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Ecology of dormancy in ladybird beetles (Coleoptera: Coccinellidae)

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Abstract. When environmental conditions become unfavourable most invertebrates enter into a state of reduced activity called dormancy. In ladybird beetles dormancy usually occurs in the adult stage and in many species takes up most of their lifespan. In this review, some ecological and behavioural issues related to dormancy, such as habitat selection, migration to dormancy sites, aggregation, mortality, phenology and species composition of aggregations of ladybirds in hibernation are discussed. The habit of migrating to and hibernating in high mountains is characteristic of many ladybirds and is here discussed in detail with its advantages and disadvantages highlighted. The latter include the high energy cost of migrating to and dispersing from mountain sites, high mortality often recorded in ladybird aggregations on mountain tops and phenological shifts that result in a considerable curtailment of the periods suitable for reproduction, development and accumulation of metabolic reserves compared to those of ladybirds that enter dormancy in the lowlands. Knowledge of the dormancy ecology of Coccinellidae largely relies on studies of a few species, such as *Coccinella septempunctata* Linnaeus, 1758, *Ceratomegilla undecimnotata* (Schneider, 1792) and *Hippodamia convergens* Guérin-Méneville, 1842. It is postulated that investigating other species, especially those that are more ecologically specialized, will reveal more dormancy-related strategies and provide a better insight into ladybird ecology. It is also emphasized that the use of a community approach when studying ladybird dormancy will provide valuable information, both in terms of basic knowledge and its applications (e.g. pest management, conservation of rare species).

Key words. Coccinellidae, aestivation, hibernation, aestivo-hibernation, dormancy, diapause, quiescence, migration, aggregation, mortality, phenology.

INTRODUCTION

Most terrestrial organisms experience environmental conditions that alternate between favourable and unfavourable over the course of a year. Such seasonality is especially well expressed in temperate and polar climatic zones, but also occurs in the subtropics and tropics (Wolda 1988). At high latitudes seasonality is mainly shaped by changes in temperature (cold and warm seasons), while close to the equator water availability is a principal factor (dry and rainy seasons). In some areas in the temperate zone (e.g. those with a continental climate), both factors are important and two seasons with harsh conditions can be distinguished within a year: cold winter and a hot and dry summer.

The majority of invertebrates spend periods of unfavourable conditions in a relatively inactive state called dormancy, which is characterized by low developmental and metabolic activity (Danks 1987, Košťál 2006, Belozerov 2009). Based on the period of the year in which an organism remains inactive, dormancy can be categorized as hibernation (during the cold season), aestivation (during the hot and/or dry season) or aestivo-hibernation (bridging these two periods by one prolonged period of inactivity). On the other hand, two categories of dormancy can be distinguished depending on the mechanisms involved in its regulation: quiescence, which is directly induced by the onset of adverse conditions and terminated when conditions improve, and diapause that is a genetically programmed and an endogenously regulated phase in the life cycle (Danks 1987, Koštál 2006, Belozerov 2009). According to Belozerov (2009), the former category can be further divided into stage-independent, stage-specific and post-diapause quiescence.

Ladybirds are a group of insects in which diapause and non-diapause dormancy and the physiological mechanisms regulating them have been studied over a long period of time, dating back to the pioneering concepts of Theodosius Dobzhansky (Dobrzhanskii 1922a, b). Knowledge of ladybird dormancy, in particular the ecophysiology of diapause and quiescence, is well reviewed in the chapter, diapause/dormancy, in the recently published *Ecology and Behaviour of the Ladybird Beetles* (Hodek 2012a) and in the respective chapters of earlier versions of this book (Hodek 1973, 1996). Although the physiology of dormancy in ladybirds is well studied, it is not always easy to determine whether in particular cases one is dealing with diapause or quiescence. Perhaps the most common pattern of dormancy includes diapause, which in a later phase switches to post-diapause quiescence. However, different patterns can be observed even within the same species. For example, central and western European populations of *Coccinella septempunctata* Linnaeus, 1758 enter hibernation diapause and that changes to post-diapause quiescence around December–January (Hodek 2012a, b), in some more southern areas (e.g. Greece or central Turkey) aestivo-hibernation occurs (Bodenheimer 1943, Katsoyannos et al. 1997), again with a sequence of diapause and post-diapause quiescence, while in bivoltine populations of the subspecies *C. septempunctata brucki* Mulsant, 1842 in central Japan the first generation enters summer diapause and the second generation winter quiescence (Sakurai et al. 1986). Sakuratani (1988) reports that in the mild climate of southern Honshu winter quiescence of *C. septempunctata brucki* can occur at any developmental stage (adult, pupa, larva or egg), i.e. according to Belozerov (2009) it should be classified as stage-independent quiescence.

In this review I focus on some behavioural and ecological aspects of ladybird dormancy, such as selection of habitat for dormancy, mortality during dormancy and assemblages of dormant ladybirds. I do not go deeply into physiological mechanisms as they are sufficiently discussed by Hodek (2012a). I also avoid distinguishing between diapause and quiescence and use the general term ‘dormancy’, because in many cases we cannot say with certainty whether they are in diapause or quiescent.

DEVELOPMENTAL STAGES OF DORMANT LADYBIRDS

Generally, ladybirds spend periods of dormancy as adult beetles (Hodek 2012b). There are, however, a few exceptions. The European *Scymnus impexus* Mulsant and Chinese *S. camptodromus* Yu & Liu aestivo-hibernate in the egg stage (Delucchi 1954, Keena et al. 2012). It is suggested that this serves to synchronize egg hatching in these ladybirds with that of their adelgid prey. The North American *Coccidophilus marginata* (LeConte), a predator of the pine needle scale (*Chionaspis pinifoliae* (Fitch)), is reported to overwinter as a third instar larva beneath female scales (Martel & Sharma 1970). Possibly the juvenile stages of other predatory ladybirds also use dormancy as a means of synchronizing their activity with that of their prey, e.g. with aphids that hatch from overwintering eggs in spring. The Euro-Siberian *Scymnus abietis* (Paykull), for example, is suspected of overwintering as a larva as fourth instar larvae of this species can occur very early in spring (Nedvěd & Honěk 2012). In the phytophagous *Epilachna admirabilis* Crotch in eastern Asia and Japan both larvae and adults hibernate. As a rule, this species overwinters as a fully grown larva (prepupa), but some hibernate as adults in their second year (Katakura 1976, Hoshikawa 1980, 1981). In California, *Hyperaspis lateralis* Mulsant is reported to overwinter either as a pupa or adult (Hagen 1962) and, as mentioned earlier, in southern Honshu (Japan) any developmental stage of *C. septempunctata brucki* can overwinter in a state of quiescence (Sakuratani 1988). Accepting that it is exceptional for the juvenile stages of ladybirds to become dormant, the rest of this paper will be restricted to a discussion of various aspects of imaginal dormancy.

DORMANCY HABITATS

Most species of ladybirds, or at least most of those that have been studied in detail, are highly mobile, showing several kinds of flight behaviour (Hodek et al. 1993). Some species, however, are known to complete their whole life cycle in a specific habitat or at most in a few neighbouring habitats (e.g. crop fields and their grassy boundaries). Such sedentary behaviour is sometimes associated with a reduction in the size of the membranous wings (aptery or brachyptery) and, hence, an inability to fly, as in all species of the genus *Tetrabrachys* (Kapur 1948, Pope 1977) and the European phytophagous ladybird, *Cynegetis impunctata* (Pope 1977, Kalushkov et al. 2013). Two European species of the genus *Rhyzobius*, *R. litura* and *R. chrysomeloides*, are also relatively sedentary and predominantly brachypterous (Bielawski 1955, Pope 1977). The former lives in well insolated open habitats and spends periods in dormancy in dry grass in these habitats (Bielawski 1955, Ricci 1986), whereas *R. chrysomeloides* inhabits crowns of coniferous (usually Scots pine) trees during its active life and in autumn hibernates under the bark at the bases of these trees (Bielawski 1955). Interestingly, many other conifer specialists (*Myrrha octodecimguttata*, *Aphidecta obliterata*, *Harmonia quadripunctata*, *Scymnus suturalis*), although having fully developed second pair of wings, usually do not leave their feeding and breeding sites and like *R. chrysomeloides* overwinter under the bark of their host plants (Bielawski 1961, Pulliainen 1966, Spitzer et al. 2010, Hodek 2012a). Another ladybird with functional wings that is rather sedentary is *Tytthaspis sedecimpunctata*. This polyphagous species remains in dry grassland throughout the year (Bielawski 1961).

Many ladybirds spend periods in dormancy in habitats different from those utilized for reproduction and development (Hodek 2012a). Breeding and dormancy habitats may be close to each other, as e.g. in *Coccinella septempunctata* and *Propylea quatuordecimpunctata*, which hibernate in forests or forest edges nearby the fields they occupied when active (Hemptinne 1988), or more or less distant. In the latter case, the ladybirds may undertake lengthy migratory flights. Recent investigations by Jeffries et al. (2013) using vertical-looking entomological radar reveal that some ladybirds undertake very long flights. Relatively large species such as *C. septempunctata* or *Harmonia axyridis* fly at altitudes of up to 1100 m above ground level and their displacement speed can be up to 60 km/h. Furthermore, the average duration of tethered flight of *H. axyridis* measured in the same study is 36.5 minutes, with some individuals flying continuously for more than two hours. Based on this data the authors estimate that *H. axyridis* is potentially able to travel uninterruptedly for a distance of up to 120 km and more usually for a distance of about 18 km. High values for the duration of tethered flight, similar to those reported for *H. axyridis* by Jeffries et al. (2013) and Maes et al. (2014), are recorded by Rankin & Rankin (1980) for another long-distance flier, the North American *Hippodamia convergens*. However, for *C. septempunctata*, which is a less spectacular migrant, the duration of tethered flight only rarely exceeds 15 minutes (Nedvěd et al. 2001).

There is some controversy about whether the long-distance flights undertaken by ladybirds to dormancy sites are directional (see Hodek 2012a), but the many examples of aggregations of beetles at dormancy sites at the highest points in the landscape support the hypothesis of hypsotactic orientation. Some ladybird long-distance migrants are known to select dormancy sites on high mountain peaks. Reports of such species occupying peaks higher than 1500 m a. s. l. are listed in Table 1. This list does not include mountain residents that spend their whole life at high altitudes, e.g. the North American *Hippodamia oregonensis* (Edwards 1957, Fields & McMullen

Table 1. Reports of Coccinellidae migrating and entering dormancy on the tops of mountains above 1500 m a. s. l.

species	altitude (m a. s. l.)	location	reference
Epilachninae			
Epilachna canina	2285	Nyika Plateau, Malawi	Farrell 1968
Chilocorinae			
Exochomus octosignatus	up to 2500	Central Asia	Yakhontov 1962
	2900	Palandöken Mtn., E Turkey	Özbek & Çetin 1991
Coccinellinae			
Adalia decempunctata	1855	Elmadağ, central Turkey	Bodenheimer 1943
Ceratomegilla undecimnotata	1512	Mt. Cousson, France	Kreiter & Iperti 1984
	2000 and higher	Central Asia	Yakhontov 1962
	2130	Transcaucasia	Schneider & Leder 1878, after Dobrzhanskii 1922a
	2900	Palandöken Mtn., E Turkey	Özbek & Çetin 1991
	2500–3000	Tajikistan	Ataeva 1972
Coccinella monticola	2000	Pinnacle Peak, WA, USA	Edwards 1957
	2435	Squaw Peak, MT, USA	Chapman et al. 1955
Coccinella septempunctata	1510	Mount Nif, W Turkey	Bodenheimer 1943
	1512	Mt. Cousson, France	Hodek et al. 1977
	1600	Mt. Śnieżka, Poland	Ceryngier 2000
	1700	Mount Aqraa, S Turkey	Bodenheimer 1943
	1855	Elmadağ, central Turkey	Bodenheimer 1943
	1940	Sibillini Mountains, Italy	Ricci et al. 2005
	2273	Çimen Mountain, S Turkey	Güven et al. 2015
	2530	Keshish Dagh, NW Turkey	Werner 1913, after Dobrzhanskii 1922a
	2900	Palandöken Mtn., E Turkey	Özbek & Çetin 1991
	2500–3000	Tajikistan	Ataeva 1972
	2600–3300	SE Kazakhstan (Tian Shan)	Savoiskaya 1966
	about 4570	Dhauladhar, Himalaya, India	M.S. Mani, after Edwards 1957
Coccinella undecimpunctata	2194	Mount Enys, New Zealand	Hudson 1905
Declivitata hamata	2198	Dedza Mountain, Malawi	Farrell 1968
Hippodamia caseyi	1975	Mount Kobau, BC, Canada	Fields & McMullen 1972
	2196	Beaconsfield Mtn., BC, Canada	Fields & McMullen 1972
	2200	Sheep Rock, BC, Canada	Fields & McMullen 1972
	2248	Apex Mountain, BC, Canada	Fields & McMullen 1972
	2303	Baldy Mountain, BC, Canada	Fields & McMullen 1972
	2435	Squaw Peak, MT, USA	Chapman 1954, Chapman et al. 1955
	2787	Lolo Peak, MT, USA	Chapman et al. 1955
	2990	McDonald Peak, MT, USA	Chapman et al. 1955
Hippodamia convergens	1744	Mt. Pisgah, NC, USA	Sherman 1938
	1781	Mt. Sterling, SC, USA	Sherman 1938
	2037	Mt. Mitchell, NC, USA	Sherman 1938
	2070	Mt. Locke, TX, USA	Rankin & Rankin 1980
	2200	Horsetooth Mtn., CO, USA	Hawkes 1926
	2460	Green Mtn., CO, USA	Johansson 1958, after Krell & Britton 2009
	2510	Genesee Mtn., CO, USA	Krell & Britton 2009
	2710	Doubleheaded Mtn., CO, USA	Krell & Britton 2009
	2890	Mosca Peak, NM, USA	Douglass 1930
Hippodamia glacialis lecontei	1519	Moscow Mtn., ID, USA	Piper 1897
Hippodamia quinquesignata	1676	Argus Mts., CA, USA	Th. Dobzhansky, after Edwards 1957
	1768	Lakeview Ridge, AB, Canada	Harper & Lilly 1982
	1780	Porcupine Hills, AB, Canada	Harper & Lilly 1982

Table 1. (continued)

species	altitude (m a. s. l.)	location	reference
	1829	Lightning Peak, AB, Canada	Harper & Lilly 1982
	2000	Pinnacle Peak, WA, USA	Edwards 1957
	2043	Bellevue Hill, AB, Canada	Harper & Lilly 1982
	2043	Plateau Mtn., AB, Canada	Harper & Lilly 1982
	2134	Turtle Mtn., AB, Canada	Harper & Lilly 1982
	2230	Table Mtn., AB, Canada	Harper & Lilly 1982
	2378	Crandell Mtn., AB, Canada	Harper & Lilly 1982
	2439	Sofa Mtn., AB, Canada	Harper & Lilly 1982
	2474	Glendowan Mtn., AB, Canada	Harper & Lilly 1982
	2520	Peavine Peak, NV, USA	Chapin 1946, after Edwards 1957
	2744	Mount Blakiston, AB, Canada	Harper & Lilly 1982
	2960	Logan Peak, UT, USA	Chapin 1946, after Edwards 1957
	3365	Telescope Peak, CA, USA	Edwards 1957
Hippodamia variegata	1800–2200	Hamadan, Iran	Hamedi & Maharramipour 2013
Lioadalia intermedia	2198	Dedza Mountain, Malawi	Farrell 1968
Psyllobora variegata	2198	Dedza Mountain, Malawi	Farrell 1968

1972, Belicek 1976), *Coccinella alta* (Belicek 1976) and *Hyperaspis jasperensis* (Belicek 1976) or the many species inhabiting central Asian ranges (Dobzhansky 1925, Savoiskaya 1966, Kovář 2005) and the Himalayas (Kapur 1963, Miyatake 1985, Canepari 1997). These ladybirds should be ranked as relatively sedentary species.

Ladybirds migrating to dormancy sites in mountains do not always choose the summits. Some select lower altitude sites. *Hippodamia convergens*, for example, overwinters in valleys in Sierra Nevada in California (USA) (Hagen 1962) but occupies mountain tops in eastern and interior North America (see Table 1 and references therein). In the Tian Shan mountains in Kazakhstan, Savoiskaya (1960) records migrants of *Oenopia conglobata* and *Adalia bipunctata* in the stands of the Asian spruce (*Picea schrenkiana*) growing on mountain slopes. Both species overwinter under the bark of old *P. schrenkiana* trees, at between 1500 and 1800 m a. s. l. in the case of *O. conglobata* and for *A. bipunctata* between 1500 and 2900 m a. s. l.

SPATIAL DISTRIBUTION AND POPULATION DENSITY OF LADYBIRDS AT DORMANCY SITES

In terms of their spatial distribution during dormancy, ladybirds can be roughly divided into those that form mass aggregations or occur singly or at most in small groups.

In the Palaearctic region aggregations of inactive individuals of several species of ladybirds are commonly recorded under the bark of trees: *Scymnus suturalis, Rhyzobius chrysomeloides, Chilocorus bipustulatus* (L.)*, Myrrha octodecimguttata, Harmonia quadripunctata, Aphidecta obliterata, Adalia bipunctata* and *Oenopia conglobata* (Savoiskaya 1960, Bielawski 1961, Pulliainen 1966). Of the species that select other types of dormancy habitats, long-distance migrants to the tops of hills and mountains (e.g. those mentioned in Table 1) also usually aggregate. In the case of non-migratory ladybirds, aggregative behaviour is less frequently observed, although the rather sedentary *Tytthaspis sedecimpunctata*, for example, forms large aggregations (Jones 1990, Majerus 1992, Nedvěd 2006). The North American *Coccinella novemnotata* Herbst also forms large aggregations, both aestival and hibernal, close to its breeding habitats in the San Joaquin Valley in California (USA) (McMullen 1967). A distinct category of aggregation is those formed inside buildings and other man-made structures. The best example of a ladybird gathering in such places is *H. axyridis*. In autumn, this species may enter buildings in high numbers both in its native range (Sakurai et al. 1993, Wang et al. 2011) and in areas where it is invasive (Nalepa 2007, Koch & Galvan 2008). Other species with a similar behaviour are *A. bipunctata* (Majerus 1997) and *Aiolocaria hexaspilota* (Hope) (Kuznetsov 1977). Each of these three species use man-made structures as substitute hibernacula. The natural overwintering sites of *H. axyridis* and *A. hexaspilota* are usually cracks in rocks in hilly or mountainous areas (Kuznetsov 1977, Obata 1986) and of *A. bipunctata*, under loose bark at the base of tree trunks (Savoiskaya 1960, Hemptinne 1985). As *H. axyridis* cannot survive outdoors in the cold winters experienced in Quebec (Canada) it is suggested that those that selected human houses as dormancy sites survived and thus enabled this species to successful overwinter and spread in northern regions (Labrie et al. 2008).

The high densities of ladybird beetles recorded on and close to the tops of hills and mountains can be partly explained in terms of the geometry of the area of the top of a more or less cone-shaped mountain, which is much smaller than that around its base and, therefore, the relocation of a given number of individuals from the surroundings of a mountain to its top results in a sharp increase in the numbers per unit area. After arriving at a mountain, migrants may further congregate as a result of entering specific microhabitats, such as grass tussocks, bases of shrubs, lower surfaces of stones or rock crevices (Hodek 2012a). Finally, ladybirds may attract each other resulting in a further compaction of the aggregation (Honěk et al. 2007). In some species, such as *C. septempunctata* and *Hippodamia variegata* (Goeze), the former two steps of the compaction process (migration towards summits and selection of specific microsites) are mainly, if not solely, responsible for the high population densities recorded during dormancy. Both of the above species are neither typical migrants nor typical aggregators as they often hibernate at low population densities in the lowlands (Honěk et al. 2007, Hodek 2012a).

The aggregative behaviour of some species of ladybirds is induced and maintained by chemical cues emanating from the beetles. It is postulated that alkylmethoxypyrazines, volatile compounds that serve as predator-alerting signals, also act as pheromones for attracting conspecifics (Al Abassi et al. 1998). Indeed, recent studies confirm the role of these chemicals in the formation of aggregations in *H. convergens* (Wheeler & Cardé 2013) and *A. bipunctata* (Susset et al. 2013). In addition, non-volatile cuticular hydrocarbons deposited by ladybirds at dormancy sites are attractive to *H. convergens* (Wheeler & Cardé 2014), *A. bipunctata* (Susset et al. 2013) and *H. axyridis* (Durieux et al. 2012). Substrate marking with these persistent compounds is believed to ensure the cohesion of aggregations and colonization of the same sites from year to year. The latter function of such a substrate marking, however, is questioned by Durieux et al. (2014), as they found that the chemical profile of hydrocarbons left by *H. axyridis* changes considerably over time and after one year no longer induce beetle aggregation.

The sizes of aggregations of ladybirds can be very impressive. Probably the record is the aggregation of more than 40 million specimens of *H. convergens* overwintering at a site in the Sierra Nevada Mountains in California (USA) (Hagen 1962). Another North American species, *Coleomegilla maculata* (DeGeer), aggregates in autumn in litter on the ground in oak-elm-hickory forest in Illinois (USA), where the population density can be 12 thousand individuals per square meter (Park 1930). Enormous aggregation of *T. sedecimpunctata*, estimated at over one million individuals, is recorded by Jones (1990) in a bramble hedge near London (England). Overwintering assemblages of up to hundreds of thousands of *Ceratomegilla undecimnotata* (Schneider) and *Exochomus octosignatus* (Gebler) are reported from Central Asian mountains by Yakhontov (1962). Other ladybirds that gather in large numbers in the mountains of Central Asia are the two typical montane species, *Ceratomegilla rickmersi* (Weise) and *C. heydeni* (Weise), with tens or hundreds of thousands of these species per aggregation recorded in Tian Shan, in the territory of present-day Kyrgyzstan (Dobzhansky 1925).

Aggregations of dormant ladybirds are not always monospecific. Mixed clusters are often formed by the species that overwinter under tree bark. Bielawski (1961) reports *M. octodecimguttata, H. quadripunctata, C. bipustulatus* and *S. suturalis* in heterospecific winter aggregations found under the bark of large pine (*Pinus sylvestris* L.) trees in Poland. In Finland, under the bark of the same species, Pulliainen (1966) recorded *M. octodecimguttata, S. suturalis* and *A. obliterata*, with sporadic admixture of several other species. Ladybird aggregations on mountains may also consist of more than one species. Dobzhansky (1925) describes finding about 6500 beetles clumped at the base of a shrub at about 1500 m a. s. l. in Fergana Range (central Asia, Kyrgyzstan). Of the six

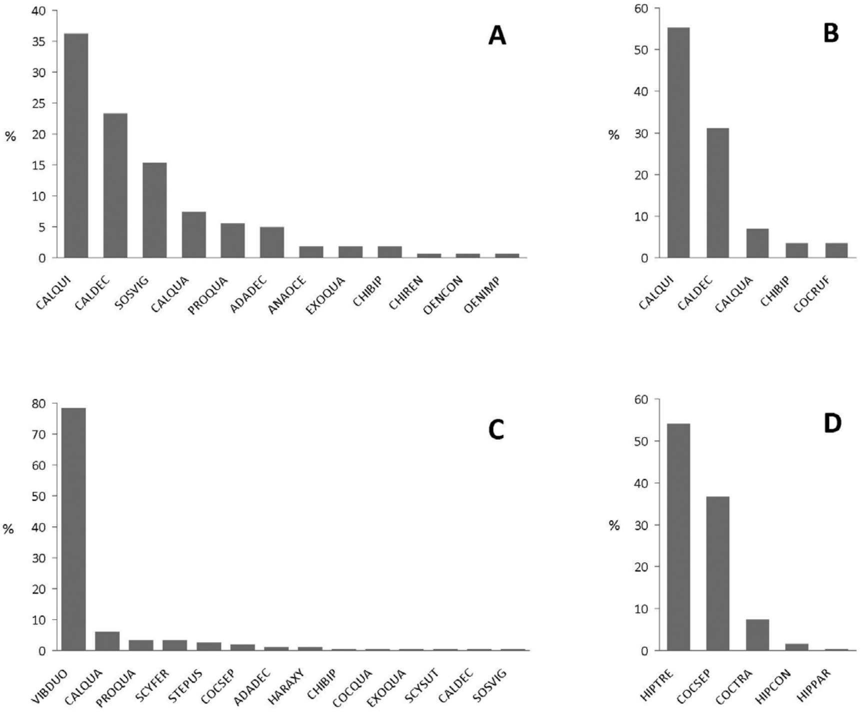

Fig. 1. Species composition of Coccinellidae overwintering in the litter in various forest habitats: A – mixed oak-pine forest in central Poland (after Godeau & Ceryngier 2011), B – alder carr forest adjacent to the previous habitat (after Godeau & Ceryngier 2011), C – floodplain forests along the river Vistula in central Poland (after Ceryngier & Godeau 2013, based on pooled numbers from six sites), D – beach-ridge forest at Lake Manitoba in Canada (after Turnock & Wise 2004, pooled numbers from autumnal samples collected over a period of 2 years). Species symbols: ADADEC – *Adalia decempunctata* (L.), ANAOCE – *Anatis ocellata* (L.), CALDEC – *Calvia decemguttata* (L.), CALQUA – *Calvia quatuordecimguttata* (L.), CALQUI – *Calvia quindecimguttata* (F.), CHIBIP – *Chilocorus bipustulatus* (L.), CHIREN – *Chilocorus renipustulatus* (Scriba), COCQUA – *Coccinula quatuordecimpustulata* (L.), COCRUF – *Coccidula rufa* (Herbst), COCSEP – *Coccinella septempunctata* L., COCTRA – *Coccinella transversoguttata* Faldermann, EXOQUA – *Exochomus quadripustulatus* (L.), HARAXY – *Harmonia axyridis* (Pallas), HIPCON – *Hippodamia convergens* Guerin, HIPPAR – *Hippodamia parenthesis* (Say), HIPTRE – *Hippodamia tredecimpunctata* (L.), OENIMP – *Oenopia impustulata* (L.), OENCON – *Oenopia conglobata* (L.), PROQUA – *Propylea quatuordecimpunctata* (L.), SCYFER – *Scymnus ferrugatus* (Moll), SCYSUT – *Scymnus suturalis* Thunberg, SOSVIG – *Sospita vigintiguttata* (L.), STEPUS – *Stethorus pusillus* (Herbst), VIBDUO – *Vibidia duodecimguttata* (Poda).

Table 2. Estimated population densities of Coccinellidae overwintering in litter in various habitats

species	region	habitat	mean density per m^2	reference
Chilocorinae				
Exochomus quadripustulatus	central Poland	oak forest	8	Bielawski 1961
Coccinellinae				
Adalia decempunctata	central Poland	hornbeam-oak forest	0.4	K. Bodzon & P. Ceryngier, unpubl.
	central Poland	oak forest	3	Bielawski 1961
Coccinella quinquepunctata	central Poland	oak forest	2	Bielawski 1961
	central Poland	pine forest	2	Bielawski 1961
Coccinella septempunctata	central Poland	hornbeam-oak forest	0.3	K. Bodzon & P. Ceryngier, unpubl.
	central Poland	mixed oak-pine forest	0.4	K. Bodzon & P. Ceryngier, unpubl.
	Hainaut, Belgium	forest interior	0.78	Hemptinne 1988
	Hainaut, Belgium	forest edge	0.98	Hemptinne 1988
	Manitoba, Canada	beach-ridge forest	31.3–45.3	Turnock & Wise 2004
Coccinella transversoguttata	Manitoba, Canada	beach-ridge forest	6.9–8.5	Turnock & Wise 2004
Coccinula quatuordecimpustulata	central Poland	oak forest	4	Bielawski 1961
	central Poland	pine forest	9	Bielawski 1961
Hippodamia convergens	Manitoba, Canada	beach-ridge forest	1.1–2.1	Turnock & Wise 2004
Hippodamia parenthesis	Manitoba, Canada	beach-ridge forest	0.13–0.4	Turnock & Wise 2004
Hippodamia tredecimpunctata	Manitoba, Canada	beach-ridge forest	47.3–65.6	Turnock & Wise 2004
Propylea quatuordecimpunctata	central Poland	hornbeam-oak forest	0.6	K. Bodzon & P. Ceryngier, unpubl.
	central Poland	mixed oak-pine forest	1.1	K. Bodzon & P. Ceryngier, unpubl.
	Hainaut, Belgium	forest edge	1.11	Hemptinne 1988
	Hainaut, Belgium	forest interior	1.41	Hemptinne 1988
	central Poland	oak forest	2–3	Bielawski 1961
	central Poland	pine forest	15	Bielawski 1961

species in that aggregation, *Ceratomegilla heydeni* and *C. undecimnotata* predominated, *Exochomus octosignatus* and *Coccinula sinuatomarginata* also occurred abundantly, while *Hippodamia variegata* and *Platynaspis luteorubra* were less numerous. A large aggregation consisting of *C. undecimnotata*, *C. septempunctata* and *E. octosignatus* was recorded at 2900 m a. s. l. in eastern Anatolia (Turkey) by Özbek & Çetin (1991). On hills at Primorye (Far East of Russia) Kuznetsov (1977) found *Aiolocaria hexaspilota* aggregating together with *H. axyridis*, *O. conglobata* and some other insects.

Non-aggregating ladybirds often spend periods inactive in the litter or on the surface of the ground in various forested and unforested habitats or in the transition zone between them (forest margins) (Hodek 1960, 2012a, Bielawski 1961, Hemptinne 1988, Godeau & Ceryngier 2011, Ceryngier & Godeau 2013). Numbers of beetles at such sites may vary but are usually low (Table 2).

Species composition of ladybird beetles that can be found in dormancy in the litter of particular habitats is rarely recorded even though it is very easy to do. Quantitative data on this topic available in a few papers are depicted in Fig. 1. Number of species reported from different types of habitats ranged from 5 to 14. Interestingly, at three central European locations (Fig. 1A–C) some species considered to be rare in Europe were common. In and/or around an alder carr forest in Poland Godeau & Ceryngier (2011) recorded an abundant overwintering population of two rare marshy forest specialists, *Calvia quindecimguttata* and *Sospita vigintiguttata* (Fig. 1A–B). Another relatively rare species, *Vibidia duodecimguttata*, is recorded as dominant in aggregations of ladybirds hibernating in the litter in floodplain forests (Ceryngier & Godeau 2013, Fig. 1C). These results indicate that studying overwintering assemblages, apart from its cognitive value, may also be important in terms of the conservation of rare species.

MORTALITY AND OTHER FITNESS-REDUCING PROCESSES ASSOCIATED WITH DORMANCY

In regions with a cold and temperate climate, ladybirds often spend longer in dormancy than active each year. *C. septempunctata* in Central Europe, for example, spends about two thirds of its lifespan in hibernation (Honěk 1989) and in the Middle East about four fifths (9 months) of its lifespan in aestivo-hibernation (Bodenheimer 1943). An equally long aestivo-hibernation is recorded for *C. undecimnotata* (Hodek 1960, 2012a). During these long periods of inactivity under unfavourable conditions many ladybirds die (e. g. Lipa et al. 1975, Honěk 1989, 1997, Ceryngier 2000, Güven et al. 2015). Dormant individuals die of various causes, such as adverse abiotic conditions, depletion of energy reserves or the action of natural enemies.

Of the abiotic factors, low temperature may, among others, result in high winter mortality. The effect of cold on the mortality of *H. axyridis* is well illustrated by the fact that none of those that hibernated in an outdoor artificial hibernacula survived whereas 25–53% of those that hibernated inside houses survived (Labrie et al. 2008). Shaefer (2003) records 40% mortality in a naturally-formed aggregation of *H. axyridis* in an observation tower in Pennsylvania (USA), which he attributes to the steel and concrete structure of the tower providing too little thermal protection for the beetles. Turnock & Wise (2004) record that the mortality of several ladybird species overwintering in the litter in a beach-ridge forest in Manitoba (Canada) was dependent on the distance of the site from the beach, with the highest percentage dying recorded at the edge of the forest near the beach due to them being buried by sand blown off the beach.

Numerous authors (Hodek & Čerkasov 1963, El-Hariri 1966, Mills 1981, Zhou et al. 1995, Hodek 2012a) emphasize the importance of energy reserves (fat, glycogen) in determining ladybird survival during dormancy. However, evidence for this is lacking and Mills (1981) reports that winter mortality in *A. bipunctata* is independent of their fat content. On the other hand, experiments conducted by Barron & Wilson (1998) show that overwintering survival of *C. septempunctata* is positively correlated with their weight relative to body size measured at the beginning of overwintering. As the differences in the 'relative weights' are clearly dependent on the size of their fat reserves, this is good indirect evidence for a relationship between fat reserves and winter mortality in *C. septempunctata*.

The natural enemies that affect the survival of dormant ladybirds have been studied by many authors (e.g. Iperti 1966, Lipa et al. 1975, Olszak 1986, Ceryngier 2000, Ormond et al. 2006, Güven et al. 2015) and the general consensus is that entomopathogenic fungi, especially the genus *Beauveria*, are the most important. Dormant ladybirds may also be heavily parasitized by parasitoids, such as *Dinocampus coccinellae* (Schrank), but in this case the ladybird hosts are parasitized before dormancy and the beetles arrive at dormancy sites already parasitized (Ceryngier 2000). In contrast, infection with pathogens may occur throughout dormancy due to the presence of pathogen spores at the dormancy sites. Indeed, places regularly used by ladybirds as hibernacula may be very rich reservoirs of the spores of *Beauveria* and other fungal pathogens. At such places, huge numbers of dead individuals (Piper 1897, Dobzhansky 1925, Hawkes 1926, Douglass 1930, Bodenheimer 1943, Edwards 1957, Harper & Lilly 1982), often covered with fungal mycelium (Iperti 1966, Hales et al. 1986, Ceryngier 2000, Güven et al. 2015), may be seen. This is especially the case at montane aggregation sites, where densities of overwintering beetles are high. In aggregations, close body contact of individuals may also favour transmission of some ectoparasites, such as the laboulbenialean fungus *Hesperomyces virescens* Thaxter (Riddick & Schaefer 2005, Nalepa & Weir 2007, Ceryngier & Twardowska 2013). Finally, although Coccinellidae are rarely eaten by other animals (Ceryngier et al. 2012), aggregations are exploited by vertebrates. For example winter aggregations of mainly *Hippodamia caseyi* Johnson are exploited by grizzly bears in the Mission Mountains in Montana (USA) (Chapman et al. 1955, Klaver et al. 1986) and shrews feed on aggregations of *C. undecimnotata* in the Czech Republic (Ceryngier & Hodek 1996).

Insects that occupy dormancy sites at high altitudes experience quite different conditions from those that remain in the lowlands. With increasing altitude, ambient temperature decreases by about 6 °C for each 1000 m and snow cover persists for longer. Furthermore, the availability of oxygen decreases with altitude and wind speed and harmful UV radiation increase (Hodkinson 2005). Dormancy at high altitudes may have some benefits for ladybirds and other insects, because, e.g. they deplete their metabolic reserves more slowly (Zhou et al. 1995) and snow cover provides protection from extreme cold (Hodkinson 2005, Hodek 2012a). On the other hand, locating and dispersing from mountain dormancy sites distant from breeding areas is costly in term of both energy and time and insects remain dormant substantially longer high in the mountains than in the lowlands where the climate is milder because at high altitudes they enter dormancy earlier and resume activity later (Honěk 1989, Ceryngier 2000, Hodkinson 2005). As a consequence, high-altitude hibernators or aestivo-hibernators may experience a phenological shift and considerable shortening of the periods suitable for reproduction and development. In extreme situations, ladybirds that occupy dormancy sites in the mountains may be unable to return to lowland breeding areas because of adverse weather conditions (low temperatures, strong winds) or may return too late, when the period suitable for breeding is over (Honěk 1989, Güven et al. 2015). Recent studies by Güven et al. (2015) indicate that *C. septempunctata* that arrive every year in enormous numbers at a high mountain aestivo-hibernation site in southern Turkey are either killed by entomopathogens during dormancy or during post-dormancy remain close to the hibernaculum as they are unable to disperse and reproduce. As the studies by Honěk (1989) and Ceryngier (2000) suggest, the fraction of ladybird populations so trapped probably mostly consists of females and relatively large individuals. Smaller, poorer quality individuals are supposedly not capable of undertaking a long-distance migration and occupy dormancy sites at lower altitudes.

As shown in Table 1, there are numerous reports of *C. septempunctata* and other ladybirds migrating to dormancy sites high in the mountains. While some of these reports also document severe mortality, phenological effects associated with high altitude dormancy sites are less frequently mentioned. Data on the phenology of *H. caseyi* overwintering on several peaks in British Columbia (Canada) (altitudes of about 2000–2300 m a. s. l.) are provided by Fields & McMullen (1972). Aggregations of the beetles on the peaks lasted from early September till mid-October when the first permanent snow appeared, and their dispersal began as late as early June when large snowfields were still present. A similar overwintering phenology is recorded for another species, *Hippodamia oregonensis*, which hibernates on the same summits as *H. caseyi* (Fields & McMullen 1972). However, unlike *H. caseyi*, *H. oregonensis* is a typical subalpine to alpine species, and does not migrate to the lowlands but stays at high altitudes. In summer, it is recorded at altitudes above 1800 m a.s.l. feeding on the pollen of wild flowers and reproduces in July and August. Feeding on pollen is perhaps a more general feature of alpine ladybirds that frequently experience shortage of aphids and other arthropod food. Savoiskaya (1970 in Hodek & Evans 2012) reports the occurrence of pollinivory in the central Asian high mountain dwellers, *Coccinella reitteri* Weise and *Ceratomegilla barovskii kiritschenkoi* (Semenov-Tian-Shanski).

CONCLUDING REMARKS

Analyzing recently published literature on aphidophagous Coccinellidae, Sloggett (2005) found that the majority of research was done on a few common species, which are all ecological generalists. He argues that studying less common species, especially those more specialized, might reveal different patterns and mechanisms and enhance our understanding of the group as a whole. This seems to hold true also for dormancy. While much is known about dormancy in such species as the North American *H. convergens* or Palaearctic *C. undecimnotata, C. septempunctata* and *H. axyridis*, little is known about dormancy in most of the other species. Interestingly, even for *H. axyridis*, whose overwintering has recently attracted much attention (e.g. Nalepa et al. 1996, Huelsman & Kovach 2004, Labrie et al. 2008, Berkvens et al. 2010, Raak-van den Berg et al. 2012a, b) because of its tendency to spend the cold season in human dwellings, there is very little information on hibernation in natural dormancy sites in the mountains.

Among the many species of Coccinellidae that have not been investigated in terms of their life cycles and dormancy ecology, the ‘extremophiles’ seem especially worthy of study. Living permanently in high-mountain, polar or arid areas, these species are exposed to long periods of unfavourable conditions. During the short periods suitable for reproduction, development and accumulation of energy reserves they still have to cope with rather hostile abiotic conditions and a general scarcity of essential food. On the other hand, such harsh conditions may reduce the adverse effect of natural enemies and competitors. That ‘extremophile’ strategies are not uncommon among Coccinellidae indicates a large number of species are limited in their occurrence to high mountains and/or the arctic tundra (Dobzhansky 1925, Savoiskaya 1966, Belicek 1976, Kovář 2005). In particular, unusually high ladybird species richness and levels of endemism are recorded in the Himalayas (Kapur 1963, Miyatake 1985, Canepari 1997).

Apart from the ecology of individual species it is also worth adopting a community ecology approach when studying dormancy sites. While relatively large amounts of information exist on communities of Coccinellidae when the individual species are active (see e.g. reviews by Honěk & Hodek 1996 and Honěk 2012), far less is known about assemblages of dormant ladybirds. Research on this topic could prove to be important for managing pests with the help of predatory ladybirds or the conservation of rare species of ladybirds.

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