abundant and may develop rapidly in eutrophic habitats. The pre-reproductive period is usually short, giving the fastest-developing species life cycles of 10–12 d in the laboratory (Table 9). Even shorter generation times may occur in the field; for example, species of Chironomini and Tanytarsini complete larval growth in only 5 to 6 d (Hauer and Benke 1991).

Table 4. Sample records of short life cycles in other prostigmatic mites.

Species	G	O	T	D	°C	Reference
Pyemotidae						
<i>Pyemotes tritici</i> (Lagrèze-Fossat and Montané)	4.0				26	Bruce 1984
Acarophenacidae						
<i>Acarophenax mahunkai</i> Steinkraus and Cross				4	23–26	Steinkraus and Cross 1993
<i>Adactylidium</i> sp.				4	30	Elbadry and Tawfik 1966
Pygmephoridae						
<i>Pediculaster flechtmani</i> (Wicht)	5.2	(7.2)		3.6	21/27	Cross and Kaliszewski 1988
Tarsonemidae						
<i>Polyphagotarsonemus latus</i> (Banks) [<i>Tarsonemus</i>]	4.5			3	27	Hambleton 1938; Jeppson <i>et al.</i> 1975
<i>Stenotarsonemus spinki</i> Smiley	5.5?			3?	30	Lo and Ho 1979
<i>Tarsonemus granarius</i> Lindquist	7.1		10.4	5.0	30	White and Sinha 1981
<i>Tarsonemus myceliophagus</i> Hussey	8			6	24	Hussey and Gurney 1967
<i>Iponemus confusum</i> (Lindquist and Bedard) [<i>Tarsonemoides</i>]	(10+)			7.5	26.7	Lindquist and Bedard 1961; Lindquist 1986
Cheyletidae						
<i>Cheyletes malaccensis</i> Oudemans	12.7			11.3	30	Yousef <i>et al.</i> 1982a
Stigmaeidae						
<i>Agistemus excertus</i> Gonzalez	7.5			6.4		Hafez <i>et al.</i> 1983
	9.7			7.3	28.5–30	Zaher <i>et al.</i> 1971
	14.3			9.9	30.5	Yousef <i>et al.</i> 1982b
	(14.5)		<21	13.0	24	White and Laing 1977
<i>Zetzellia mali</i> (Ewing)						
Diptilomiopidae						
<i>Rhyncaphyoptus ficifoliae</i> Kiefer	7.15		14.6	6.5	29	Abou-Awad <i>et al.</i> 1999b
Eriophyidae						
<i>Metaculus mangiferae</i> (Attiah)	7.5			5	27	Abou-Awad 1981
<i>Phyllocoptura oleivora</i> (Ashmead)			8.85	6.1	29	Allen <i>et al.</i> 1995
<i>Epirimerus pyri</i> (Nalepa)	(10.5)			8	25	Bergh 1994
<i>Aceria ficus</i> (Cotte)	12.45		17.9	11.75	29	Abou-Awad <i>et al.</i> 1999b
<i>Eriophyes datura</i> Soliman and Abou-Awad	14.0			10.2	26	Abou-Awad 1980
<i>Vasates lycopersicae</i> (Masse)				6.5	30	Rice and Strong 1962

Note: Conventions as in Table 1.

Table 5. Sample records of short life cycles in astigmatic mites.

Species	G	O	T	D	°C	Reference
Acaridae						
<i>Sancassania boharti</i> (Cross)	6.8			5.6	26	Cross and Bohart 1990
<i>Acotyledon formosani</i> Phillipsen and Coppel	7.0		9.6		30	Phillipsen and Coppel 1977a
<i>Caloglyphus anomalus</i> Nesbitt	7.25 (11)	(19)	18.4	6.0 9.5 9.7	25 30 23 27.8	Pillai and Winston 1969 Woodring 1969 Barker 1974 Okabe 1993
<i>Histiogaster</i> sp.	(7.3)	(?15)		7.1 6.9 6.6	30 33 25	Timms <i>et al.</i> 1981 Pimentel <i>et al.</i> 1960 Rodriguez and Stepien 1973 Barker 1967
<i>Caloglyphus bertesi</i> (Michael)	7.5 9		14 14.1	8.1 9.1	26.7 27 32.2	Sánchez-Ramos and Castañera 2001 Rivard 1961 Davis and Hunter 1963
<i>Tyrophagus putrescentiae</i> (Schrank)	11.5			7.2 10.9 9.6	30 30 27	Woodring 1969 Gerson <i>et al.</i> 1983 Woodring 1969
<i>Histiogaster anops</i> Griffiths	11.1			12	23	
<i>Histiogaster rotundus</i> Woodring	(13)	(22)		11.1	27	
<i>Rhizoglyphus robini</i> (Claparede)	(13)	(26)	19.5	11.4	23	
<i>Schwiebea falcatus</i> Woodring	(13)			11.9	25	Kasuga and Amano 2000
<i>Tyrophagus similis</i> Volgin	13.6	(27)	22.5	13.2	23	Woodring 1969
<i>Schwiebea rocketti</i> Woodring	(15)	(27)		14.1	23	Woodring 1969
<i>Histiogaster arborsignis</i> Woodring	(15)	(27)				
Histiostomatidae (Anoetidae)						
<i>Histiostoma polypori</i> (Oudemans)	3.7			3.1	26	Behura 1957
<i>Histiostoma cataglyphi</i> Yousef	5.9			5.3	25	Yousef <i>et al.</i> 1979
<i>Histiostoma formosana</i> Phillipsen and Coppel	6.9				25	Phillipsen and Coppel 1977b

Note: Conventions as in Table 1.

Table 6. Sample records of short life cycles in Aphidae (virginoparae).

Species	G	O	T	D	°C	Reference
<i>Aphis glycines</i> Matsumura	3.9			3.3	27	Hirano <i>et al.</i> 1996
<i>Rhopalosiphum padi</i> (L.)	4.9			4.6	25	Dean 1974
	4.9			4.6	27.5	Asin and Pons 2001
	5.2			5.0	26	Villanueva and Strong 164
	5.3		12.4	4.7	26	Elliott and Kieckhefer 1989
	6.3				20	Simon <i>et al.</i> 1991
<i>Aphis gossypii</i> Glover	5.0	(8)			26	Pettit <i>et al.</i> 1994
	5.2		6.4	4.6	30	Xia <i>et al.</i> 1999
	5.5			4.0	25	Aldyhim and Khalil 1993
	6.0				Field	Saha and Raychaudhuri 1996
			7.3	4.1	25	Peng 2002
	6.2		7.4		29.7	Komazaki 1982
<i>Aphis fabae</i> Scopoli			10.4	4.5	30	Kersting <i>et al.</i> 1999
	5.4	(10.4)		5.4	28.5	Tsitsipis and Mittler 1976
	(6)			(6)	25	
	6.7		12.2		20	Frazer 1972
<i>Schizaphis graminum</i> (Rondani)	6.8				25/20	Fernandez-Quintanilla <i>et al.</i> 2002
	5.5				21/25	Kerns <i>et al.</i> 1989
	5.7				27.7	Peters <i>et al.</i> 1988
				4.8	30	Kirkland <i>et al.</i> 1981
				5.1	25	
<i>Aphis craccivora</i> Koch					21	Summer <i>et al.</i> 1986
	8.2		13.7		24	Michels <i>et al.</i> 1997
			13.8	4.1		Girma <i>et al.</i> 1990
	8.6				27–29	Gutierrez <i>et al.</i> 1971
			5.8		20	Abdel-Malek <i>et al.</i> 1982
<i>Aphis spiraeicola</i> Patch [<i>A. citricola</i> van der Groot]	5.5		7.4	5.1	25	Komazaki 1982
	7.3		11.7		25	Neubauer <i>et al.</i> 1981
	(8)		11.4	7.3	28	Wang and Tsai 2000

Table 6 (continued).

Species	G	O	T	D	°C	Reference
<i>Lipaphis erysimi</i> (Kaltenbach)				5.0	30	Liu and Meng 2000
<i>Toxoptera aurantii</i> (Boyer de Fonscolombe)	5.8				28.4	Rout and Senapati 1968
<i>Rhopalosiphum maidis</i> (Fitch)	(6.0)		9.5	5.3	28	Wang and Tsai 2001
<i>Acyrtosiphon pisum</i> (Harris)	6.2	(10)		5.5	28/24	Branson and Ortman 1967
				4.9	25	Lamb 1992
	6.6		10.3	5.4	26.1	Campbell and Mackauer 1975a
	6.6			5.7	26.1	Campbell and Mackauer 1977
	(7)		9.0	8.5	21	Kouamé and Mackauer 1992
	(7.2)	(10.3)		6.8	26.7	Morgan <i>et al.</i> 2001
	7.6		(11.7)	6.2	25	Siddiqui <i>et al.</i> 1973
	7.7		11.3		25	Hutchison and Hogg 1984
	8.0		12.6		20	Frazer 1972
	9.0				20	Mackauer 1973
	(9)				24	Hughes and Bryce 1984
<i>Toxoptera citricida</i> (Kirkaldy)				7.2	20.1	Cartier 1960
	6.2		11.9	8.5	26.7	Morgan <i>et al.</i> 2001
			13.7			Campbell and Mackauer 1975b
			8.5		27.6	Komazaki 1982
			8.5	5.5	30	Tsai and Wang 1999
	7.1		9.4	6.3	30	Tang <i>et al.</i> 1999
<i>Brachycaudus rumexicolens</i> (Patch)					27.9	Scott and Yeoh 1999
<i>Aphis pomi</i> De Geer			7.2		28	Carroll and Hoyt 1986a
			(11.6)	5.2	25.8	Graf <i>et al.</i> 1985
<i>Monelliopsis pecanis</i> Bissell	6.3		10.0	4.7	28	Carroll and Hoyt 1986b
<i>Rhopalosiphum insertum</i> (Walker)			(11.0)	5.1	Field	Kaakeh and Dutcher 1992
<i>Myzus persicae</i> (Sulzer)	6.5			5.1	25.8	Graf <i>et al.</i> 1985
	6.8			5.8	25	El Din 1976
	7.0	(10)			25/20	Fernandez-Quintanilla <i>et al.</i> 2002
			5.4		26	Pettit <i>et al.</i> 1994
					26.7	Jansson and Smilowitz 1985

Table 6 (continued).

Species	G	O	T	D	°C	Reference
	7.6			5.25	22	Hodjat and Bishop 1978
				5.4	22–29	Eggers-Schumacher 1983
	7.8				28	Liu and Meng 1999
			12.5	7.6	20	Nikolakakis <i>et al.</i> 2003
<i>Dysaphis plantaginea</i> (Passerini)			(10.9)	6.15	20	Tamaki <i>et al.</i> 1982
<i>Aphis nasturtii</i> Kaltenbach	(<6.7)		9.2	5.7	25.8	Graf <i>et al.</i> 1985
	(<7.6)		8.3	6.6	30	Wang <i>et al.</i> 1997
	7.0		10.1	5.8	35	
<i>Acyrtosiphon kondoi</i> Shinji				7.9	26.7	Summers <i>et al.</i> 1984
				7.6	20	Wellings 1985
<i>Brachycaudus schwartzi</i> (Bömer)			10.4	7.6	30	Satar and Yokomi 2003
<i>Hyperomyzus lactucae</i> (L.)	(7)		11.1	6.7	24	Liu and Hughes 1987
				6.6	22	Liu and Hughes 1984b
<i>Sitobion avenae</i> (Fabr.) [<i>Macrosiphum</i>]	7.2			6.6	25	Lykouressis 1985
	7.6			7.3	20	Simon <i>et al.</i> 1991
	8.2			7.5	25	Asin and Pons 2001
	8.4			7.5	22.5	Dean 1974
				10.1	29	Kieckhefer <i>et al.</i> 1989
<i>Brachycorynella asparagi</i> (Mordvilko)	7.4		11.6	7.7	21.7	Wright and Cone 1988
	7.7	(12)		7.7	23	Hayakawa <i>et al.</i> 1990
			14.8	8.1	25	Tamaki <i>et al.</i> 1983
<i>Monellia caryella</i> (Fitch)	7.5		8.6	6.3	Field	Kaakeh and Dutcher 1992
<i>Metapolophium dirhodum</i> (Walker)	7.8			7.4	20	Dean 1974
	8.5			7.5	25	Asin and Pons 2001
	13.0			11.9	15	Grüber and Dixon 1988
				12.4	Field	Cannon 1984
<i>Diuraphis noxia</i> (Kurdjumov)	8.2	(25.2)		8.2	20	Aalbersberg and Du Torr 1987
				8.6	27–29	Girma <i>et al.</i> 1990
			8.6?	9.9	30	Nowierski <i>et al.</i> 1995
<i>Rhopalosiphum nymphaeae</i> (L.)		(8)		6.8	30.6	Ballou <i>et al.</i> 1986

Table 6 (concluded).

Species	G	O	T	D	°C	Reference
<i>Timocallis caryaefoliae</i> (Davis) [<i>Melanocallis</i>]	9.1		12.6	7.7	Field	Kaakeh and Dutcher 1992
<i>Aphis nerii</i> Boyer de Fonscolombe			11.8		30	Kuo and Chiang 1999
<i>Macrosiphum albifrons</i> Essig	9.4		16.6	7.4	24.2	Frazer and Gill 1981
<i>Pemphigus betae</i> Doane	9.7		14.2		24	Campbell and Hutchison 1995
<i>Chaitophorus leucomelas</i> Koch	10.5	(17)		9.0	25	Hintze-Podufal and Thorns 1979
<i>Cinara watsoni</i> Tissot	12.2			9.2	27.2	Brooks and Warren 1964
<i>Cinara</i> sp. (nr. <i>cupressi</i> (Buckton))			16.3	9.2	25	Kairo and Murphy 1999
<i>Eutachmus agilis</i> (Kaltenbach)	13.3			12.0	21.1	Bliss and Kearby 1971

Note: Conventions as in Table 1.

A few species of other small Nematocera develop very rapidly, too (Table 9). Some ceratopogonids develop rapidly, but adult blood feeding and egg development extend generation times and other reports, even for species shown in Table 9, record slower development. Larval feeding of many cecidomyiid midges is rapid (*e.g.*, Harris and Schreiner 1992), and the preoviposition period may last only one day (*e.g.*, Caresche and Wapshere 1975), but other stages are slower and only a few species can complete a generation in less than 15 d. However, when food is abundant, some fungivorous species have paedogenetic life cycles (much shorter than their sexual cycles) that have arisen in four distinct groups within the family (Wyatt 1967). At least one species of psychodid that eats decaying materials has a short generation time even though longer developmental times are more common, especially in the blood-feeding phlebotomines.

Among the Brachycera (Table 10), many cyclorrhaphan flies have relatively short life cycles, but few have very short ones. Scattered records suggest that egg to adult development can be completed in as little as 14 or 15 d in some Aschiza (*e.g.*, Patro and Behera 2002 for a syrphid). Among the acalyptrates, one might expect that families of small phytophagous flies that have been studied especially because of their agricultural relevance would contain rapidly developing species. However, almost all generation times are at least 15 d, typically because development throughout the life cycle is not especially rapid, because the pupal stage is relatively long (as in Agromyzidae), or because the preoviposition period is long (as in many Tephritidae). However, egg to adult development can take less than 15 d in a few species of Agromyzidae, including *Liriomyza trifolii* (Burgess) (*e.g.*, Leibe 1984; Miller and Isgar 1985; Smith and Hardman 1986). *Drosophila melanogaster* Meigen develops rapidly in the laboratory, and even faster strains can be selected (Table 10). Some other acalyptrate families, such as Ephydriidae (Table 10) and Piophilidae (Hegazi *et al.* 1978), also have species with very short life cycles, at least among those with short preoviposition periods.

The maggots of calyptrate flies such as the muscids, sarcophagids, and calliphorids that develop in decaying material, dung, or carrion are well known for their very rapid development. For example, Levot *et al.* (1979) reported larval developmental times of 2.25 to 5.2 d for eight species of calliphorids and one sarcophagid. A

Table 7. Sample records of short life cycles in Anthocoridae.

Species	<i>G</i>	<i>O</i>	<i>T</i>	<i>D</i>	°C	Reference
<i>Orius strigicollis</i> (Poppius)				11.4	30	Ohta 2001
<i>Orius sauteri</i> (Poppius)	(14.7)		21.9	12.7	30	Nagai and Yano 1999
	16.0	(26)		12.0	25	Honda <i>et al.</i> 1998
				11.9	30	Nakata 1995
<i>Orius minutus</i> (L.)	14.7	(25)		11.7	25	Honda <i>et al.</i> 1998
<i>Orius insidiosus</i> (Say)				8.3	35	McCaffrey and Horsburgh 1986
				12.1	32	Isenhour and Yeargan 1981
<i>Orius albidipennis</i> Reuter			14.8	7.7	35	Cocuzza <i>et al.</i> 1997
				10.9	30	Gitonga <i>et al.</i> 2002
<i>Orius tristicolor</i> White	(14)			(11.5)	33.3	Askari and Stern 1972
<i>Orius laevigatus</i> (Fieber)			20.4	10.1	35	Cocuzza <i>et al.</i> 1997

Note: Conventions as in Table 1.

Table 8. Sample records of short life cycles in Thripidae.

Species	<i>G</i>	<i>O</i>	<i>T</i>	<i>D</i>	°C	Reference
<i>Thrips hawaiiensis</i> (Morgan)	8.0			7.0	30	Murai 2001a
<i>Scolothrips sexmaculatus</i> (Pergande)	11.3		17.9	10.6	30	Coville and Allen 1977
<i>Frankliniella fusca</i> (Hinds)	(12)		13.2	11.5	35	Lowry <i>et al.</i> 1992
<i>Thrips setosus</i> Moulton	12.2		19.6	11.2	25	Murai 2001b
				10.4	30	
<i>Thrips tabaci</i> Lindeman	12.6		16.9	10.6	30	Murai 2000
	14.2			13.2	25	Abdel-Gawaad and El-Shazli 1971
	14.8		20.4	12.9	25	van Rijn <i>et al.</i> 1995
<i>Frankliniella occidentalis</i> (Pergande)		(12)		9	26.5	Lopes and Alves 2000
	(14)	(16)		11.5	30	Gaum <i>et al.</i> 1994
			24	12.0	25	Hulshof <i>et al.</i> 2003
			29	11.7	25	
	14.2		20.1	12.4	25	van Rijn <i>et al.</i> 1995
	(14.3)		15.5	13.8	25	Lowry <i>et al.</i> 1992
	15.0			12.6	30	Lublinkhof and Foster 1977
<i>Thrips obscuratus</i> (Crawford)	14.3			10.3	27	Teulon and Penman 1991
<i>Scirtothrips dorsalis</i> Hood	(14.4)			13.4	20	Tatara 1994
	14.4			13.4	29.4	Tatara 1994
				13.9	30	Shibao 1996
<i>Thrips palmi</i> Karny			15.2	11.8	32	Tsai <i>et al.</i> 1995

Note: Conventions as in Table 1.

few species have minimum generation times just below 15 d (Table 10). Nevertheless, stages other than larvae commonly take longer, and total generation times are not strikingly short in most species. In particular, in typical muscoid flies the teneral adult must harden, mate, feed,

and develop eggs before oviposition, thus requiring preoviposition intervals of at least several days (*e.g.*, Parr 1962; Hughes *et al.* 1972; Kuramochi 1985). Larvae of some species of tachinid parasitoids not constrained by host development likewise develop very rapidly

in their hosts, but again the life cycle is seldom very short because of longer pupal and preoviposition intervals. Mean generation times tend to be longer still because the oviposition period is prolonged.

Lepidoptera

The typical phytophagous caterpillars of most Lepidoptera develop relatively slowly, as do the pupae. No species of Lepidoptera has strikingly rapid development. However, some small moths can complete egg to adult development in as little as 11 d (*e.g.*, Plutellidae: Liu *et al.* 2002) and a generation in 15 to 20 d (*e.g.*, Lyonetidae: Parrella and Kok 1977; Gelechiidae: Shanower *et al.* 1993), suggesting that a few species might have even shorter life cycles under especially favourable conditions.

Hymenoptera

The order Hymenoptera contains both rapidly and slowly developing taxa. Most sawflies (phytophagous), bees (phytophagous), and wasps (predaceous) have relatively long and often seasonal life cycles. Species in many families of the suborder Apocrita, comprising chiefly parasitoids of other arthropods, develop rapidly. However, many other related species develop more slowly, especially on hosts with slow development. Species in which adults have complex behaviours for mating and feeding on the host less commonly have very short generation times.

Species in the major family Braconidae (including Aphidiinae, solitary parasitoids of aphids) attack many kinds of insects. Many species of internally and externally feeding species attacking hosts in various taxa, especially the host larval stages, have rapid larval development and short preoviposition intervals, giving minimum life cycles of 10 to 15 d (Table 11). There are numerous other reports of related species with rapid larval development that undoubtedly also have similarly short cycles. Many more species with somewhat longer cycles are known. The major family Ichneumonidae likewise contains diverse, mostly solitary parasitoids of arthropods, but very few species complete a generation in less than 15 d (Table 11). However, many species have only slightly longer generation times (*e.g.*, Giron 1978; Isenhour 1986; Smith *et al.* 1990). Some species with rapidly developing larvae spend much more time in the pupal stage (*e.g.*, Rahoo and Luff 1987). In typical species,

reproduction is prolonged, extending mean generation times.

Rapid development is characteristic of several families of small chalcidoids (Table 12), typically endoparasitoids or hyperparasitoids of insects. Mymarids and trichogrammatids parasitize chiefly eggs; eulophids and elasmids attack eggs, larvae, or pupae; aphelinids specialize chiefly on aphids and scale insects; and pteromalids have a wide range of mainly larval and pupal hosts. A few encyrtids have life cycles close to 15 d (*e.g.*, Umeh 1988), but most species have longer life cycles. Other hymenopterous parasitoids with rapid development in the larval stage (Table 13) include scelionids, which attack insect eggs and typically have very short preoviposition intervals, ceraphronids (*e.g.*, 9.4 d for immature development of *Dendrocerus niger* (Howard) at 25.9 °C: Campbell and Mackauer 1975a), and a few species of bethylids, although most species take much longer to develop, attacking chiefly larvae.

Correlates of short life cycles

Phylogeny

The above taxonomic review shows that short life cycles are much more prevalent in some taxa than in others. Taxa containing species with life cycles of less than 15 d are summarized in Table 14. The distribution of taxa suggests that phylogenetic origin and evolutionary advancement, as well as ecological niche and body size, govern the rate of development.

In general, highly derived groups develop more rapidly than their primitive relatives. Primitive groups tend to retain many moults: up to 30 in Thysanoptera (Nishizuka *et al.* 1998), normally 15–25 in mayflies (Fink 1980; Brittain 1982), and up to 24 in stoneflies (Vaught and Stewart 1974; Baumann 1987). Most families of flies, wasps, and other endopterygotes develop more rapidly than exopterygotes such as orthopterans. Even in oribatid mites (most of which develop slowly), the phylogenetically advanced species develop more rapidly than more primitive ones (Lebrun 1970, 1971). However, life cycles that have become complex tend to be prolonged (*e.g.*, Proctor and Pritchard 1990 for water mites).

Few species with very long adult lives have short generation times. Therefore, many well-known families of beetles and other insects are missing from the list in Table 14.

Table 9. Sample records of short life cycles in Nematocera.

Species	G	O	T	D	°C	Reference
Culicidae						
<i>Culex tritaeniorhynchus</i> Giles	10.6 (18.5?)		22.2 (~21)	(~8)	27–29	Reisen <i>et al.</i> 1979
<i>Culex nigripalpis</i> Theobald				8.5	28	Shahid and Reisen 1981
<i>Anopheles albimanus</i> (Wiedemann)	(13.1)		18	7.5	32?	Nayar 1968
<i>Culex pipiens</i> L.	(14.7)			(10.3)	26	Mahmood 1997
<i>Anopheles sinensis</i> Wiedemann				8.2	30	Madder <i>et al.</i> 1983
				14.4	28	Shono and Hirano 1993
Chironomidae						
Chironomini and Tanytarsini spp.				5–6	Field, 21–24	Hauer and Benke 1991
Various species				9–16	22	Gray 1981
<i>Chironomus strenzkei</i> Fittkau	10	(12)			28	Syrjämäki 1965
<i>Chironomus sancticaroli</i> Strixino and Strixino	12			11	25	Strixino and Strixino 1982
<i>Chironomus</i> sp. nr. <i>attenuatus</i> Walker	(12?)			(10)	28.9	Biever 1965
<i>Chironomus circumdatus</i> (Kieffer)				12	37	Sankarperumal and Pandian 1991
<i>Tanytarsus dissimilis</i> Johansen	12.2			12	28	Nebeker 1973
<i>Chironomus imicola</i> Kieffer	(14)			12.2	Field	McLachlan 1983
<i>Corynoneura scutellata</i> Winnertz				10.5	25	Olsen <i>et al.</i> 2003
<i>Chironomus pulcher</i> Wiedemann				13.3	30	Dejoux 1971
Ceratopogonidae						
<i>Culicoides variipennis</i> (Coquillett)	14?				Field	Barnard and Jones 1980
				10?	23–25	Boorman 1974
				14.5	30	Mullens and Rutz 1983
				11–13	26–33	Allingham 1991
<i>Culicoides brevitarsis</i> Kieffer		17			28	Bishop <i>et al.</i> 1996
<i>Probezzia</i> sp.				11.5	22	Gray 1981
Cecidomyiidae						
<i>Feltiella acarisuga</i> (Vallot)	(12?)			10	27	Gillespie <i>et al.</i> 2000
<i>Feltiella minuta</i> (Felt)		(12)		9.5	30	Ho and Chen 1998
<i>Contarinia sorghicola</i> (Coquillett)	(12.5)			11.9	36	Baxendale <i>et al.</i> 1984

Table 9 (concluded).

Species	G	O	T	D	°C	Reference
<i>Mycophila speyeri</i> (Barnes) (paedogenetic generation)	6			5	?	Wyatt 1964
<i>Heteropeza pygmaea</i> Winnertz (paedogenetic generation)	7			4	25	Ulrich <i>et al.</i> 1972
<i>Miastor metraloas</i> Meinert (paedogenetic generation)	12			6	?	Wyatt 1963
Psychodidae				5	?	Wyatt 1967
<i>Psychoda alternata</i> Say	(15?)			13.1	24	Redborg <i>et al.</i> 1983

Note: Conventions as in Table 1.

Finally, even in families characterized by rapid development there may be genera with slower or much slower development. For example, species of *Mansonia* have slower larval development than many other mosquitoes.

Strain

Different strains within a species may differ widely in life-cycle duration. Typically there are differences among populations from different regions (or among different laboratory colonies). Many of the intraspecific differences shown in Tables 1–13, albeit modified by food and other experimental conditions, reflect such differences among geographic strains. The strain differences accord chiefly with differential selection in places with different conditions (see review by Danks (1987), Chapter 9), but some of them result from other factors. For example, sublethal pathogens typically slow down the development of their hosts but can have the reverse effect: the aphid *Sitobion avenae* (Fabr.) takes 7.9 d to develop when infected by virus but 9.3 d when not infected (Feres *et al.* 1989).

Different aphid clones collected in the same place may differ. For example, minimum generation time of *Rhopalosiphon padi* (L.) lasts from 6.3 to 8.1 d, depending on strain (Simon *et al.* 1991), and immature development of *S. avenae* lasts from 6.6 to 9.4 d (Lykouressis 1985). Such differences may also accord with other traits of interest, such as resistance to insecticides (*e.g.*, Eggers-Schumacher 1983).

Rapid development in all stages

For complete life cycles to be very short, all stages must develop relatively rapidly. In contrast, for various reasons, most groups of insects spend much longer in one or more particular stages than in the others, even during diapause-free development. Short *mean* generation times occur chiefly in species in which the majority of offspring are produced soon after reproduction begins. Most such species have relatively short adult lives (*e.g.*, Trichogrammatidae), and many of them do not feed as adults.

Such patterns in the life cycle, some of which were noted in the taxonomic review, depend largely on phylogeny. For example, even some small insects with relatively rapid larval and pupal development (*e.g.*, tingids, thrips) require longer periods for egg development. In other taxa, the larval stages are somewhat prolonged (*e.g.*, cicadellids, most families of moths). A relatively long pupal stage is characteristic of

Table 10. Sample records of short life cycles in Brachycera.

Species	<i>G</i>	<i>O</i>	<i>T</i>	<i>D</i>	°C	Reference
Cyclorrhapha: Acalyptratae						
Agromyzidae						
<i>Liriomyza sativae</i> Blanshard	(14)	(<18)		13.1	30	Parkman <i>et al.</i> 1989
Ephydriidae						
<i>Scatella stagnalis</i> Fallen	14.6		18.4	11.4	25	Vänninen 2001
				10.1	28.5	
<i>Scatella picea</i> (Walker)	15			12.8	24	Connell and Scheiring 1982
Drosophilidae						
<i>Drosophila melanogaster</i> Meigen						
Selected line	(9)			7.9	25	Chippindale <i>et al.</i> 1997
Selected line				6.2	25	Prasad <i>et al.</i> 2000
	(10.5)			9.0	25	Summary of others by Chippindale <i>et al.</i> 1997
				9	25	Bakker and Nelissen 1963
Cyclorrhapha: Calyptratae						
Muscidae						
<i>Stomoxys calcitrans</i> (L.)	(14)		(24)	12	30	Lysyk 1998a
				13.7	35	Kunz <i>et al.</i> 1977
<i>Musca domestica</i> L.	15.1			10.5	28	Mishra 1979
				8.8	35	Lysyk and Axtell 1987
<i>Musca vetustissima</i> Walker				7.1	38	Vogt <i>et al.</i> 1990
<i>Fannia femoralis</i> (Stein)				14.4	30	Meyer and Mullens 1988
<i>Haematobia thirouxii</i> <i>potans</i> (Bezzi)				9.4	30	Fay 1985
<i>Haematobia irritans</i> (L.)				9.3	30	Depner 1961
	20			15.3	25	Lysyk 1991
Calliphoridae						
<i>Chrysomya rufifacies</i> (Macquart)	~15?			~9	~30	Baumgartner 1993
				7.9	35	Byrd and Butler 1997
<i>Protophormia terraenovae</i> (Robineau-desvoidy)				9.2	35	Greenberg and Tantawi 1993
<i>Phaenicia pallescens</i> (Shannon)				10.4	35	Ash and Greenberg 1975
<i>Phormia regina</i> (Meigen)				11	35	Byrd and Allen 2001

Note: Conventions as in Table 1.

several families of flies (*e.g.*, agromyzids, muscids). Finally, many species with rapid larval and pupal development mature eggs only after a relatively long preoviposition interval, often requiring adult foods, as in many Coleoptera and Diptera. A characteristic of nearly all of the species listed in Tables 1–13 is that these sorts of stage-specific delays are minimized, except

in some mites in which larval development is so rapid that it can compensate for a relatively long-lasting egg stage (*e.g.*, Bounfour and Tanigoshi 2001). Short life cycles are virtually unknown in species with complex social interactions, including ants and theirinquilines, or in species with resistant dormant stages, except when these stages can be omitted in

favourable conditions (as for the hypopal stages of some mites). Moreover, dormancy responses include not only complete suppression of development but also the slowing of development in response to token stimuli such as photoperiod, and there are also several more complex options. This remarkable range of responses for adaptive timing of the life cycle in insects as a whole (Danks 2002a), coupled with the normal stage-specific delays just summarized, means that relatively few species develop rapidly in all stages.

Size

Species of small size are more likely to develop rapidly than larger ones. Not only do fewer resources have to be accumulated, but also metabolic rate is faster in smaller organisms (Schmidt-Nielsen 1984). Many of the characteristic families shown in Table 14 contain mainly small species. These taxa with short life cycles consist chiefly of mites, small flies, and parasitoid wasps attacking hosts of small size, especially eggs, or living gregariously on their hosts (*e.g.*, many chalcidoids). Within a given family, the smaller species typically develop most rapidly (see below). Nevertheless, even among small parasitoids such as mymarids there are species with relatively slow development. Moreover, Walter and Proctor (1999, Fig. 4.7) showed that developmental rates were similar in 15 species of mesostigmatid mites differing in size by more than an order of magnitude.

Temperature

Rapid development takes place at high temperatures, and short life cycles are best known from laboratory rearing at the temperature at which development is fastest. Norton (1994) pointed out that much laboratory rearing has been carried out at temperatures much higher than those normally experienced in the field. Some field observations suggest that development may be slower in the field than in warm, well-fed laboratory colonies (Mackey 1977). Nevertheless, many natural habitats are relatively warm and, moreover, warm microhabitats can be chosen by individuals during development or by ovipositing females and enhanced by basking behaviour (see Habitat). Indeed, many short life cycles have been reported from the field as well as the laboratory.

Typically, as temperature increases, developmental rate increases up to a maximum and then declines again as the temperature reaches an

unsuitable level. For an outline of such features and models and many further references see Laudien (1973), Lamb *et al.* (1984), Lactin *et al.* (1995), and Danks (2000). However, the temperatures at which larval/nymphal growth, larval/nymphal survival, postemergence egg development, fecundity, or adult survival are maximized may be different, potentially resulting in different temperatures for the fastest immature development, shortest minimum or mean generation times, and maximum reproductive rate. The effects of temperature on generation time are exemplified by data for the eriophiid mite *Phyllocoptruta oleivora* (Ashmead) (Allen *et al.* 1995). Mean calculated generation time is 8.85 d at 29 °C, is slower at higher temperatures (9–10 d at 31–33 °C), and is much slower at low temperatures (37.2 d at 14 °C).

Not only the level but also the consistency of temperature is important. Cold nights may greatly slow development even when days are hot. Therefore, short life cycles in nature have been reported especially from tropical and subtropical regions, which maintain fairly constant temperatures throughout the diel, and from warm stable habitats (see Habitat).

Food

Some species that eat very nourishing food in continuous supply develop very rapidly in the larval stage (Plowright and Pendrel 1977 for *Bombus* larvae). Food of poor quality or in limited supply greatly slows development even in species capable of fast growth. For example, in the phytoseiid mite *Phytoseius plumifer* (Canestrini and Fanzago), mean female immature development varied from 3.8 d on a diet of immature spider mites to 10.5 d on date pollen (Zaher *et al.* 1969). A similar pattern is seen in many other species of mites and insects. Many studies of herbivores, such as aphids, show how different host plants affect developmental rates. In one typical example, immature development of *Aphis gossypii* Glover varied from 4.1 to 8.2 d on different hosts, and calculated generation time varied from 7.3 to 12.7 d (Perng 2002). A number of the papers listed in Table 6 report similar results. Thus, in nature the potential growth rate of some herbivores changes through the season in parallel with changes in food-plant quality (*e.g.*, levels of fibre, nutrients, water, or antifeedants) that influence the duration of feeding and growth (*e.g.*, Yang and Joern 1994). In some species the effect of food plants

Table 11. Sample records of short life cycles in Braconidae and Ichneumonidae.

Species	G	O	T	D	°C	Reference
Braconidae						
<i>Bracon instabilis</i> Marsh.	(9.5)			9.2	30	Abbas and Abou-Zeid 1983
<i>Lysiphlebus testaceipes</i> (Cresson)	(10)			(9.5)	24	Tyler and Jones 1974
				8.9	26	Royer <i>et al.</i> 2001
<i>Trioxys utilis</i> Muesebeck	10			12.4	24	Salto <i>et al.</i> 1983
			11.6	10	21.1	Schlinger and Hall 1961
<i>Bracon kirkpatricki</i> (Wilkinson)	10.1			9.3	29.4	Force and Messenger 1964
<i>Aphidius gifuensis</i> Ashmead	(10.5)			7.6	35	Engroff and Watson 1975
			13.2	9.7	25	Ohta <i>et al.</i> 2001
<i>Microplitis brassicae</i> Muesebeck	10.7	(15)		10.7	32.2	Ohta and Ohtaishi 2004
<i>Aphidius colemani</i> Viereck	(11.0)			10.0	25	Browning and Oatman 1985
<i>Microplitis rufiventris</i> Kokujev	(11.4)			10.9	30	van Steenis 1993, 1995
	(14.1)			13.6	26	Hutchison <i>et al.</i> 1986
				13.1	28	McCutcheon and Harrison 1987
<i>Praon palitans</i> Muesebeck	11.9			10.5	21.1	Altahtawy <i>et al.</i> 1976
<i>Leitophron uniformis</i> (Gahan)	(12)			9.8	25	Schlinger and Hall 1960
<i>Apanteles marginiventris</i> (Cresson)	(12)			(12)	30	Debolt 1981
				12.2	30	Boling and Pitre 1970
<i>Cotesia plutellae</i> (Kurdjumov)	(<12.4)			11.4	25	Kunnalaca and Mueller 1979
<i>Bracon</i> sp. (<i>hancocki</i> (Wilkinson))	12.5			10.0	24–30	Kawaguchi and Tanaka 1999
<i>Aphidius rhopalosiphii</i> De Stefani-Perez	(12.8)			11.3	25	Olaifa and Akingbohunge 1982
<i>Ephedrus californicus</i> Baker	(12.8)	(17.3)		12.3	26.4	Sigsgaard 2000
<i>Microplitis feltiae</i> Muesebeck	12.8			12.3	30	Cohen and Mackauer 1987
<i>Aphidius sonchi</i> Marshall				12.5	20	Puttler and Thewke 1970
				9.1	26	Liu and Carver 1985
				11.0	22	Liu and Hughes 1984a
			13.1		22	Liu 1985
<i>Aphidius ervi</i> Haliday	(13.1)			11.6	25	Sigsgaard 2000
				10.1	25.9	Campbell and Mackauer 1975b
<i>Aphidius smithi</i> Sharma and Subba Rao				9.5	21	Fox <i>et al.</i> 1967
			15.7	9.9	25.9	Campbell and Mackauer 1975b
				(12.5)	20.5	Mackauer 1983

Table 11 (concluded).

Species	G	O	T	D	°C	Reference
<i>Diaeretiella rapae</i> (M*Intosh)	(14)	(15)		13.7	30	Hayakawa <i>et al.</i> 1990
<i>Bracon hebetor</i> Say	(14)		20	13	27	Nikam and Pawar 1993
<i>Meteorus autographae</i> Muesebeck	(14.5)	(20)		6.7	35	Jackson and Butler 1984
<i>Orgilus elasmopalpi</i> Muesebeck	(15?)			14.0	27	Grant and Shepard 1984
Ichneumonidae				14.1	32.2	Johnson and Smith 1980
<i>Diadromus collaris</i> (Gravenhorst)	(11)			10.4	30	Liu <i>et al.</i> 2001
<i>Hyposoter exiguae</i> (Viereck)	(15)			14	32.2	Browning and Oatman 1981
				12.8	?	Bloem and Duffy 1990
				14	26	Jowyk and Smilowitz 1978

Note: Conventions as in Table 1.

on developmental rate depends on the instar, and the differences among food plants may even be reversed from one instar to another (Capinera *et al.* 1981).

Similar food-related differences take place in species in other circumstances, including aquatic species (*e.g.*, Meier and Torres 1978; Richardson 1991) and parasitoids. In many parasitoids, developmental rate depends not only on the host species but also on host condition, size, or instar (*e.g.*, Fox *et al.* 1967; Weseloh 1984; Umeh 1988; Liu and Stansly 1996), and even on the food eaten by the host (*e.g.*, Altahtawy *et al.* 1976). Predators as well as parasitoids are very well represented among the fast-developing taxa.

Species that use rich but ephemeral sources of food must develop rapidly to exploit the source before it becomes unsuitable, disappears, or is preempted by competitors. For example, larval development of flies living in dung and carrion is characteristically rapid (Greenberg and Tantai 1993). Many species in decaying vegetation and fungi, including paedogenetic cecidomyiids, also characteristically develop rapidly.

Other factors

Some other conditions are occasionally but not consistently correlated with generation time through their effect on larval growth rate. Photoperiod modifies growth rate directly in a surprisingly large number of insect species (Abdel-Malek *et al.* 1982 and Aldyhim and Khalil 1993 for *Aphis* spp.; Table 33 in Danks 1987). In some species, especially species of small mites, growth rate depends on humidity (*e.g.*, Bonato *et al.* 1995). Growth rates can also depend on density: development may be more rapid under crowded conditions (see review by Danks (1987)). There are some unexpected effects too: two species of whiteflies develop more rapidly in mixed cultures than when reared separately (Tsueda and Tsuchida 1998).

Habitat

The habitat type of a given species is especially important because temperature and food availability greatly affect developmental rate. Warm, food-rich habitats favour species that develop rapidly. Species from warm, shallow, eutrophic ponds develop faster than related species from deep, cold lakes. Sunshine warms favoured habitats of various sorts. For example, shallow water warms up rapidly by solar heating of the bottom and cools down more slowly

Table 12. Sample records of short life cycles in Chalcidoidea.

Species	G	O	T	D	°C	Reference
Mymaridae						
<i>Gonatocerus</i> sp.	(8.6)	(9.6)	10.15	8.6	30	Sahad 1982
<i>Gonatocerus cinctipennis</i> Sahad					32	Miura 1990b
	(9.3)			8.3	32	Miura 1990a
<i>Anaphes listronoti</i> Huber [not <i>A. sordidatus</i> (Girault), see Huber <i>et al.</i> 1997]	(9.2)	(10.5)		8.7	29	Collins and Grafius 1986
<i>Anagrus giraulti</i> Crawford	(10)			9.1	32	Meyerdirk and Moratorio 1987
<i>Anaphes flavipes</i> (Foerster)				7.25	32.2	Anderson and Paschke 1969
				8.5	30	Anderson and Paschke 1968
Trichogrammatidae						
<i>Trichogramma chilonis</i> Ishii	(<8)		8.2		28	Miura and Kobayashi 1995
<i>Trichogramma pretiosum</i> Riley	(6.9)		8.4		25	Prattisoli and Parra 2000
	(7.2)		8.6	6.8	30	Pak and Oatman 1982b
	(7.7)			7.2	30	Harrison <i>et al.</i> 1985
	(7.7)			6.6	32	Butler and Lopez 1980
	10.2–10.8	(8.6)		7.6	32.5	Naranjo 1993
	(11)	(15)	12.8	9.9	25	Orphanides and Gonzalez 1971
	(7)			10.1	25	Cônsoli and Parra 1996
	(<9)			10.4	25	Cônsoli <i>et al.</i> 1999
<i>Trichogramma minutum</i> Riley	(7.0)			6.85	30	Yu <i>et al.</i> 1984
			11.7	(8.0)	25	Smith and Hubbes 1986
<i>Trichogramma exiguum</i> Pinto and Platner				7.0	35	Harrison <i>et al.</i> 1985
<i>Trichogramma turkestanii</i> Meyer	(7.3)			7.0	30	Hansen 2000
<i>Trichogrammatoidea bactrae</i> Nagaraja	(7.4)	(7.8)		7.1	30	Hutchison <i>et al.</i> 1990
<i>T. b. fumata</i> Nagaraja	(9)	(8.3)		7.3	29.5	Naranjo 1993
<i>Trichogramma evanescens</i> Westwood		(11.5)		8.75	26.2	Lim 1986
<i>Trichogramma australicum</i> Girault	(8)			7.2	29.3	Farghaly 1975
	(8.7)			7.6	24, 28	Dahlan and Gordh 1996, 1998
				7.6	28	Dahlan and Gordh 1996

Table 12 (continued).

Species	G	O	T	D	°C	Reference
<i>Trichogramma brevicapillum</i> Pinto and Platner	(8.6)		10.2	8.0	29	Jarjees and Merritt 2002
<i>Trichogramma papilionis</i> Nagaraja	10.1	(11)		8.5	30	Pak and Oatman 1982b
<i>Trichogramma dendrolimi</i> Matsumura		(11?)		10	25	Pak and Oatman 1982a
<i>Trichogramma</i> sp.	9			9	25	Hussein <i>et al.</i> 1996
	9.5			9	25	Takada <i>et al.</i> 2000
	(11)	(14.5)		9.5	25	Stavraki 1976
<i>Trichogramma galloi</i> Zucchi	(12)	(14)		11	21	
<i>Paracentrobia andoi</i> (Ishii)	(11.5)		12.5	11.3	25	Cónsoli and Parra 1996
<i>Trichogramma retortidum</i> Girault	12.4		14.4	10.3	25	Cónsoli <i>et al.</i> 1999
				11.0	32	Miura 1990c
				10.9	25	Orphanides and Gonzalez 1971
Eulophidae						
<i>Ooencyrtus papilionis</i> Ashmead	(9.6)			9.1	30	Rahim <i>et al.</i> 1991
<i>Sympiesis marylandensis</i> Girault	(10)			8.2	31	Ridgway and Mahr 1990
	(13)	(22)		10.9	23	
<i>Cirrospilus</i> sp. nr. <i>lyncus</i>	10.4		12.2	8.2	30	Urbaneja <i>et al.</i> 1999, 2001
<i>Edovum puttleri</i> Grissell [<i>Euplectrus</i>]	(12.5)	(16.5?)		10	30	Puttler <i>et al.</i> 1980
	(14.5?)			11.3	29.4	Obrycki <i>et al.</i> 1985
	(14)			11.2	29.4	Ruberson <i>et al.</i> 1988, 1989
<i>Elachertus ceramidae</i> Burks	(14.2)			13	?	Harrison 1965
<i>Ooencyrtus trinidadensis</i> Crawford	(15)		19.5	14.0	28	Gerling <i>et al.</i> 1976
<i>Cirrospilus vittatus</i> Walker	(16)			12.9	30	Urbaneja <i>et al.</i> 2002
<i>Euplectrus kuwanae</i> Crawford				13.3	25	Uematsu 1981a, 1981b
<i>Pediobius foveolatus</i> Crawford				13.5	25	Bledsoe <i>et al.</i> 1983
Aphelinidae						
<i>Aphelinus asychis</i> (Walker)			13.2	9.5	32.2	Raney <i>et al.</i> 1971
<i>Aphelinus semiflavus</i> Howard				10.4	29.4	Force and Messenger 1964
<i>Aphytis lingnanensis</i> Compere				10.4	32	Kfir and Luck 1984
<i>Aphytis melinus</i> DeBach				11.0	32	Kfir and Luck 1984
<i>Aphytis chrysomphali</i> (Mercet)				11.3	29	Kfir and Luck 1984

Table 12 (concluded).

Species	G	O	T	D	°C	Reference
<i>Eretmocerus longipes</i> Compere				11.4	35	Sengonca and Liu 1998
<i>Aphelinus albipodus</i> (Hayat and Fatima)			15.2		26.7	Bernal <i>et al.</i> 1997
<i>Encarsia transvena</i> (Timberlake)	(13.3)			11.3	25–30	Antony <i>et al.</i> 2003
<i>Encarsia pergandiella</i> Howard				11.6	26.7	Liu and Stansly 1996
<i>Aphelinus mali</i> (Haldeman)				11.8	30	Asante and Dantharayana 1992
<i>Aphelinus niger</i> (Lagace) [<i>Mesidia nigra</i>]	(13)			12	25.6	Lagace 1969
<i>Encarsia deserti</i> Gerling and Rivnay	(13)	(17)		12	25	Gerling <i>et al.</i> 1987
<i>Eretmocerus eremicus</i> Rose and Zolnerowich				13.7	32	Greenberg <i>et al.</i> 2000
Elasmidae						
<i>Elasmus broomensis</i> Naumann and Sands	(13?)			12.4	25	Naumann and Sands 1984
Pteromalidae						
<i>Anisopteromalus calandrae</i> (Howard)	10.4		12.3	10.4	35	Smith 1992
	(12)		14.6	11.45	25	Smith 1993
	13.6			12.6	28	Begum 1999
<i>Amblymerus bruchophagi</i> (Gahan)	(12.0)			10.5	27	Saunders and Hsiao 1970
<i>Pteromalus venustus</i> Walker	(12)			11.2	32	Whitfield and Richards 1985
<i>Trichomalopsis sarcophagae</i> Gahan	12		(13.5)	12	30	Lysyk 1998b
<i>Urolepis rufipes</i> (Ashmead)	(12.5)			10.5	30	Smith and Rutz 1986
<i>Eurytoma nesiotis</i> Crawford	12.5	(23?)		12.5	?	Tiwari 1974
<i>Muscidifurax raptorellus</i> Kogan and Legner	(13)		(15)	12.7	30	Lysyk 2001b
<i>Hypopteromalus tabacum</i> (Fitch)	(13.4)			(13)	27	McNeil and Rabb 1973
<i>Catolaccus aeneoviridis</i> (Girault)	(13.4)			(13)	27	McNeil and Rabb 1973
<i>Muscidifurax zaraptor</i> Kogan and Legner	(14)		(16)	13.9	30	Lysyk 2001a
	20	(25.4)		19	24–28	Coats 1976
<i>Rhopalicus tutela</i> (Walker)	14.8			14.8	25	Krüger and Mills 1990
<i>Catolaccus grandis</i> (Burks)	15.1		23.9	13.3	30	Morales-Ramos and Cate 1992b
				11.8	33	Morales-Ramos and Cate 1993
<i>Muscidifurax raptor</i> Girault and Sanders			18	10.6	35	Morales-Ramos and Cate 1992a
					32.3	Ables <i>et al.</i> 1976

Note: Conventions as in Table 1.

Table 13. Sample records of short life cycles in other Hymenoptera.

Species	<i>G</i>	<i>O</i>	<i>D</i>	°C	Reference
Scelionidae					
<i>Telenomus reynoldsi</i> Gordh and Coker	(10?)		9.3	33	Cave and Gaylor 1988
<i>Trissolcus oenone</i> (Dodd)	(10.7?)		9.7	30	James and Warren 1991
<i>Telenomus triptus</i> Nixon	(<11)		9.0	30	Icuma and Hirose 1996
<i>Telenomus podisi</i> Ashmead	(11)		10.2	29.4	Yeargan 1980
	(11)	(16)		21	Yeargan 1982
<i>Gryon gnidus</i> Nixon	(11)	(12)	10.5	30	Egwuatu and Taylor 1977
<i>Gryon clavigrallae</i> Mineo	11.5	(17.5)	10.5	30	Romeis <i>et al.</i> 2000
<i>Trissolcus semistriatus</i> (Nees)	(12.5)		11.0	26	Kivan and Kilic 2002
<i>Trissolcus basalis</i> (Wollaston)	(13)	(15.5)	10.2	27	Awan <i>et al.</i> 1990
			7.8	33	Orr <i>et al.</i> 1985
			10	32.2	Powell <i>et al.</i> 1981
<i>Trissolcus mitsukurii</i> (Ashmead) [Asolcus]	(13)		12.2	25	Hokyo <i>et al.</i> 1966
<i>Paratelenomus</i> <i>saccharalis</i> (Dodd)	<13.7		11.7	30	Takagi and Murakami 1997
<i>Telenomus chloropus</i> (Thompson)			11.6	30	Orr <i>et al.</i> 1985
<i>Trissolcus euschisti</i> (Ashmead)			10.2	30	Yeargan 1983
Bethylidae					
<i>Goniozus legneri</i> Gordh	(10)		8.1	35	Butler and Schmidt 1985

Note: Conventions as in Table 1.

than the air because of the high specific heat of water. Therefore, temperatures above 25 °C can be maintained for long periods in summer even in cool temperate regions. The soil surface and clumps of vegetation also heat up when insolated, leading to temperatures many degrees above ambient even in the Arctic (Corbet 1972). Such conditions allow insects to gain heat through basking and other active behaviours (see Use optimal conditions). Conversely, development in many species from specialized habitats tends to be slow. Typical mosquitoes have relatively rapid larval development, but some species from small container habitats develop slowly; for example, immature stages of a predatory species that lives in bamboo internodes take 25–45 d to develop at 28 °C, and adults oviposit over about 2 months (Okazawa *et al.* 1986). Many habitats are unsuitable for development for large parts of the year when dry summers,

cold winters, or limited food prevent rapid development (Danks 1987, 1992).

On a very small scale, habitat influences potential developmental rate by modifying conditions, not only temperature but also various other factors such as humidity and ease of movement. Different leaves with different textures and other properties affect the generation time of mites eating prey on those leaves (El-Banhawy *et al.* 2000).

On a larger scale, the permanence and seasonality of habitats mediate longer-term influences on life-cycle duration. The need for rapid development on ephemeral food sources was noted above. Likewise, species from ephemeral habitats must complete development before those habitats become unsuitable. Macrochelid mites inhabiting dung have short life cycles (*e.g.*, Cicolani 1979). Nevertheless, many such species with rapid larval development do not have short life cycles because the egg stage or adult

Table 14. Families of mites and insects in which species have very short life cycles (for details see Tables 1–13 and text).

Acari

Mesostigmata
 Phytoseiidae
 Macrochelidae
 Ascidae
 Species in some other families, *e.g.*, Digamasellidae, Laelapidae, Pachylaelapidae

Prostigmata
 Tetranychidae
 Tarsonemidae
 Eriophyidae
 Species in some other families, *e.g.*, Acarophenacidae, Pyemotidae, Pygmephoridae, Cheyletidae, Stigmaeidae

Astigmata
 Acaridae
 Histiosomatidae

Probably at least a few species in many other families in most major groups

Insecta

Hemiptera
 Aphididae
 A few species in some other families, *e.g.*, Anthocoridae

Diptera
 Chironomidae
 Species in some other families of Nematocera, *e.g.*, Culicidae, Ceratopogonidae, Cecidomyiidae
 A few to several species in some cyclorrhaphan families, *e.g.*, Ephydriidae, Drosophilidae
 Probably a few to several species in many other families

Hymenoptera
 Braconidae
 Mymaridae
 Trichogrammatidae
 Eulophidae
 Aphelinidae
 Pteromalidae
 Scelionidae
 Species of some other families, *e.g.*, Ichneumonidae, Elasmidae, Bethyidae
 Probably a few to several species in many other families of Parasitica

life is prolonged. Snowmelt mosquitoes (*Aedes* spp.) develop rapidly after hatch, before their temporary spring pools evaporate, but the months of winter are spent in the egg stage (Wood *et al.* 1979). Similarly rapid development is known in insects from desert streams (Gray 1981). In many habitats, nest parasites such as cuckoo bees save time by taking over the nests of industrious species (*cf.* Wcislo 1987). Many astigmatic mites are adapted to colonize and develop in scattered and temporally restricted habitats, and these adaptations include faster development (O'Connor 1994).

Although long life cycles are seen in parasitoids that remain dormant in a particular stage to wait for host development, other species are subject to a restricted time frame imposed by the limited duration of host suitability, and they develop rapidly. Such parasitoids face challenges of timing because they cannot use the whole host life cycle, because the host itself may develop rapidly, and because competitors may preempt the host tissues. Consequently, many parasitoids, especially on rapidly developing hosts, have fast development (*cf.* Table 12; Sequeira and Mackauer 1992).

Table 15. Summary of potential mechanisms to abbreviate life cycles.

Reduce resources required
Reduce size
Reduce fecundity
Reduce adult longevity
Simplify structures
Eliminate stages
Larvipary
Reduced numbers of instars
Rapid or non-feeding instars
Parthenogenesis
Paedogenesis
Accelerate stages
Rapid metabolism
Low thresholds and heat requirements
Dark colours and hairiness
Rapid moulting
Group effects
Rapid reproduction
Use optimal conditions
Warm habitats or microhabitats
Basking
Rich food sources

Mechanisms for short life cycles

This section summarizes the ways in which the various stages can be abbreviated, using selected examples including some species in which only part, rather than all, of the life cycle is completed very rapidly.

Possible mechanisms to abbreviate life cycles are listed in Table 15, although various constraints limit the degree to which each method is feasible in a given taxon or a given environment. Life cycles are shortened when stages are eliminated or accelerated, a process that is enhanced by reducing resource use, exploiting favourable sites, and minimizing variations in developmental rate.

Reduce resources required

Reductions in size, fecundity, longevity, and structural complexity all limit the resources, and hence the time, required to complete the life cycle. Both within and between species, smaller individuals require fewer resources and develop faster, other things being equal, as already

noted for characteristic families. Thus, smaller species generally develop much more rapidly than their larger relatives (Danks 1978, 1992; Bonner and Horn 1982; Norton 1994).

Less fecund adults need fewer resources, whether these resources are carried through from the larval stage or are acquired in adulthood. For example, data from many species of mites (Sabelis 1991) show that developmental rates are higher when fecundity and oviposition rates are lower. Adults that live for a shorter time, and hence reproduce closer to emergence, likewise tend to require fewer resources. The gall midge *Masakimyia pustulae* Yukawa and Sunose lives for only 6 to 12 h (Sunose 1985), and some mayflies live for only a few hours (*e.g.*, Kureck and Fontes 1996); few insect species that are so short lived as adults feed in that stage. Short life cycles are favoured in such species provided that the larval stages can develop rapidly and food is abundant.

Reducing the complexity of structure conserves energy and hence allows faster development. Wing development provides the best-known examples. In many species with more than one wing form, brachypterous or apterous individuals develop faster than winged ones, even when no ovarian dormancy is correlated with wing form or dispersal. For example, development from birth to adult of most aphids lasts 2 or 3 d less in apterae than in alatae (*e.g.*, Noda 1960; Campbell and Mackauer 1975a; Kieckhefer *et al.* 1989). Other species with short wings do not develop especially rapidly but instead devote the resources saved to egg production, as in some lygaeid bugs (Solbreck *et al.* 1990) and in *Orgyia* moths (Lymantriidae) and other species with heavy-bodied wingless females and winged males.

Eliminate stages

Time can also be saved during development by reducing or eliminating any of the substages of the life cycle, although, of course, such adaptations may relate to protection, dormancy, or other features as well as to possible influences on the rate of development (Danks 2000). Egg stages are eliminated by larvipary, which is relatively widely distributed among the arthropods. At least in aphids, some Diptera, some thrips, and some macrochelid and phytoseiid mites, it contributes to very rapid development. A few specialized species telescope the life cycle even further through development of eggs to the late larval stage within the mother, as in louse flies,

bat flies, and tsetse flies (Danks 2002b). Adult male podapolipid mites hatch directly from the egg (females retain an active larval instar), and in some families (e.g., Pyemotidae) adult females produce adult males and females (Lindquist 1986; Wrensch and Bruce 1991).

Larval stages can be abbreviated by reducing the number of instars and by interpolating rapid, usually non-feeding, instars. The number of juvenile instars has been reduced during the evolution of many different insect and mite groups (e.g., references in Danks 2000, p. 286). In groups with relatively few instars, the first or second instar may also be especially abbreviated, as in some moths, in chironomid midges, and in other insects and mites. Even within a species, the rapid development possible under favourable conditions may take place with fewer instars than slower development under less favourable conditions, as in some species of moths (e.g., Neunzig 1969; Kamata and Igarashi 1995) and spiders (e.g., Miyashita 1997).

The adult stage can be abbreviated by parthenogenesis, which avoids the necessity for mating; moreover, eggs or even larvae can then begin development before adult emergence, as in aphids in which the annual sexual reproduction of overwintering eggs is much slower than the parthenogenetic reproduction by apterae in summer. Indeed, several generations are present in one parthenogenetic female aphid because embryonic development can begin before the mother is born (Uichanco 1924 and later references). In a few species, adults have been eliminated (at least in some generations), and eggs or young are produced by a preadult stage (paedogenesis), further abbreviating the life cycle. The best-known examples are in some fungivorous cecidomyiids, in which larvae of the next generation develop within the mother larva (see references in Table 9). Crowding or exhaustion of available food triggers a switch to the slower sexual cycle, but by preventing these influences up to 250 continuous paedogenetic generations can be reared (Nikolei 1961).

Accelerate stages

Faster development is assisted by more rapid metabolism (at a given temperature), by reducing the amount of heat required for development, by low threshold temperatures for development, by adaptations of structure or colour to assist heat gains, and in several other ways (Table 15). Many of these adaptations related to temperature are best developed in species from cold

environments (reviewed by Danks 1981, 2004), although they occur elsewhere. Apparently, they are not common in warmer habitats partly because such adaptations would be disadvantageous at the upper end of the temperature range.

The thresholds for development and the heat sums (day-degrees) required for development have been studied in many species and stages. Even within a species, stages have different thresholds, so that the speed of development depends on the most demanding link. Although in many species stage-to-stage differences are very small, or only about 2 °C (e.g., *Coleomegilla maculata* (De Geer), egg 10.2 °C, pupa 12.2 °C; Obrycki and Tauber 1978), greater differences are known (e.g., *Cylas formicarius elongatulus* (Summers), egg 9.0 °C, larva 17.4 °C; Mullen 1981).

The average temperature threshold for development in insects is about 10 or 11 °C (Utida 1957; Honěk and Kocourek 1990). Some species from cold habitats and Arctic and alpine zones have much lower developmental thresholds: for example, -1.5 °C for cave-dwelling *Trichocera* spp. (Plachter 1983) and 1 to 2 °C for cold stream stoneflies (Mutch and Pritchard 1986; Økland 1991). Many such species are active at still lower temperatures, even below 0 °C (Jonsson and Sandlund 1975; Aitchison 1983, 1984; Catley 1992; Block *et al.* 1994). Some temperate species have developmental thresholds below 5 °C, including many species of aphids (e.g., Wellings 1981; Lamb 1992), flies (McLeod *et al.* 1985; Kim and Eckenrode 1987), and aquatic species in addition to stoneflies (e.g., 2.5 to 4 °C for chironomids and mayflies: Ohno 1981; Rosillon 1988). Despite these low thresholds, few such species develop very rapidly because their habitats are so cold.

Based on the summaries for 294 mostly temperate species by Honěk and Kocourek (1990), typical species require about 400 day-degrees above the threshold for development from egg to adult, and some require much more, but the lowest requirements, notably in aphids and various parasitic Hymenoptera, are only about 100 or 200 day-degrees for the same interval. For example, the aphidiine braconid *Aphidius ervi* Haliday requires only 73 day-degrees for immature development (Sigsgaard 2000). A generation (*T*) can be completed with only 130.5 day-degrees in the mymarid *Trichogramma minutum* Riley (Lawrence *et al.* 1985) and with

only 144 day-degrees in the aphid *Myzus persicae* (Sulzer) (Jansson and Smilowitz 1985).

Acquisition of the heat necessary for development is assisted in many species by dark colours and hairiness which, coupled with habitat choice and basking behaviour, enhance and retain heating by the sun. These adaptations are well known in Arctic and alpine species (for reviews see Danks 1981, pp. 266–274; Danks 2004) but are common in temperate species too. Possible overheating at higher temperatures can be partly offset by behaviour. Some species even change colour seasonally, with darker colours in the cooler spring, for example, and lighter colours in summer (Fields and McNeil 1988).

In some species, group effects enhance developmental rate. The “tents” of gregarious caterpillars such as *Malacosoma* species have been supposed to enhance heat gain (see review by Klok and Chown 1999). Some fly larvae raise the temperature and liquify food by group action, making the food more readily available to members of the group (Marchenko and Vinogradova 1984). Other increases in the rate of development depend not on group influences on the habitat but rather on pheromones or on contacts among individuals, as in cockroaches (Nakai and Tsubaki 1986) and some moth larvae (Fitzgerald 1993).

Time might also be saved by reducing the time required for moulting, which in many species occupies a substantial fraction, even as much as half, of the developmental time (Oetting and Yonke 1971; Ayres and MacLean 1987; Ayres and Scriber 1994). Finally, generation time is reduced when reproduction is completed very rapidly. Rapid mating is ensured in many species by protandry (so that males are available upon emergence of females). Some species emerge with eggs fully developed, and many of these do not feed as adults. In other species, females may feed later but lay the first clutch rapidly without feeding (*e.g.*, McLachlan and Yonow 1989 for a chironomid). Even in groups of biting flies well known for developing eggs after the adult feeds on the blood of vertebrate hosts, there are autogenous species that develop eggs more rapidly from larval food reserves.

Use optimal conditions

Temperatures and food supplies vary from place to place on a wide range of scales and through the season, so that habitat choice greatly influences rates of development. Females of many species oviposit in favourable

locations for their offspring, and immature stages may seek out the most favourable sites. Basking behaviour, usually coupled with adaptations of colour and structure, further enhances heat gain, increasing the speed of adult activity or the developmental rate of larvae. Remarkable increases in temperature above ambient temperature can be achieved by melanin, basking individuals such as larvae of the butterfly *Euphydryas aurinia* (Rottentburg), which can reach 30 °C (Porter 1982). More commonly the increases are in the range of 3 to 8 °C (Rawlins and Lederhouse 1981; James 1986), but even so such basking may halve larval developmental time (Rawlins and Lederhouse 1981). The effectiveness of basking depends strongly on size and favours larger individuals (*e.g.*, Bishop and Armbruster 1992); however, very rapid development is less common in large than in small individuals even at high temperatures.

Most species focus active development into a particular part of the year and pass less favourable conditions in a dormant state. Development tends to be especially rapid when the period with the most favourable conditions is very narrow. However, these seasonal adaptations do not necessarily shorten the life cycle as a whole but only promote rapid larval or nymphal development.

Conclusions

The life cycles of some insects and mites are remarkably short, and some species complete a generation within 1 week. The fastest minimum generation times listed here belong to the histiostomatid mite *Histiostoma polypori* (Oudemans) (3.7 d), the aphid *Aphis glycines* Matsumura (3.9 d), the parasitoid pyemotid mite *Pyemotes tritici* (Lagrèze-Fossat and Montané) (4.0 d), and the predatory phytoseiid mites *Neoseiulus womersleyi* (Schicha) and *N. fallacis* (Garman) (4.0 d). The fastest mean generation times that have been calculated (4.5–5.2 d) belong to four species of predatory *Macrocheles* mites (Macrochelidae).

The species with very fast life cycles come chiefly from a number of families characterized by small species that live in warm climates, habitats, or microhabitats with rich and abundant food. Specific adaptations that favour rapid development include reducing the resources required (by reducing size or fecundity); eliminating life stages, especially instars; accelerating certain stages, especially by physiological

adaptations; and choosing optimal conditions. The most rapid development is seen in aphids and in certain mites and in some insect parasitoids, all of which are small and have adaptations among those just enumerated. Typical short life cycles thus accord both with intrinsic predisposition through taxonomic affinity and with ecological correlates that can be summarized as a lack of adversity or stress, coupled with physiological and behavioural adaptations for rapid development. Within insects and mites as a whole, therefore, species with very short life cycles are relatively rare.

At the other extreme are species with very long life cycles, even prolonged beyond a year when conditions are cool or unpredictable, food is poor, scattered, or unreliable, individuals are large, and natural enemies are abundant (Danks 1992). Many more species from cool temperate regions have long life cycles typified by univoltinism (Danks and Footitt 1989). Most other species complete a generation relatively rapidly in summer (*e.g.*, between 15 and 45 d, but not more rapidly) but typically much more slowly or not at all in winter. The life-cycle delays in these sorts of species serve to adjust development to ensure seasonal coincidence, especially through control of growth rate, or to withstand adversity, especially through developmental arrests in a resistant stage (Danks 1987, 1994, 2001, 2002*a*). Evidently, these constraints apply to nearly all species, and few species can avoid or overcome them to the extent necessary to complete the life cycle very quickly.

Species with very rapid life cycles belong to two main categories. First, many species living in continuously equable conditions have continuous, overlapped cohorts with very high rates of increase and explosive population growth. A few species reproduce continuously but the cohorts do not overlap. Even in continuously reproducing populations, however, a few individuals may take much longer to complete the life cycle, apparently providing insurance against unpredictability (Danks 1983). Second, species from habitats where conditions are ideal for only a very short time develop in a single burst during the brief suitable period. Although many such species from seasonal habitats are dormant in between these bursts, a few continue to develop rapidly by moving to new habitats that are available all year, including rich but ephemeral sources of dung, carrion, and other decaying materials.

Short life cycles therefore respond to both specific and general forces. Some specific environmental characteristics make rapid development essential: if favourable habitats, food quality, or food supply are restricted, there may be only a short window of opportunity for development. Even when the window is not restricted, however, more rapid development has a simple general demographic advantage: the potential rate of increase of a population depends to the greatest degree on the generation time (Birch 1948; many subsequent papers). Moreover, by limiting the exposure of developing stages to lethal environmental elements, fast development tends to reduce mortality (Cornell 1990, 1991). Given these advantages, in fact, the absence of rapid development in most species is more striking than its presence in a few. Certainly development is constrained: the necessary processes take time and cannot always be telescoped, and many taxa retain all developmental instars. In particular, however, slower development stems from the many constraints present in most environments, notably the seasonality of temperature and resources, as well as their heterogeneity, that force development to follow specific timing and incorporate resistant stages that greatly prolong generation time beyond the theoretical minimum.

Insects and mites with short life cycles are instructive because they provide clues to the complex set of environmental and phylogenetic features that govern the life-cycle traits of a given species. Critical features of timing and resource relationships are brought into focus especially clearly when the life cycle lasts for only a short time. These findings also confirm the remarkable adaptability of the arthropods. Few other taxa encompass a range of generation times from less than 4 days to more than 20 years.

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