

Intraspecific Variability in Number of Larval Instars in Insects

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J. Econ. Entomol. 100(3): 627–645 (2007)

ABSTRACT The number of larval instars varies widely across insect species. Although instar number is frequently considered to be invariable within species, intraspecific variability in the number of instars is not an exceptional phenomenon. However, the knowledge has remained fragmentary, and there are no recent attempts to synthesize the results of relevant studies. Based on published case studies, we show that intraspecific variability in the number of larval instars is widespread across insect taxa, occurring in most major orders, in both hemimetabolous and holometabolous insects. We give an overview of various factors that have been observed to affect the number of instars. Temperature, photoperiod, food quality and quantity, humidity, rearing density, physical condition, inheritance, and sex are the most common factors influencing the number of instars. We discuss adaptive scenarios that may provide ultimate explanations for the plasticity in instar number. The data available largely support the compensation scenario, according to which instar number increases in adverse conditions when larvae fail to reach a species-specific threshold size for metamorphosis. However, in Orthoptera and Coleoptera, there are some exceptional species in which instar number is higher in favorable conditions. In more specific cases, the adaptive value of the variability in instar number may be in reaching or maintaining the developmental stage adapted to hibernation, producing additional generations in multivoltine species, or increasing the probability of surviving in long-lasting adverse conditions.

KEY WORDS instar number, developmental polymorphism, plasticity, threshold size, life history

Understanding the life histories of insects is crucial, not the least when the species involved have an economic significance. In these cases, detailed knowledge of the life cycle, and how it responds to environmental factors, is the necessary raw material for forecasting, and for developing successful control programs (Nylin 2001). In insects, various aspects of the complex individual growth trajectory should be viewed as life history traits of central importance because these traits proximally determine adult sizes, and thereby fecundities; and also the time span the often vulnerable larvae are exposed to predators.

During their immature development, larvae of insects and other arthropods molt regularly, i.e., replace their exoskeletons. As a result, the larval period of insects is divided into several discrete stages. The period between two successive molts is usually called an instar, although some debate exists considering the terminological issues (Carlson 1983, Fink 1983, Jones 1983). In the present article, we use the term *instar* to designate the period from one molt to another, as well as referring to the periods from hatching to the first larval molt (the first instar). Accordingly, the last instar is the period from final molt to either pupal or

prepupal stage (in the case of holometabolous insects) or eclosion of an imago (hemimetabolous insects).

The number of larval instars varies widely across insect taxa. The hymenopteran egg parasitoid *Trichogramma australicum* (Girault), for example, has been reported to have only one larval instar (Jarjees and Merritt 2002), whereas the larvae of the ephemeropteran *Leptophlebia cupida* (Say) go through as many as 34 instars (Clifford et al. 1979). Most commonly, however, insects tend to have three to eight larval instars, but in some phylogenetically older orders (Ephemeroptera, Odonata, and Plecoptera), where larvae have heavily sclerotized, nonexpansible exoskeletons, instar number is usually >10 (Sehnal 1985, Nijhout 1994).

However, instar number is much more canalized at the intraspecific level. Moreover, within species, instar number is perhaps usually considered to be constant in most insects. Still, there are a considerable number of species in which instar number varies intraspecifically (partially reviewed by Calvert 1929, Uvarov 1966 for Orthoptera; Wigglesworth 1972, Corbet 1999 for Odonata). Nevertheless, data about this phenomenon, sometimes also referred to as developmental polymorphism (the term proposed by Schmidt and Lauer 1977), are scattered, and we are unaware of any recent attempt to synthesize results of the numerous case studies. Thus, there is little general understanding with respect to how widespread is the intraspecific

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variability in instar number among insects. Moreover, it is not clear which factors can elicit such variability, and what are the physiological mechanisms involved.

In the present review, we summarize published case studies reporting intraspecific variability in instar number in insects. We investigate how widely plasticity in instar number occurs among insects, and we discuss which factors elicit such a plastic change. We also discuss different scenarios that may explain the adaptive role of intraspecific variability in the number of instars. Finally, we examine whether additional instars serve as a compensatory mechanism for achieving a species-specific threshold size in poor conditions, or are they rather used as a means enabling to attain particularly large adult sizes in conditions permitting fast growth.

Materials and Methods

To find case studies that report intraspecific variability in instar number in insects, major ecological and entomological journals (40 in total) were systematically surveyed for relevant studies. The emphasis was on the issues from the past three decades. However, many older relevant works also were included. We could not aim to provide a perfectly complete coverage of relevant studies. Such a task would be unreasonably hard to complete because variability in instar number is usually reported as a by-product in respective case studies, and it is not reflected in title or abstract. However, we think that the 173 articles we were able to trace present a survey of existing knowledge sufficient to reveal qualitative trends.

The present review is restricted to winged insects (Pterygota), which do not molt as adults. Cases in which differences in instar number were caused by an unnatural factor (e.g., injecting analogues of hormones involved in the molting process, treating larvae with pesticides) were not considered. Only studies in which the number of larval instars was determined directly by regularly observing larvae were included. This restriction was applied because indirect methods of determining instar number are often inappropriate in species with a varying number of instars. For example, one of the most common of such indirect methods, used primarily in field studies, is based on distribution peaks of head capsule widths. Head capsules from larvae of different ages are measured, and each peak of the distribution is considered to represent one instar. This method is based on Dyar's rule, which states that head widths in successive instars follow a regular geometric progression (Dyar 1890). However, the method has been repeatedly shown to be unreliable for species with a varying instar number (Gaines and Campbell 1935, Beck 1950, Kishi 1971, Schmidt et al. 1977, Fink 1984, Daly 1985, Weatherby and Hart 1986, Gold et al. 1999, García-Barros 2006). Therefore, investigations in which instar number was determined on the basis of the distribution of head capsule widths are not considered in the present review. Unfortunately, this restriction implied that only articles based

on laboratory studies passed our qualification requirements.

To further reduce the possibility of mistakes in determining the number of larval instars, several restrictions related to methods and sample size were applied. Only studies in which variability in instar number was observed within the framework of a single experiment were included, i.e., cases when different authors reported a different instar number in a particular species were not considered. Only studies in which the total sample was no less than ten individuals were included. Instar number was considered to vary intraspecifically when at least three individuals developed through a different number of instars than did their conspecifics.

When analyzing the influence of different factors on the number of instars, those studies were always considered in which instar number had been reported to differ significantly between respective groups. However, the difference between treatments in the number of instars had frequently not been confirmed statistically by original authors, and the data had often been presented in a way that did not allow us to perform proper statistical tests either. Therefore, as a substitute criterion, the particular factor was decided to have an influence on the number of instars when the difference in average instar number between the groups being compared was at least 0.2 instars. For example, diet quality was considered to have an influence on instar number if all larvae developed through four instars on one host plant, but 20% of the larvae had five instars on another host species. Additionally, sample sizes of at least 10 individuals in all treatments were required, with at least five more individuals having an "untypical" instar number in one treatment, compared with the other.

When testing whether the additional instars do preferentially occur in favorable or adverse conditions, the following approach was taken. Only studies in which the effect of environmental factors could be expected to be directly mediated via environmental quality were considered. This implies that the cases in which the difference in instar number had arisen due to a factor used more likely as a cue (e.g., photoperiod) of future conditions were not included. Such cues may well function as a signal of environmental quality, but their interpretation in this context is often idiosyncratic as well as equivocal. The treatments were included into the comparison when the sample sizes were at least 10 individuals in both treatments, and the instar number was reported to differ significantly between treatments. If the difference had not been confirmed statistically by the original authors, treatments were considered to differ when the difference between the average instar number was at least 0.2 instars, with at least five more individuals having an "untypical" instar number in one treatment, compared with the other treatment. Always only two treatments, one treatment representing the "favorable" and the other treatment the "adverse" condition, were considered. If more than two treatments had been applied, those with the largest difference in the indicators of environmental quality were chosen. In some

cases (e.g., presence versus absence of injuries, starved versus nonstarved individuals), the very nature of the treatments allowed them to be unambiguously classified as adverse or favorable. In less straightforward cases, the following parameters were used as the indicators of adverse conditions: higher mortality, smaller body size in early instars (i.e., before the variability in instar number becomes apparent), and final body size (size of pupae or adults). The treatments were considered to be different in their quality when at least one of these indicators had been reported to show a statistically significant difference, or, if the difference had not been confirmed statistically by the authors, when the respective values differed by at least 10%. Cases in which different indicators provided contradictory evidence with respect to the quality of the treatments, were not considered in this comparison.

Variability in Intraspecific Instar Number across Insect Taxa

The confirmed cases of the occurrence of intraspecific variability in instar number across insect taxa are summarized in Table 1. In the total 173 case studies fulfilling our qualification criteria (see above), intraspecific instar number has been reported to be variable in 145 insect species, which represented 12 orders and 49 families. It can thus be concluded that intraspecific variability in instar number is a widespread phenomenon among insects, occurring in almost all major orders, in both hemimetabolous and holometabolous taxa. Typically, the intraspecific range of variability in the number of instars remains as low as 1–3 (Table 1). However, there are several remarkable exceptions. One of the most extreme examples is the moth *Prionoxystus robiniae* (Peck) in which larvae may have from eight to 31 instars, depending largely on whether the larvae represent the univoltine (larval period lasts 1 yr) or the semivoltine (2–3 yr as a larvae) developmental pathway (Solomon 1973). The larvae of some species may go through an undetermined number of additional molts if starved (Beck 1971), reared on poor-quality diet (Titschack 1926), or reared in groups (Quennedey et al. 1995) or under conditions inducing larval diapause (Chippendale and Yin 1973, Kfir 1991). Usually, stationary, or even regressive molts (i.e., linear measurements of larvae do not increase, or even decrease in molting from one instar to another) are involved in species that exhibit an extremely high variability in the number of larval instars.

Although it is clear that intraspecific variability in the number of instars is widespread across major insect taxa, it is, at the present, hard to tell whether some taxa are more prone than others to display this type of plasticity. Although as much as a half of the insect species, in which variability in instar number has been reported, belong to the order Lepidoptera, the main reason for the disproportion is likely the overrepresentation of these insects in ecological studies. However, there still seem to be disproportionately few spe-

cies with intraspecific variability in instar number in such well-studied insect orders as Diptera and Hymenoptera (excluding sawflies), as well as among true bugs (Hemiptera: Heteroptera) and butterflies (Lepidoptera: Papilionoidea). In contrast, the relatively high number of roach species (Dictyoptera: Blattaria) in which instar number is reported to vary may indicate that this phenomenon is more common in this taxon than in insects in general.

Interestingly, various insect species showing variability in the number of instars are economically important pests. For example, instar number is reported to be variable in such serious pest species such as *Locusta migratoria* (L.), *Schistocerca gregaria* (Forsk.), *Tenebrio molitor* (L.), *Lymantria dispar* (L.), *Pieris brassicae* (L.), and *Tineola biselliella* (Hummel) (Table 1). It is tempting to speculate that a high level of plasticity in life history parameters, such as developmental time and size, provided by the plastic instar number, might contribute to a species' tendency to become an opportunistic pest.

Despite that there are >100 insect species in which the number of larval instars has been proven to vary, invariability in instar number perhaps still seems to be considered the typical, or "normal" case by many entomologists. Nevertheless, because invariability in instar number is likely considered uninteresting, respective statements are not easy to find in the literature. Moreover, it is, even philosophically, impossible to prove the negative. Still, there are several insect species in which, despite of being subjected to versatile and extensive ecological research, no variation in instar number seems to be recorded. To mention the most marked examples, there seems to be no variability in instar number in the particularly well-studied *Drosophila* flies (invariably three instars; Hutchinson et al. 1997), and Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (four instars; Hare 1990). Of Lepidoptera, we can add at least the geometrid *Epirrita autumnata* (Borkhausen) (five instars; Tammaru 1998) and the tortricid *Cnephasia jactatana* (Walker) (five instars; Ochieng'-Odero 1990). Moreover, with a few exceptions, instar number is always five in true bugs (Hemiptera: Heteroptera) (Štys and Davidová-Vilimová 1989), and invariably three or four within several families of Coleoptera (Crowson 1981).

Factors Causing Plasticity in Instar Number

Of environmental factors, temperature, photoperiod, food quality and quantity, rearing density, and humidity are the most common ones affecting the instar number in various insects (Table 1). In addition, presence of injuries has been observed to influence the number of instars in some species. Humidity, physical condition as well as food quantity and quality (with very few exceptions) affect the instar number in the same direction. In particular, low humidity, the presence of injuries and low food quality (mature leaves, diet lacking some important component) and quantity (transient starvation) increase the instar number in many insect species (Tables 1 and 2). The

Table 1. Intraspecific variation in the number of larval instars in insects

Taxa	Instar range	Factors influencing no. of instars	More instars (higher mean instar no.) in	Reference
Dermatoptera				
Labiuridae				
<i>Labidura riparia</i>	5-6 (♂) ^a	Sex, sex*vsc ^b	Males	Shepard et al. (1973)
Dictyoptera				
Blaberidae				
<i>Diploptera punctata</i>	3-5	Sex, density*sex, vsc	Females, singly reared males	Willis et al. (1958), Woodhead and Paulson (1983), Holbrook and Schal (1998)
<i>Leucophaea maderae</i>	7-8	Sex, physical condition, vsc	Females, injured larvae	Willis et al. (1958)
<i>Nauphoeta cinerea</i>	7-8	Sex, vsc	Females	Willis et al. (1958)
<i>Opisthoptalia orientalis</i>	5-7	Sex, photoperiod, sex*photoperiod*temperature, vsc	Females, short daylength (12-h light), high temperature (30°C) at short daylength in females, low temperature (25°C) at long daylength (16-h light) in males	Zhu and Tanaka (2004)
<i>Pycnoscelus surinamensis</i>	8-10 (12) ^c	Physical condition, vsc	Injured larvae	Willis et al. (1958)
Blattellidae				
<i>Blattella germanica</i>	5-8 (9) ^c	Sex, physical condition, food quality, vsc	Females, injured larvae, low-quality diet	Seamans and Woodruff (1939); Willis et al. (1958); Tanaka (1981, 1982); Tanaka and Hasegawa (1979); Tanaka et al. (1987)
<i>B. vaga</i>	5-7	Sex, vsc	Females	Willis et al. (1958)
<i>Supella supellecillum</i>	6-8	Vsc		Willis et al. (1958)
Blattidae				
<i>Blatta orientalis</i>	7-10	Sex, vsc	Females	Willis et al. (1958)
<i>Eurycotis floridana</i>	6-7 (8) ^c	Vsc		Willis et al. (1958)
<i>Periplaneta americana</i>	9-14	Inheritance ^d , vsc	In one of two populations	Willis et al. (1958), Mira and Raubenheimer (2002)
<i>P. australasiae</i>	10-12	Vsc		Willis et al. (1958)
<i>P. japonica</i>	7-9	Vsc		Shindo and Masaki (1995)
Hemiptera				
Aphididae				
<i>Nasanoia ribisnigri</i>	4-5	Temperature, temperature*vsc (variation only at extreme temperatures)	Extreme temperatures (8 and ≥26°C)	Diaz and Fereres (2005)
Cicadellidae				
<i>Colladonus montanus</i>	5-6	Vsc		Severin and Klostermeyer (1950)
<i>Hordnia circellata</i> (<i>Neokolla circellata</i>) ^e	4-6	Vsc		Severin (1949)
Delphacidae				
<i>Peregrinus maidis</i>	4-6	Vsc		Tsai and Wilson (1986)
Miridae				
<i>Creontiades dilutus</i>	4-6	Vsc		Foley and Pyke (1985)
<i>Cyrtorhinus lividipennis</i>	3-5	Food quality, vsc	Certain prey species (<i>Drosophila</i> sp.)	Liquido and Nishida (1985), Geetha et al. (1992)
Odonata ^f				
Coenagrionidae				
<i>Argia vivida</i>	12-13 (14) ^c	Vsc		Leggott and Pritchard (1985)
<i>Coenagrion pulchellum</i> (<i>Agrion pulchellum</i>)	10-13	Vsc		Balfour-Browne (1909)
Libellulidae				
<i>Brachythemis contaminata</i>	11-12	Temperature	Low temperature (27°C)	Mathavan (1990)
<i>Orthetrum sabina</i>	14-15	Temperature	High temperature (37°C)	Mathavan (1990)
Orthoptera				
Acrididae				
<i>Acrotylus insubricus</i>	5-7	Vsc		Haniffa and Periasamy (1981)
<i>Chorthippus brunneus</i>	4-5 (♀) ^a	Sex, sex*food quality, sex*inheritance, sex*temperature, food quality*inheritance, temperature*inheritance, sex*vsc	Females, females in high-quality diet, some (southern) populations, high temperature (≥30°C)	Hassall and Grayson (1987), Grant et al. (1993), Willott and Hassall (1998), Telfer and Hassall (1999)
<i>Locusta migratoria</i>	5-6 (♀) ^a	Sex, sex*inheritance	Females in some populations	Key (1936)
<i>Melanoplus differentialis</i>	6-8	Density, density*sex, vsc	Singly reared nymphs, singly reared females (not found by Hodge 1933)	Hodge (1933), Dingle and Haskell (1967)
<i>M. femurrubrum</i>	6-7 (8) ^c	Sex, temperature, vsc	Females, high temperature (35-38°C)	Bellinger and Pienkowski (1987, 1989)
<i>M. sanguinipes</i> (<i>M. bilituratus</i>)	5-6	Food quality, inheritance, vsc	Certain host plant (<i>Avena sativa</i>), red-back phenotype	Smith (1959), Hodson and Chapco (1986)

(continued)

Table 1. Continued

Taxa	Instar range	Factors influencing no. of instars	More instars (higher mean instar no.) in	Reference
<i>Nomadacris septemfasciata</i>	6-7	Density, inheritance, density*inheritance, vsc	Singly reared nymphs (solitarious phase), progeny of solitarious	Albrecht and Blackith (1957)
<i>Omocestus viridulus</i>	4-5 (♀) ^a	Sex, sex*inheritance, sex*vsc	Females from certain (low-altitude) population	Berner and Blanckenhorn (2006)
<i>Ornithacris turbida</i>	6-7	Density, sex, vsc	Singly reared nymphs, females	Antoniou (1973)
<i>Schistocerca gregaria</i>	5-6	Density, inheritance, density*inheritance, sex, vsc	Singly reared nymphs (solitarious phase), progeny of solitarious individuals, females	Albrecht and Blackith (1957), Injeyan and Tobe (1981)
Gryllidae				
<i>Allonemobius fasciatus</i>	6-7 (8) ^c	Photoperiod, vsc	Long daylength (16-h light)	Tanaka and Brookes (1983)
<i>Gryllus bimaculatus</i>	8-10	Temperature, vsc	High temperature (34°C)	Behrens et al. (1983)
<i>Modicogryllus siamensis</i>	7-14	Photoperiod (larval diapause), photoperiod*vsc (variation only in short photoperiod)	Diapaused larvae at short daylength (12-h light)	Taniguchi and Tomioka (2003)
<i>Pteronemobius nitidus</i>	7-12	Photoperiod, temperature (larval diapause), photoperiod*temperature, vsc	Long daylength (≥15-h light), high temperature (28°C), low temperature (20°C) at short daylength (12-h light)	Tanaka (1979)
Pauliniidae				
<i>Paulinia acuminata</i>	5-6	Vsc		Thomas (1980)
Pyrgomorphidae				
<i>Zonocerus variegatus</i>	5-6	Density, sex, vsc	Low density (10 nymphs per cage), females	Chapman et al. (1977), Theagwan (1981)
Tettigoniidae				
<i>Euthypoda acutipennis</i>	5-7	Vsc		Eluwa (1970)
Phasmida				
Heteronemiidae				
<i>Diapheromera femorata</i>	4-5 (6) ^c	Sex, vsc	Females	Severin and Severin (1911)
Plecoptera				
Nemouridae				
<i>Nemoura avicularis</i>	12-13 (14) ^c	Vsc		Brittain (1973)
Coleoptera				
Anobiidae				
<i>Falsogastrallus sauteri</i>	4-12	Vsc		Xiong (1992)
Bostrichidae				
<i>Lyctus brunneus</i>	4-6 (7) ^c	Vsc		Iwata and Nishimoto (1984)
Cerambycidae				
<i>Anoplophora malasiaca</i>	7-9 ^g , 11-15 ^h	Temperature, vsc	Fluctuating temperature corresponding to the late summer conditions in the beginning of larval period	Adachi (1994)
<i>Monochamus carolinensis</i>	3-6	Temperature, vsc	High temperature (25-30°C)	Pershing and Linit (1988)
<i>Psacotheta hilaris</i>	4-6 ^f , 5-9 ^j (10) ^c	Photoperiod (larval diapause), temperature, inheritance, photoperiod*temperature*inheritance, food quantity, vsc	Short daylength (12-h light), low temperature (20°C), individuals from certain populations, nonstarved larvae	Shintani and Ishikawa (1997, 1998), Shintani et al. (1996), Muniyiri et al. (2003)
Curculionidae				
<i>Cosmopolites sordidus</i>	5-8	Vsc		Gold et al. (1999)
<i>Hyllobitelus xiaoi</i>	5-7	Vsc		Wen et al. (2004)
<i>Sitophilus oryzae</i>	4-5	Humidity, vsc	Low humidity (40% RH)	Pittendrigh et al. (1997)
Dermestidae				
<i>Anthrenus coloratus</i>	7-9	Vsc		Ali (1997)
<i>A. sarnicus</i>	5-17	Sex, temperature, humidity, vsc	Females, extreme temperatures (15 and 30°C), extreme humidities (20% and 90% RH)	Armes (1990)
<i>Attagenus fasciatus</i>	8-14 (15) ^c	Vsc		Ali (1993)
<i>A. unicolor</i> (<i>A. megatoma</i>)	5-12	Vsc		Baker (1977)
<i>Dermestes lardarius</i>	5-10	Humidity, temperature, vsc	Low humidity (50% RH), extreme temperatures (17.5 and 25-30°C)	Fleming and Jacob (1986)
<i>Trogoderma glabrum</i>	5-9 ^k	Sex, humidity, humidity*temperature, food quantity, vsc	Females, low humidity (30% RH), transient starvation	Beck (1971), Archer and Strong (1975)
<i>T. inclusum</i>	5-10	Sex, vsc	Females	Strong (1975)
<i>T. simplex</i>	6-10	Sex, vsc	Females	Strong and Mead (1975)
<i>T. variabile</i>	5-9 (10) ^c	Sex, humidity, humidity*temperature, vsc	Females, low humidity (30%, RH)	Partida and Strong (1975)

(continued)

Table 1. Continued

Taxa	Instar range	Factors influencing no. of instars	More instars (higher mean instar no.) in	Reference
Silvanidae				
<i>Oryzaephilus surinamensis</i>	3-5	Humidity, temperature, inheritance, vsc	Low humidity (30% RH), extreme temperatures (20 and 35°C), certain strains (reared in laboratory for generations)	Collins et al. (1989), Beckett and Evans (1994)
Tenebrionidae				
<i>Lagria hirta</i>	7-8	Vsc		Zhou and Topp (2000)
<i>Tenebrio molitor</i>	12-24	Temperature, food quality/humidity, inheritance*humidity, vsc	High temperature (30°C), diet with low water content, larvae from certain genetic strain reared at low humidity	Ludwig (1956), Ludwig and Fiore (1960), Urs and Hopkins (1973)
<i>Zophobas atratus</i>	12-13 ^l (11) ^c	Density, vsc	Group-rearing in late larval life	Quennedey et al. (1995)
Diptera				
Simuliidae				
<i>Simulium vittatum</i>	7-9 (11) ^c	Vsc		Colbo (1989)
Tabanidae				
<i>Tabanus lineola</i>	8-10	Sex, vsc	Females	Orminati and Hansens (1974)
<i>T. nipponicus</i>	5-7	Vsc		Matsumura (1995)
Hymenoptera ^m				
Argidae				
<i>Arge nigrinodosa</i>	5-7	Sex, density, vsc	Females, high density (20 larvae in group)	Adachi (1981)
<i>A. nipponensis</i>	5-7	Sex, density*sex, vsc	Females, high density (5-10 larvae in group) in females	Adachi (1981)
Megachilidae				
<i>Megachile rotundata</i>	4-5	Vsc		Whitfield et al. (1987)
Tenthredinidae				
<i>Nematus oligospilusⁿ</i>	5-7	Temperature, vsc	Extreme temperatures (11 and 29°C)	Charles and Allan (2000)
Lepidoptera				
Arctiidae				
<i>Apantesis phalerata</i>	6-8	Vsc		Bachelor and Habeck (1974)
<i>A. vittata</i> (<i>A. radians</i>)	6-7 (8) ^c	Sex, vsc	Females	Bachelor and Habeck (1974)
<i>Hyphantria cunea</i>	6-7	Inheritance, sex, food quality, vsc	Progeny of bivoltine population, Progeny of one (southern) of the trivoltine populations, females, leaves of <i>Populus nigra</i>	Gomi (1996), Gomi et al. (2003, 2005)
<i>Pyrharctia isabella</i>	7-12	Photoperiod, vsc	Long daylength (15-17-h light)	Goettel and Philogène (1978, 1979)
<i>Spilosoma lubricipedum</i>	6-7	Vsc		Esperk and Tammaru (unpublished)
Bombycidae				
<i>Bombyx mori</i>	5-6	Diet quantity, diet quality, vsc	Transient starvation, diet containing low proportion of nutritional components at first instar	Kellogg and Bell (1903), Kato and Sumimoto (1968)
Cossidae				
<i>Prionoxystus robiniae</i>	8-12 ^c (13, 15) ^c , 14-30 ^b (31) ^c	Inheritance/temperature, sex, vsc	Progeny of one (semivoltine) female in lower temperature (22-30°C), females	Solomon (1973)
Crambidae				
<i>Chilo partellus</i>	6-7 ^d	Food quantity, food quantity*sex, food quantity*vsc (variation only in starvation)	Transient starvation, females (in starvation treatment)	Kfir (1991), Ochieng'-Odero et al. (1994)
<i>Crambus teterrellus</i>	7-9 (10) ^c	Vsc		Ainslie (1930)
<i>Diatraea grandiosella</i>	5-6 ^d	Sex, photoperiod*temperature (larval diapause), vsc	Females, short daylength (≤ 12 -h light) and low temperature ($< 20^\circ\text{C}$) at early instars (diapaused larvae)	Jacob and Chippendale (1971), Chippendale and Yin (1973)

(continued)

Table 1. Continued

Taxa	Instar range	Factors influencing no. of instars	More instars (higher mean instar no.) in	Reference
<i>D. lineolata</i>	5-7	Sex*temperature, vsc	Females in extreme temperatures (22 and 30°C)	Rodríguez-del-Bosque et al. (1989)
<i>D. saccharalis</i>	5-7	Sex, vsc	Females, vsc	Roe et al. (1982)
Gelechiidae <i>Pectinophora gossypiella</i>	4-5	Vsc		Watson and Johnson (1974)
Geometridae <i>Ennomos subsignaria</i>	5-6	Vsc		Drooz (1965)
<i>Selenia tetralunaria</i>	4-5	Photoperiod, vsc	Short daylength (12-h light)	Tammaru et al. (unpublished data)
Gracillariidae <i>Marmara gulosa</i>	4-6 ^p	Vsc		Guillén and Heraty (2004)
Lasiocampidae <i>Malacosoma disstria</i>	5-8	Food quality, inheritance	Mature leaves, progeny of certain individuals	Jones and Despland (2006)
<i>Streblote panda</i>	5-7	Sex, food quality, vsc	Females, certain host plant (<i>Vaccinium</i>) cultivars	Calvo and Molina (2004)
Lycaenidae <i>Lycaena hippothoe</i>	4-5	Temperature, temperature*sex, vsc	Low temperature (15-20°C), males (in low temperature)	Fischer and Fiedler (2001)
<i>Lycaena phlaeas</i>	4-5	Photoperiod*temperature (at oviposition and during larval period), vsc	Short daylength (<11-h light) and low temperature (<20°C) at oviposition (egg stage) or in larval stage (larval diapause)	Endo et al. (1985), Ballmer and Pratt (1989)
<i>Paralucia aurifera</i>	5-7	Ant-tending, vsc	Larvae not tended by ants	Cushman et al. (1994)
Lymantriidae <i>Lymantria dispar</i> (<i>Porthetria dispar</i>)	4-8	Sex, inheritance, food quantity, density, temperature, vsc	Females, transient starvation (only at first instar), larvae reared in groups, low temperature (18.5°C)	Leonard (1966, 1968, 1970a, 1970b); Nagasawa (1988); Esperk and Tammaru (2006)
<i>Orgyia antiqua</i>	4-7	Sex, food quality, food quantity, vsc	Females, poor quality diet (mature leaves), transient starvation	Esperk and Tammaru (2006, unpublished data)
<i>O. pseudotsugata</i>	4-6	Sex, vsc	Females	Beckwith (1976)
Noctuidae <i>Agrotis ipsilon</i>	6-9	Food quality, humidity, temperature, vsc	Certain diet treatment (leaves of <i>Zea mays</i>), low humidity (40-60% RH), extreme temperatures (13 and 34°C)	Archer et al. (1980), Santos and Shields (1998)
<i>A. orthogonia</i>	6-7	Food quantity, vsc	Transient starvation	McGinnis and Kasting (1959), Byers (1992)
<i>Anomis flava</i>	5-6	Vsc		Essien and Odebiyi (1991)
<i>Anticarsia gemmatilis</i>	5-10	Food quality, vsc	Certain host species (<i>Lespedeza stipulacea</i> , <i>Phaseolus vulgaris</i>)	Conti and Wadill (1982), Waters and Barfield (1989)
<i>Autographa gamma</i> (<i>Plusia gamma</i>)	5-7	Vsc		Long (1953)
<i>Bellura gortynoides</i>	6-7 (9) ^c	Vsc		Levine and Chandler (1976)
<i>Copitarsia decolora</i>	4-7	Food quality, temperature, food quality*temperature, vsc	Certain diet treatment (stem of <i>Asparagus</i> sp.), low temperature (10-20°C), high temperature (30°C only in <i>Asparagus</i> diet)	Gould et al. (2005)
<i>Euxoa auxiliaris</i>	6-7	Vsc		Byers (1992)
<i>E. messoria</i>	6-8	Vsc		Cheng (1973)
<i>Heliothis armigera</i> (<i>Helicoverpa armigera</i>)	5-7	Food quality, vsc	Certain diet treatment (leaves of <i>Lycopersicon esculentum</i>)	Casimero et al. (2000)
<i>H. cirescens</i>	5-6	Vsc		Gunaseena et al. (1989)
<i>Lacanobia oleracea</i> (<i>Diataraxia oleracea</i>)	6-7 (8) ^c	Vsc		Long (1953)
<i>Mythimna separata</i> (<i>Leucania separata</i>)	6-7	Vsc		Tateishi et al. (1988)
<i>Pseudopulsia includens</i>	5-7	Food quality (host species), vsc	Certain host species (<i>Pueraria montana</i>)	Strand (1990), Kidd and Orr (2001)
<i>Pyrria exprimens</i>	5-6 (7) ^c	Vsc		Hardwick (1970)
<i>Sesamia nonagrioides</i>	6-7 ⁱ , 8-15 ^j	Photoperiod (larval diapause), vsc	Diapaused larvae at short daylength (\leq 12-h light)	Fantinou et al. (1996), Gadenne et al. (1997)
<i>Simyra henrici</i>	7-8	Vsc		Decker and Maddox (1971)
<i>Spodoptera frugiperda</i>	5-9	Food quality, temperature, food quality*temperature, vsc	Certain host species (<i>Cyperus esculentus</i> , <i>Gossypium</i> sp.), low temperature (17°C), certain host species at low temperature (17-21°C)	Pencoe and Martin (1981, 1982), Ali et al. (1990)

(continued)

Table 1. Continued

Taxa	Instar range	Factors influencing no. of instars	More instars (higher mean instar no.) in	Reference
<i>S. littoralis</i>	5-7	Vsc		Duodu and Biney (1981), Hegazi et al. (1988)
<i>S. litura</i>	6-8	Food quality, density, inheritance, density*inheritance, vsc	Transient starvation (in early instars), high density (≥ 20 larvae in group), progeny of group-reared parents	Morita and Tojo (1985)
<i>Trichoplusia ni</i>	5-6	Inheritance, vsc	Progeny of 6-instar type individuals	Jones et al. (1981)
<i>Xestia c-nigrum</i> (<i>Amathes c-nigrum</i>)	5-7 ⁱ , 7-8 ^j	Photoperiod (larval diapause), sex, vsc	Short daylength (8-h light) in early instars (inducing diapause), females	Honěk (1979)
Notodontidae				
<i>Syntypistis punctatella</i> (<i>Quadricalcarifera punctatella</i>)	4-5	Rainfall in early instars (diet quantity), temperature, vsc	Continuous rainfall during 1st instar (transient starvation), high temperature (20-25°C)	Kamata and Igarashi (1994, 1995)
Nymphalidae				
<i>Acraea acerata</i>	5-7	Vsc		Anioke et al. (1995)
<i>Coenonympha pamphilus</i>	4-5	Photoperiod (larval diapause), vsc	Short daylength (13-14-h light), diapaused larvae	García-Barros (2006)
<i>Mycalesis sirius</i>	5-6	Vsc		Braby and Jones (1994)
<i>Pararge aegeria</i>	4-5	Sex, temperature, vsc	Females, low temperature (12-20°C)	Shreeve (1986)
<i>Sasakia charonda</i>	5-6	Photoperiod, photoperiod*vsc (variation only in long daylength conditions (16-h light))	Short daylength (12-14-h light)	Kato (1989)
Pieridae				
<i>Pieris brassicae</i>	4-6	Temperature	Low temperature ($\leq 15^\circ\text{C}$)	Klein (1932)
Pyralidae				
<i>Argyroactis subornata</i>	5-6	Vsc		Forno (1983)
<i>Corcyra cephalonica</i>	6-12 (13; 15) ^c	Sex, humidity	Females, low humidity (10%-30% RH)	Russell et al. (1980)
<i>Galleria mellonella</i>	7-9 ^d	Food quality, temperature, vsc	Temporal exposure to low temperature (0°C for >1/2h) or protein-free diet	Allegret (1964), Cymborowski and Boguś (1976), Pipa (1976)
<i>Herpetogramma licarsisalis</i>	5-6	Temperature, temperature*vsc (no variation at highest temperature 25°C)	Low temperature (15°C)	Jensen and Cameron (2004)
<i>Hypsipyla robusta</i>	5-6	Vsc		Atuahene and Souto (1983)
<i>Samea multiplicalis</i>	5-6	Food quality (nitrogen content) in early instars, vsc	Diet of low nitrogen content (<1.35%) in 1st and 2nd instar	Taylor (1984)
Sphingidae				
<i>Manduca sexta</i>	5-7	Food quantity, food quantity*vsc (variation only in starvation treatment)	Transient starvation	Nijhout (1975), Jones et al. (1980)
Tineidae				
<i>Tineola bisselliella</i>	5-16 ^d	Food quality, sex, vsc	Diet containing low proportion of nutritional components, females	Titschack (1926)
Tortricidae				
<i>Acleris minuta</i>	5-7	Temperature, food quality, vsc	Low (15-17°C) and high (27°C) temperature, certain host plant (<i>Malus domestica</i>) cultivars	Weatherby and Hart (1986)
<i>Adoxophyes orana</i>	5-6	Food quality, temperature	Artificial diet, low temperature (14-17°C)	Milonas and Savopoulou-Soultani (2000)
<i>Argyrotaenia spheralepta</i>	5-7	Food quality, vsc	Certain host plant (<i>Vitis vinifera</i>)	Bentancourt et al. (2003)
<i>Bactra verutana</i>	4-6	Food quality, vsc	Artificial diet	Frick and Wilson (1978)
<i>Bonagota cranaoides</i>	5-7	Food quality, food quality*sex, vsc	Certain host plant (<i>Vitis vinifera</i>), mature leaves, females (in 4 from 5 diet treatments)	Bentancourt et al. (2004)
<i>Choristoneura fumiferana</i>	5-7	Vsc		Schmidt and Lauer (1977)
<i>C. occidentalis</i>	5-7 (8) ^c	Diet quality, diet quality*sex, vsc	Certain diet treatment (<i>Pseudotsuga menziesii</i>), females (only in artificial diet)	Schmidt and Lauer (1977)
<i>C. retiniana</i> (<i>C. viridis</i>)	6-8	Sex, vsc	Females	Schmidt and Lauer (1977), Schmidt et al. (1977)

(continued)

Table 1. Continued

Taxa	Instar range	Factors influencing no. of instars	More instars (higher mean instar no.) in	Reference
<i>Ctenopseustis obliquana</i>	5-6	Sex, vsc	Females	Clare and Singh (1988)
<i>Platynota idaeusalis</i>	5-6 ^f , 6-13 ^g	Photoperiod (larval diapause), photoperiod*temperature, vsc	Short daylength (10-14-h light), low temperature (16-21°C) at short daylength	Rock and Shaffer (1983), Shaffer and Rock (1983)
<i>P. stultana</i>	5-6 (♀) ^a	Sex, sex*temperature, sex*vsc	Females, low temperature (15°C), low and high temperatures (15-20°C and 30-35°C)	Zenner-Polania and Helgesen (1973)
Zygaenidae <i>Harrisina brillians</i>	4-5	Temperature, vsc	Low temperature (18-23°C)	Roltsch et al. (1990)
Raphidioptera Raphidiidae <i>Raphidia bicolor</i>	10-11	Vsc		Kovarik et al. (1991)

The number of instars is presented as the total range across different treatments and case studies. Only data for individuals that survived to pupal/adult stage are presented. Factors affecting instar number are presented only when the respective difference in instar number was reported to be significant in original studies or when difference between treatments was at least 0.2 instars (see Materials and Methods for details). Species in which instar number differs between sexes with no variation within sexes are not presented. The classification of insects is based on the Tree of Life Web Project (<http://tolweb.org>).

^a Variation in instar number occurred only in particular sex.

^b Vsc, variation within standardized rearing conditions.

^c Only one individual developed through particular number of instars.

^d Includes both genetical inheritance and maternal effects.

^e If the name used in the original paper differs from the current usage, the former is given in the parentheses.

^f Instar number is given without the nonfeeding pronymphal stage.

^g Univoltine development.

^h Semivoltine development.

ⁱ Directly developing individuals.

^j Individuals having larval diapause.

^k Larvae had undetermined number of additional molts when exposed to continuous starvation.

^l Larvae had undetermined number of additional molts when reared in group.

^m Instar number is given without nonfeeding prepupal (eonymph) stage.

ⁿ Studied population consisted only (thelytokous) females.

^o Diapaused larvae may go through several additional molts.

^p Instar number is given without nonfeeding larval instars.

^q Larvae had undetermined number of additional molts when exposed to low-quality diet.

influence of these factors is expected to be mediated via environmental quality and their different levels could be often classified as representing favorable or adverse conditions (discussed in more detail below).

Temperature can influence the number of instars in different ways. Some species tend to have more instars when reared under low temperatures; others do so in high temperatures, whereas sometimes both extremes increase the number of instars (Table 1). Although temperature can affect instar number by changing the quality of environment, it also can have an indirect influence to the number of instars serving as a cue for the duration of the favorable season (e.g., Adachi 1994). For example, low temperature combined with short photoperiod is often used as a cue for an upcoming unfavorable season and induces slow development together with additional instars in several species (Chippendale and Yin 1973, Rock and Shaffer 1983, Ballmer and Pratt 1989, Shintani and Ishikawa 1997).

Photoperiod is commonly used by temperate insects as a cue to estimate calendar date and thereby the time available for development (Beck 1980, Tauber et al. 1986). However, in some rare cases, photoperiod may directly affect the quality of environment and thereby instar number. For example, increased daylength may influence larval develop-

ment in night-active species by decreasing the time available for feeding and thereby causing starvation and increasing the number of instars (Goettel and Philogène 1978). Although, in several cases instar number tends to be higher when larvae are exposed to short-day conditions, the opposite is true for other species (Table 1). It has been proposed that short-day conditions, often in concert with low temperature, accelerate the growth of univoltine insects, but they slow the growth of multivoltine species (Shaffer and Rock 1983). In support of this hypothesis, all three species that showed increased number of instars, and prolonged larval period when exposed to long daylength, were univoltine (Goettel and Philogène 1978, Tanaka 1979, Tanaka and Brookes 1983). Because insects are usually capable of surviving the unfavorable season only in a certain developmental stage, slowing down the larval development in long daylength conditions, or accelerating growth under short daylength, is likely an adaptation for insects in univoltine populations, allowing them not to reach the hibernating stage too early or too late (Goettel and Philogène 1978). Consistently, additional instars in short daylength conditions often seem to be an adaptation enabling individuals to stay in the larval stage in those species that hibernate as a larva. These extra instars may be inserted under the diapause-inducing condi-

Table 2. Comparison of mean instar number in treatments with different quality (see text for explanation)

Species	Order	Treatments				Adverse n	Instars	Indicators of treatment quality	Reference
		Treatment with more instars		Favorable					
		n ^a	Instars ^b	n ^a	Instars ^b				
<i>Blattella germanica</i>	Dictyoptera	Adverse	Uninjured	Injured (amputation of legs)	73	6.4	c	Seamans and Woodruff (1939)	
<i>Diploptera punctata</i>	Dictyoptera	Favorable	Low density (reared singly)	High density (reared in groups)	136	3.2 (♂) ^d	Adult mass	Woodhead and Paulson (1983)	
<i>Leucophaea maderae</i>	Dictyoptera	Adverse	Uninjured	Injured (amputation of legs)	23	7.7	c	Willis et al. (1958)	
<i>Pycnoscelus surinamensis</i>	Dictyoptera	Adverse	Uninjured	Injured (amputation of legs)	37	8.9	c	Willis et al. (1958)	
<i>Chorthippus brunneus</i>	Orthoptera	Favorable	High-quality diet (ungrazed grass)	Low-quality diet (grazed grass)	≥10	4.0 (♀) ^e	Mass in earlier instars, adult mass	Hassall and Grayson (1987)	
		Favorable	Temperature 25°C	Temperature 35°C	14	4.0 (♀) ^e	Adult mass	Willott and Hassall (1998)	
<i>Melanoplus differentialis</i>	Orthoptera	Favorable	Low density (reared singly)	High density (reared in groups)	34	6.0	Adult hew ^f	Dingle and Haskell (1967)	
<i>Dermestes lardarius</i>	Coleoptera	Adverse	Humidity 80% RH (at 25°C)	Humidity 50% RH (at 25°C)	56	6.0	Mortality, adult mass	Fleming and Jacob (1986)	
<i>Monochamus carolinensis</i>	Coleoptera	Favorable	Temperature 25°C	Temperature 20°C	18	4.3	Hew in 3rd instar, final instar hew	Pershing and Linit (1988)	
<i>Orizaphilus surinamensis</i>	Coleoptera	Adverse	Humidity 70% RH (30°C)	Humidity 30% RH (30°C)	34	3.3	Mortality	Beckett and Evans (1994)	
<i>Psacotha hilaris</i>	Coleoptera	Favorable	Food ad libitum	Starvation from the 2nd day of 4th instar	27	4.6	Mortality, pupal mass	Munyiri et al. (2003)	
<i>Tenebrio molitor</i>	Coleoptera	Adverse	High humidity	Low humidity	27	12.2	Pupal mass	Urs and Hopkins (1973)	
<i>Agrotis ipsilon</i>	Lepidoptera	Adverse	Artificial diet	Leaves of <i>Zea mays</i>	360	6.0	Mortality, mass in earlier instars	Santos and Shields (1998)	
<i>Anitarsia gemmatilis</i>	Lepidoptera	Adverse	Leaves of <i>Glycine max</i>	Leaves of <i>Lespedeza stipulacea</i>	46	5.7	Mass in fifth instar, pupal mass	Waters and Barfield (1989)	
<i>Bombix mori</i>	Lepidoptera	Adverse	Food ad libitum	Temporal starvation	>200	5.0	Pupal mass	Kellogg and Bell (1903)	
<i>Bonagota cranaodes</i>	Lepidoptera	Adverse	Young leaves of <i>Morus domestica</i>	Mature leaves of <i>M. domestica</i>	>40	5.0	Pupal mass	Bentancourt et al. (2004)	
<i>Corejra cephalonica</i>	Lepidoptera	Adverse	Humidity 70% RH	Humidity 20% RH	21	6 (♂) ^g 7 (♀) ^g	Adult mass	Russell et al. (1980)	
<i>Heliothis armigera</i>	Lepidoptera	Adverse	Artificial diet	Leaves of <i>Lycopersicon esculentum</i>	85	5.2	Mortality, pupal mass	Casimero et al. (2000)	
<i>Hyphantria cunea</i>	Lepidoptera	Adverse	Artificial diet	Mature leaves of <i>Populus nigra</i>	73	6.0	Pupal mass	Gomi et al. (2005)	
<i>Lampantria dispar</i>	Lepidoptera	Adverse	Food ad libitum	Temporal starvation (in first instar)	141	5.1 (♂) 6.1 (♀)	c	Leonard (1970a)	
<i>Malacosoma disstria</i>	Lepidoptera	Adverse	Young leaves of <i>Populus tremuloides</i>	Mature leaves of <i>P. tremuloides</i>	28	5.8	Pupal mass	Jones and Despland (2006)	
<i>Manduca sexta</i>	Lepidoptera	Adverse	Food ad libitum	Temporal starvation at 3rd instar	>50	5.0	5th instar hew	Nijhout (1975)	
<i>Paralucia aurifera</i>	Lepidoptera	Adverse	Presence of ants	Absence of ants	19	5.5	Pupal mass	Cushman et al. (1994)	

(continued)

Table 2. Continued

	Lepidoptera	Adverse	Temperature 25°C	Temperature 5°C	59	5.2 (♀) ^e	Temperature 15°C	13	6.0 (♀) ^e	Mortality, hew in early instars	Zenner-Polania and Helgesen (1973)
<i>Platymota stultana</i>	Lepidoptera	Adverse	Leaves of <i>Glycine max</i>	Leaves of <i>Glycine max</i>	189	5.3	Leaves of <i>Pueraria montana</i>	123	6.8	Mortality, 4th instar mass, pupal mass	Kidd and Orr (2001)
<i>Pseudoplusia includans</i>	Lepidoptera	Adverse	Leaves of <i>Elysiine indica</i>	Leaves of <i>Elysiine indica</i>	20	6.0	Leaves of <i>Cyperus esculentus</i>	16	7.0	Mortality, pupal mass	Penceo and Martin (1982)
<i>Spodoptera frugiperda</i>	Lepidoptera	Adverse	Control (no rain)	Control (no rain)	12	4.0	Continuous rainfall in 1st instar (starvation)	28	5.0	Mortality, mass in the end of 1st instar	Kamata and Igarashi (1994)
<i>Syngrapha punctatella</i>	Lepidoptera	Adverse	Diet containing high proportion of nutritional components	Diet containing high proportion of nutritional components	19	7.5	Diet containing low proportion of nutritional components	11	10.6	Mortality, adult mass	Tischack (1996)

^a Number of individuals who reached to the pupal/adult stage.
^b Mean number of larval instars in particular treatment.
^c Injuries and starvation were a priori defined as adverse conditions.
^d Only males were considered as instar number was invariable in females.
^e Only females were considered as instar number was invariable in males.
^f Hew, Head capsule width.
^g Typical instar number in respective treatment.

tions before the actual diapause (e.g., Shintani and Ishikawa 1998) or even during the diapause (Chippendale and Yin 1973, Honěk 1979, Kfir 1991). However, especially in the latter case, stationary and/or regressive molts are usually involved.

Some multivoltine species may omit an instar in long daylength conditions, thereby shortening their developmental time at the cost of reduced size at maturation. The adaptive explanation for this may be the resulting opportunity to develop an additional generation in the current year. As a result, a “saw-tooth” pattern of generation length may occur: the generation time increases with the increasing of the favorable season until the point when an additional generation becomes possible. Then, with increased voltinism, generation length decreases abruptly and starts to increase again with continuing prolongation of the favorable season (Roff 1983). In the arctiid moth *Hyphantria cunea* (Drury), the incidence of the additional instar was higher, and developmental time was longer in larvae from a bivoltine population compared with those of a trivoltine population even when larvae were reared under the same environmental conditions (Gomi 1996). Moreover, when larvae from two trivoltine populations were reared under the same conditions, insects from the more southern population had more often an additional instar and a longer developmental time (Gomi et al. 2003), perhaps because in the field they have more time available for the three generations. In the geometrid moth *Selenia tetralumaria* (Hufnagel), two seasonal morphs exist that usually go through a different number of instars. The summer morph is induced when larvae are reared under long-day conditions, where it tends to omit an instar compared with the spring morph and it has a shorter larval period (Mikkola et al. 1989, T.T. et al., unpublished data).

Rearing density has been observed to affect the instar number in several grasshopper species (Orthoptera) but also in a few species of roaches (Dictyoptera), beetles (Coleoptera), sawflies (Hymenoptera), and noctuids (Lepidoptera) (Table 1). In orthopterans, and some noctuids, rearing density induces morphologically and behaviorally different morphs called the solitary phase (individually reared larvae) and the gregarious phase (larvae reared in groups), respectively (for review, see Pener 1991). One of the specific characters of the solitary phase of Orthoptera is a higher number of larval instars; the same has been proposed for some polyphenic noctuids (Long 1953). In contrast, in insects other than Orthoptera, high rearing density tends to increase the number of instars (Leonard 1968, Adachi 1981, Morita and Tojo 1985). It has been proposed, however, that at least in some cases, shortage of food (i.e., transient starvation) accompanied by the high rearing density rather than rearing density itself may influence the number of instars (Morita and Tojo 1985). Larvae of the tenebrionid beetle *Zophobas atratus* (F.) may have an undetermined number of instars, and they are not able to pupate when reared in crowded conditions (Quennedey et al. 1995). Although these larvae may

achieve body masses of twice of that of normal larvae, they often go through stationary and/or regressive molts.

Of other, more unconventional environmental factors, the larvae of a notodontid moth have an additional instar when exposed to artificial rainfall (Kamata and Igarashi 1994). However, transient starvation rather than direct influence of rain seems to affect instar number in the latter case, because the larvae tend to hide, and they do not feed when it is raining. In some species, an undetermined number of regressive molts may occur when larvae are deprived of food (Beck 1971) or reared on a poor-quality diet (Titschack 1926). The adaptive function of negative growth of linear measurements during the molts is proposed to be an increase in surviving probability under long-lasting adverse conditions, by means of reduced requirement of energy and water (Beck 1973, Kfir 1991). Moreover, as a highly specific example, the aquatic larvae of the mayfly *Cloeodes hydatation* (McCafferty and Lugo-Ortiz) always have a stationary molt when they are taken out of water and then rehydrated (Nolte et al. 1996). The authors propose that this kind of desiccation-induced molting may serve the purpose of replacing the old cuticle, deformed by drying.

Of factors other than environmental factors, inheritance and sex most commonly affect instar number (Table 1). With very few exceptions, if instar number is sexually dimorphic, females tend to have a higher number of instars than males (discussed in Esperk et al. 2007). The inherited factors affecting instar number may be either genetical or achieved via maternal effects, which in turn may depend on environmental conditions experienced by a parent. Instar number may be genetically different in larvae from different populations (Nagasawa 1988, Telfer and Hassall 1999, Mira and Raubenheimer 2002), between genetically determined phenotypes (Hodson and Chapco 1986), or between the offspring of different individuals from the same population (Jones et al. 1981, Morita and Tojo 1985). Additionally, instar number may differ genetically between subspecies (Byers and Lafontaine 1982), or between long- and short-winged individuals (McCafferty and Page 1978, Westermann 1993). Environmental conditions during the larval period of parents or at the time of oviposition may influence instar number of progeny via maternal effects. Nymphs of locusts *Nomadacris septemfasciata* (Serville) and *S. gregaria* tended to have more instars when their parents had been reared in isolation during nymphal period (Albrecht and Blackith 1957, Injeyan and Tobe 1981). In contrast, larvae of the moth *Spodoptera litura* (F.) had more instars when their parents were reared in crowded conditions (Morita and Tojo 1985). In the butterfly *Lycaena phlaeas* (L.), there were generally four instars when larvae developed from eggs laid in long-day and high-temperature conditions, whereas the majority of larvae developing from eggs laid in short-day and low-temperature conditions underwent five instars (Ballmer and Pratt 1989). Larvae of the gypsy moth developing from the

last laid, smaller eggs of particular females tended to have more instars (Leonard 1970b).

There are some further, specific factors that may influence the instar number. In some social insects, termites in particular, the larvae belonging to different castes may have a different number of larval instars (Roisin 2000). In a lycaenid butterfly, which lives in association with ants (myrmecophily), larvae tend to go through more instars and achieve lower pupal weights when ants are not present (Cushman et al. 1994). Because larvae not tended by ants spent less time feeding, the original authors propose that low amount of food consumed may still form the proximate cause of the increased number of instars.

Although several factors may determine the number of instars in isolation, complicated interactions between various factors influencing instar number also may occur. For example, in some species, environmental factors influence instar number in one sex only (Shepard et al. 1973, Woodhead and Paulson 1983, Hassall and Grayson 1987, Zhu and Tanaka 2004) and/or only in some populations or genetic lines (Urs and Hopkins 1973, Hassall and Grayson 1987, Shintani and Ishikawa 1997). Interactions between different environmental factors in affecting intraspecific number of instars are not rare either (Partida and Strong 1975, Rock and Shaffer 1983, Endo et al. 1985, Ali et al. 1990).

Interestingly, in most species exhibiting intraspecific variability in the number of instars, some variation also occurs in standardized rearing conditions (Table 1). This trend may indicate that if the potential for variability has once evolved, instar number remains highly plastic at the intraspecific level. There seems to be a general tendency, however, that when reared under similar conditions, larvae that are initially smaller tend to go through a higher number of instars (T.E., unpublished data).

More Instars under Favorable or under Adverse Conditions?

It has been proposed that, in insects, there is a certain species-specific threshold size that larvae have to achieve to be able to initiate metamorphosis (Nijhout 1975, 1994). Accordingly, additional larval instars should serve as a compensatory mechanism in adverse conditions when the larvae fail to reach the threshold size by a "normal" number of instars (Nijhout 1994). However, an alternative plausible scenario would be to have more instars under circumstances when growth rates are high (e.g., under exceptionally favorable environmental conditions), to take the advantage of the possibility to attain large size at relatively low cost (in terms of lower cumulative mortality). Body size, in turn, has often been shown to correlate positively with various components of fitness (Honěk 1993, Blanckenhorn 2000, Rhainds and Ho 2002, Tammaru et al. 2002).

Comparisons of favorable and adverse conditions with a significant difference in instar number (see Materials and Methods for details) were available for

27 species. Sixteen of these species represented the order Lepidoptera; the rest were divided between Dictyoptera, Orthoptera, and Coleoptera (Table 2). Factors such as injuries, diet quantity and quality, humidity, temperature, rearing density, intensity of rainfall, and presence or absence of ants produced environments of different quality, with differences in instar number. In 22 species (including all the lepidopterans), a higher number of instars had been observed in adverse conditions (Table 2). This result indicates that, in most cases, the compensation scenario is likely to hold true. Moreover, many more studies suggested that the number of instars is higher in adverse conditions; unfortunately, these reports did not completely meet our qualification criteria (see above).

In five species, however, larvae tended to develop through a higher number of instars in favorable conditions (Table 2). In particular, female nymphs of one of the two populations of the grasshopper *Chorthippus brunneus* (Thunberg) were heavier already in earlier instars when reared on high-quality diet, but they added an instar compared with nymphs reared on low-quality diet, and achieved a 1.8 times higher adult body mass as a consequence (Hassall and Grayson 1987). As an additional indication of a higher number of instars in favorable conditions, females of this species tend to have an additional instar more frequently under high (favorable) temperatures, and to achieve higher body mass thereby (Willott and Hassall 1998). However, the compensation scenario seems to be involved to some extent even in this species, because females that are smaller at hatching tend to have the additional instar more frequently (Grant et al. 1993). Larvae of the cerambycid beetle *Psacotheta hilaris* (Pascoe) had four instars when exposed to starvation treatments, whereas in the control group (food ad libitum), only 40% of the larvae had four, whereas 60% had five, instars (Munyiri et al. 2003). However, the interpretation of the original authors is that instead of having an additional instar in favorable conditions, larvae of this species rather omit an instar and pupate prematurely at the cost of smaller final size when the food supply is limited. These authors further discuss that because the larvae of this beetle do not move from one host individual to another, it is highly adaptive for them to complete development prematurely when resources become exhausted. In another cerambycid beetle, *Monochamus carolinensis* (Olivier), larvae in the higher temperature treatment were larger already earlier in life, had additional instar more often and achieved larger final body size than those reared under lower temperature (Pershing and Linit 1988). Nymphs of the grasshopper *Melanoplus differentialis* (Thomas) (Dingle and Haskell 1967), and male nymphs of the roach *Diploptera punctata* (Eschscholtz) (Woodhead and Paulson 1983) tend to have more instars and achieve larger adult size when isolated compared with group-reared larvae (Table 2). However, because of the frequently observed specific influence of rearing density on larval development (Pener 1991, Tammaru et al. 2000), these two cases

may not represent the "classical" comparisons of good and adverse conditions. With the exception of such often unequivocal effects of rearing density, there was hardly any indirect evidence of the opportunistic scenario, i.e., no "nonqualifying" studies suggesting that larvae might be likely to go through more instars in favorable conditions.

It can be preliminarily concluded that in most insect species, higher instar number is related to adverse conditions, and instar number is most likely adaptively explained by the compensation scenario. However, this possibility is not the only possibility: at least in some species, the larvae tend to have a higher number of instars in favorable conditions.

Conclusions

Intraspecific variability in the number of larval instars is a widespread phenomenon across insect taxa; it has been documented for >100 species, spread across most major insect orders, both hemimetabolous and holometabolous (Table 1). In most species, instar number varies only over a limited range, although remarkable exceptions exist. However, in most insects, instar number may still be considered at least effectively invariable. There are several examples of well-studied insect species in which the number of instars is never observed to vary, and even if rare exceptions can never be entirely ruled out, variation in instar number can be safely ignored in, for example, life history models of such species.

Various factors have been shown to affect the number of instars. In particular, temperature, photoperiod, food quantity and quality, humidity, injuries, inheritance, and sex are the most common factors influencing instar number (Table 1). Interestingly, in most species that show variability in the number of larval instars, some variability in instar number between conspecifics tends to be invariably present, even within standardized rearing conditions. It follows that although perhaps in most insect species the number of instars is rigidly determined, it remains highly plastic in those species in which variability in instar number has evolved.

Typically, instar number tends to increase under adverse rather than favorable conditions (Table 2). This conclusion is consistent with the compensation scenario, according to which additional instars are inserted in poor conditions when larvae fail to reach a species-specific threshold-size with the "normal" instar number. However, there are exceptions, as in some species instar number tends to increase in favorable conditions. Nevertheless, it seems as insertion of extra instars is not the typical expected response to relaxed time stress, e.g., not the primary proximate mechanism causing latitudinal variation in insect size, as envisaged by Roff (1983) (p. 258).

In many cases, plasticity in instar number is also used as a mechanism ensuring that the developmental stage capable of surviving the unfavorable season is reached at the right time of the year. Stationary molts, in which linear measurements of the larvae do not

increase at molting, are often involved. Some multivoltine species tend to omit an instar to be able to have an extra generation in a particular year. Regressive additional molts (negative growth of linear measurements) occur in some species and are expected to increase the probability of survival in highly adverse conditions (e.g., continuous starvation).

Acknowledgments

We thank John Trumble for kindly inviting this review to the *Journal of Economic Entomology*. We also thank Dmitry L. Musolin, Enrique García-Barros, J. Daniel Hare, Scott Costa, Gaétan Moreau, Robert G. Breene, Kathleen A. Kidd, and Mohsen M. Ramadan for fruitful discussions as well as Vitali Ivanov for technical assistance. The study was supported by Estonian Science Foundation grant 5746, Estonian National Scholarship Programme 'Kristjan Jaak' to T.E. and grants from the Swedish Research Council to S.N.

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Received 9 October 2006; accepted 11 February 2007.