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Apollo Butterfly (*Parnassius apollo* L.) in Europe – its History, Decline and Perspectives of Conservation

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ABSTRACT

Parnassius apollo colonized Europe in Neogen. Migrations during interglacial episodes probably resulted in its diversification into more than 200 identified subspecies inhabiting mainly grasslands both in lowland and mountainous areas throughout Europe. According to trophic preferences two main groups can be distinguished: 'telephiophagous' that prefer *Sedum telephium*, and 'albophagous' that feed predominantly on *Sedum album*. This division reflects a vertical distribution of occupied habitats and migration history. Subspecies inhabiting mountain ranges in western and southern Europe fall into the 'albophagous' group, while the forms from lowland habitats across Europe and from the Eastern Carpathians are 'telephiophagous'. Since the 19th century Apollo has been in decline due to combined negative impact of: a) natural factors including long-term climatic changes, habitat succession, and short-term weather anomalies; b) anthropogenic factors that include broad impact of industrialization and butterfly over-collecting; and c) intrapopulation factors that include genetic erosion and behavioural changes in small demes. Habitat loss is undoubtedly the most destructive for Apollo's long-term survival. In this review we describe all these reasons in detail. Subsequently, various protective measures that were, are or should be undertaken to stop further decline are discussed.

Keywords: Apollo breeding, food-plants, habitat protection, population decline, protective measures, reintroduction, *Sedum*

CONTENTS

APOLLO HISTORY IN EUROPE

It has been assumed that the genus *Parnassius* evolved in early Paleogen in Laurasia. In Miocene collision of the Indian tectonic plate to the Asian continent dramatically changed habitats in the adjacent areas and boosted radiation within the genus in mountainous regions of Central Asia (today Karakoram, the Pamir Mts and the Himalayas)

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Invited Review

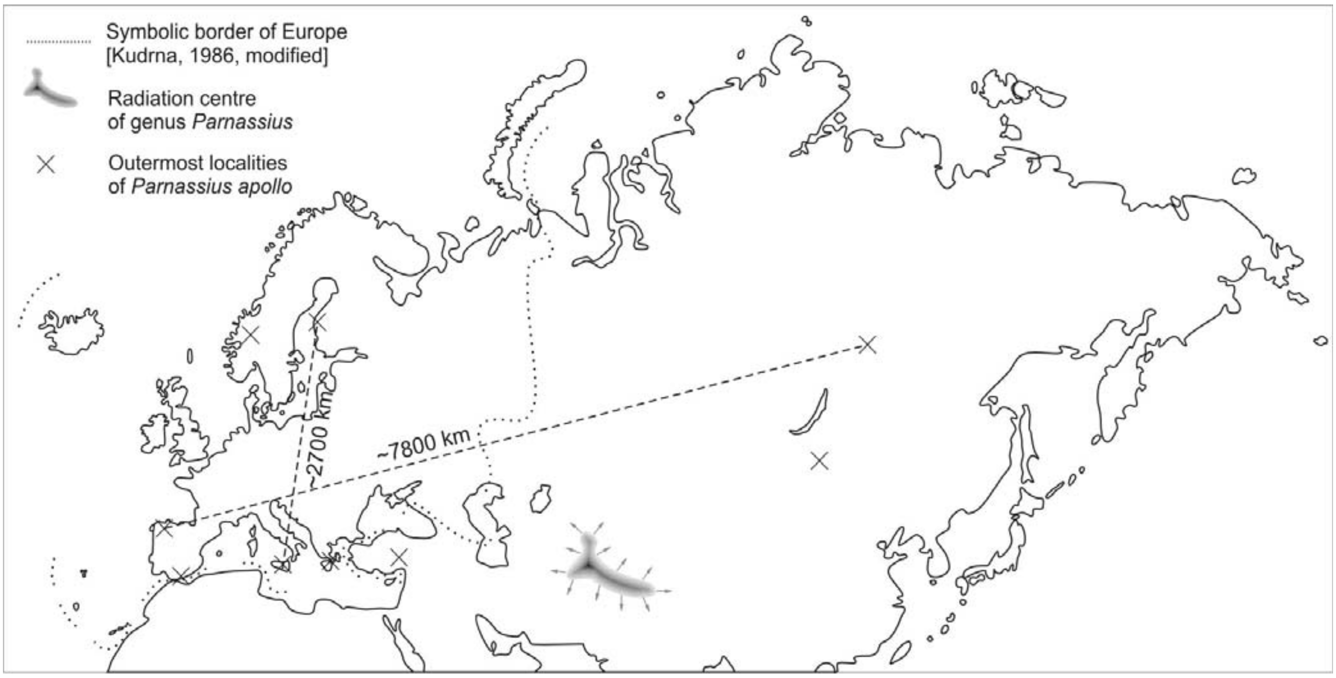


Fig. 1 Schematic Palearctic range of *Parnassius apollo*.

(Caradja 1934/35; Żukowski 1959a; Ackery 1975; Häuser 1993). Recent genetic analyses of some mtDNA sequences suggest relatively rapid radiation of *Parnassius* into more than 50 identified species. Constructed phylogenetic trees showed that the genus constitute a monophyletic group, comprising a number of cluster groups that correspond to these recognized on the morphological basis (Chen *et al*. 1999; Omoto *et al*. 2004; Katoh *et al*. 2005). One of them, *P. apollo* L. 1758, already in Neogen, dispersed widely westward, reaching Europe, and northward as far as the permanent snow line. Formerly this species probably colonized vast steppe areas, but during the first glaciation in Europe *P. apollo* drove southward from its habitats into refuges. Subsequent interglacial and glacial episodes resulted in corresponding expansions from refuges and withdrawals. Most probably these migrations brought about subspecific evolution. Shrinking steppe biotopes imposed selective pressure onto local Apollo populations, which resulted in their adaptation to new habitats – mountain screes and meadows. Gradually, Apollo shifted from a typical steppe species into a mountain-steppe species. This occurred in the Alps and, probably, at southern, calcareous slopes of the Carpathians, and resulted in the emergence of numerous forms and subspecies. Similar processes, but less dynamic, took place also in Asian part of the species range. Hence, there are a few Apollo subspecies in this vast area in comparison with Europe. Consequently, Asian and East-European forms are considered more primitive. They are, however, direct ancestors of present forms that inhabited Middle Europe and Scandinavia, in post-glacial period at the end of Pleistocene (Caradja 1934/35; Slabý 1952a, 1954; Hoffmann 1956; Żukowski 1959a).

Nowadays *P. apollo* has wide Palaearctic distribution with the range extending from 7° W (the Cantabrian Mts (Cordillera Cantábrica) in N-W Spain) to 110° E (the Khentei Mts (Hèntèjn nuruu) in Mongolia), and even to 120° E (Yakutia in the river Lena basin in Russia). Latitudinal distribution ranges from 62° N (western coast of Finland and Oppland in the Scandinavian Mts) to about 38° N (the Sierra Gádor in Spain, La Madonie massif in Sicily, Mt. Erímanthos at Peloponnese in Greece, and West Taurus massif in N-E Turkey) (Antonowa 1985; Casale and Cecchin 1990; Glassl 1993; Gómariz Cerezo 1993; Tarrier 1994 (1995); Aagaard *et al*. 1997; Gantingmaa 2004; Turlin and Manil 2005) (**Fig. 1**). As steppe and mountain-subalpine-subboreal species, Apollo occupies – within its range – different habitats (Krzywicki 1963; Descimon 1995). It is

Table 1 Biotopes inhabited by *Parnassius apollo* according to CORINE classification.

Biotopes		N1	N2
Heaths and scrubs:	Heath and scrub	2	
Grasslands:	Alpine and subapline grasslands	10	3
	Dry calcareous grasslands and steppes	8	2
	Mesophile grasslands	4	1
	Dry siliceous grasslands	2	
	Humid grasslands and tall herb communities	1	
Forests:	Broad-leaved deciduous forests	3	1
	Coniferous woodland	3	1
	Mixed woodland	1	
Unvegetated areas:	Inland cliffs and exposed rocks	5	2
	Screes	4	1
	Cliffs and rocky shores	2	
	Islets and rocky stacks	2	

N1 – number of mentions by national compilers (van Swaay and Warren 1999)
N2 – number of European countries (van Swaay *et al*. 2006)

found in heaths, scrubs, various grasslands communities in lowland biotopes, and also in forest glades. Among the most typical habitats there are alpine and subalpine grasslands and dry calcareous grasslands and steppes in upland areas. Screes and rocky habitats (up to 3,000 m a.s.l. in the Sierra Nevada, 2,500 m a.s.l. in the Alps, and 1,800 m a.s.l. in the Carpathians) are also suitable for this species (**Table 1**). Irrespective of habitat type, there must be available food-plant for the larvae – one of a few Crassulacean species (mainly *Sedum* – see next section). Nowadays particular Apollo forms and subspecies occupy small areas, sometimes limited to single mountain massif or even hillside, as it was documented in the Alps and the Carpathians (Glassl 1993) (see **Box 1**).

Site-specific conditions resulted in differences within *P. apollo*. They involve wings colouring pattern (the presence, size and appearance of the eyespots, and width and colouring intensity of the submarginal forewing bands), trophic preferences and body size (**Fig. 2; Plate 1A, 1B**). Considering morphological features lepidopterologists described about 200 subspecies and many more forms (**Table 2**). Adult polymorphism is quite common in butterflies, so it is reasonable to assume some of the described forms as manifestation of phenotypic variability related to the relative elasticity of the genes encoding the wing pattern (Capdeville 1980; Napolitano *et al*. 1990; Rivoire 1998; Brakefield

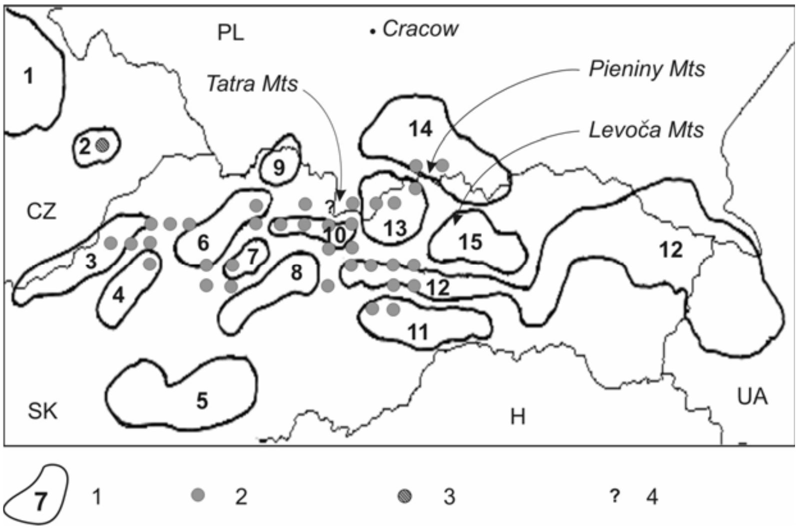
BOX 1. APOLLO HISTORY IN THE CARPATHIANS

Glacier withdrawal to the northern parts of Europe enabled migrations of Apollo populations from their southern refuges. These migrations followed expansion of their larval food-plants: *S. telephium* toward the west and north-west of Europe, and *S. album* toward the north (Pax 1915; Pekarsky 1953, 1954; Slabý 1954; Żukowski 1959a; Krzywicki 1963). Both main migratory routes probably crossed in the Western Carpathians (today Czech and Slovakia territory) what could result in a mosaic pattern of particular subspecies distribution, or even in crosses between neighbouring subspecies. It is quite possible that some 'albophagous' forms shifted again into *S. telephium*, or that some 'telephiophagous' forms had to change their food-plant into *S. album* as they colonized biotopes at higher altitudes (Slabý 1964).

Detailed morphological studies on Apollo living in the arch of the Carpathians have been carried out for more than a century. They resulted in description of 20 subspecies (see also Capdeville (1980)). Four of them inhabited the southern part of the arch in Romania, and one - vicinities of Eger in Hungary. The other 15 subspecies were found in the western part, within present borders of Poland, Czech and Slovakia (Pekarsky 1953, 1954; Krzywicki 1963; Slabý 1964; Glassl 1993). Nowadays all Apollo populations within the Czech Republic borders, and more than half of those from Slovakia should be considered extinct (see figure below) (Konvička and Fric 2002; Žlkovanová *et al*. 2004). One of the survived was *P. apollo* ssp. *frankenbergeri*. According to Glassl (1993), it occupied the whole Pieniny Mts (Pieniny), the Gorce mountains range (Gorce), and the Island Beskid (Beskid Wyspowy). In fact, it was never found in the Gorce range due to absence of food-plant for its larvae (Schille 1895; Żukowski 1959b; Witkowski 1989). Moreover, it is spatially isolated, by 15-20 km wide farmlands, from ssp. *candidus* that inhabits the eastern part of the Tatras Mts (Tatry). The Poprad river valley separates it from ssp. *braniskoi*, living about 10 km southward at the Lewoča Mts (Levočske Vrchy). It is noteworthy, that ssp. *frankenbergeri* was described in 1955 by Slabý as distinct from ssp. *carpathicus*. Ssp. *braniskoi*, described 22 years later, was separated from ssp. *sztrecsnoensis* (Glassl 1993). Both ssp. *carpathicus* and ssp. *sztrecsnoensis* have inhabited this region in the course of post-glacial migratory wave that originated in the east and moved along arch of the Carpathians. These recently described forms suggest that formerly identified *P. apollo* subspecies may undergo further adaptive changes.

Another example that confirms this suggestion was given by Żukowski, who studied morphological changes of Apollo in the Pieniny Mts. He found that specimens he collected in the 1940s and 1950s were morphologically different from those, obtained from the 19th century collections. The latter specimens constituted relatively homogenous group. He also found differences among spatially separated sub-populations. For example a forest barrier that in the 1940s and 1950s separated population at Trzy Korony (BrE: Three Crowns massif), in the eastern part of the Pieniny range (see also **Fig. 6** and **Plate 1H**), from another one that inhabited area a few kilometers westward (in Czorsztyn), led to noticeable differences among their individuals. Moreover, it appeared that butterflies from Czorsztyn displayed some typical traits of ssp. *candidus* from neighbouring population in the Tatras. Unfortunately the studies were given up due to death of Żukowski and extinction of Apollo in Czorsztyn environs in the 1960s (Żukowski 1959b; Witkowski *et al*. 1993).

These quoted examples point out that both natural and anthropogenic factors shaped the present distribution and variability of Apollo populations in this region.



Historical and actual distribution of Apollo subspecies in the Western Carpathians. 1 - area occupied by particular subspecies according to Glassl (1993); 2 - UTM grid squares with confirmed presence of *Parnassius apollo* (Žlkovanová *et al*. 2004); 3 - locality of introduced *P. apollo* ssp. *antiquus* in Štramberk; 4 - doubtful site of *Parnassius apollo* in Polish Tatra Mts. Numbers in the drawing refer to particular subspecies: 1 – *albus* (*sicinius*); 2 – *strambergensis* (*vistulicus*); 3 – *interversus*; 4 – *antiquus*; 5 – *nitriensis*; 6 – *sztrecsnoensis*; 7 – *zelnyi*; 8 – *djumbirensis*; 9 – *oravensis*; 10 – *liptauensis*; 11 – *rosnaviensis*; 12 – *carpathicus*; 13 – *candidus*; 14 – *frankenbergeri*; 15 – *braniskoi*.

Table 2 Number of *Parnassius apollo* subspecies according to different authors.

Author	No of subspecies	Unique subspecies*
Felix Bryk (1935)	167	26
Helmut Glassl (1993)	213	15
Edwin Möhn (2003)	202	61

* – subspecies described only by the author and not listed by others

and Gates 1996). There are, however, contradictory opinions that all Apollo forms represent different genetic inheritance, independent of external conditions (Napolitano *et al*. 1990; Rivoire 1998).

Kudrna (1986) made the following evaluation of biogeographic disposition and condition of *Parnassius apollo*:

1. Disposition (CI between 4 and 14 score: 4 – indicator of the most successful species, 14 – indicator of endemic (European) species):
   a. RS (range size) – 3: species distributed over one or more smaller parts of Europe (i.e. a 'medium sized' distribution);
   b. RC (range composition) – 3: predominantly isolated colonies, with a good proportion of more continuous distributions ('headquarters') in significant central parts of the species' range;
   c. RA (range affinity) – 2: 'neutral' species with distribution 'headquarters' both within and outside Europe, regardless of respective range proportions;
   d. CI (chorological index: RS + RC + RA) – 8.
2. Conditions (between 1 and 6 score: the higher vulnerability index (VI) the greater anthropogenic threat to the species):
   a. DR (decline recorded) – 1: vulnerable species;
   b. HV (habitat vulnerability) – 1: some habitats are fragile;
   c. SV (species vulnerability) – 1: threatened by collectors (overcollecting);
   d. VI (vulnerability index: DR + HV + SV) – 3: seriously threatened but not in acute danger.

More recent status of this species in Europe was pre-

Plate 1 (**A**) Typical colouration of female *P. apollo* ssp. *frankenbergeri* (from the Pieniny Mts). Inset: colouration of the bottom side of the wings. (**B**) Typical colouration of male *P. apollo* ssp. *frankenbergeri*. (**C**) Apollo larvae feeding on sprouts of *Sedum telephium* in breeding colony in Pieniny National Park. Please note their aposematic colouration. Inset: marks of feeding on *S. telephium* sprouts in natural conditions. (**D**) Apollo larvae feeding on *Sedum album* (experiment carried out in Pieniny National Park). Please note size of the larva and the food-plant (compare with **C**). (**E**) Scree at the slope of Trzy Korony massif in the Pieniny Mts – the last natural site of *P. apollo* ssp. *frankenbergeri* in Poland in the 1990s. Inset: stumps remaining at the scree during Apollo habitat 'clearing'. (**F**) Scree at Nowa Góra slope (the Pieniny Mts) – former site of Apollo from which tree and shrubs were removed during reintroduction programme. Maintenance of the site needs regular removal of shrubs. (**G**) Scree at Długa Grapa (the Pieniny Mts) do not need any treatments now. Apollo disappeared here due to site isolation; successfully re-established during the programme in the 1990s. (**H**) Panoramic view of Trzy Korony massif – nowadays site of most abundant Apollo population and the main tourist attraction of the Pieniny Mts.; famous top view on the Dunajec river gorge became also Apollo observation point in June and July. In the middle part of the massif the scree depicted in **E** can be seen. (**I**) Panoramic view of the river Mosselle valley from Cohem at Valwig, where *P. apollo* ssp. *vinningensis* was successfully reinforced. Nowadays Apollo is a local tourist attraction (see inset). Photos: M. Nakonieczny.

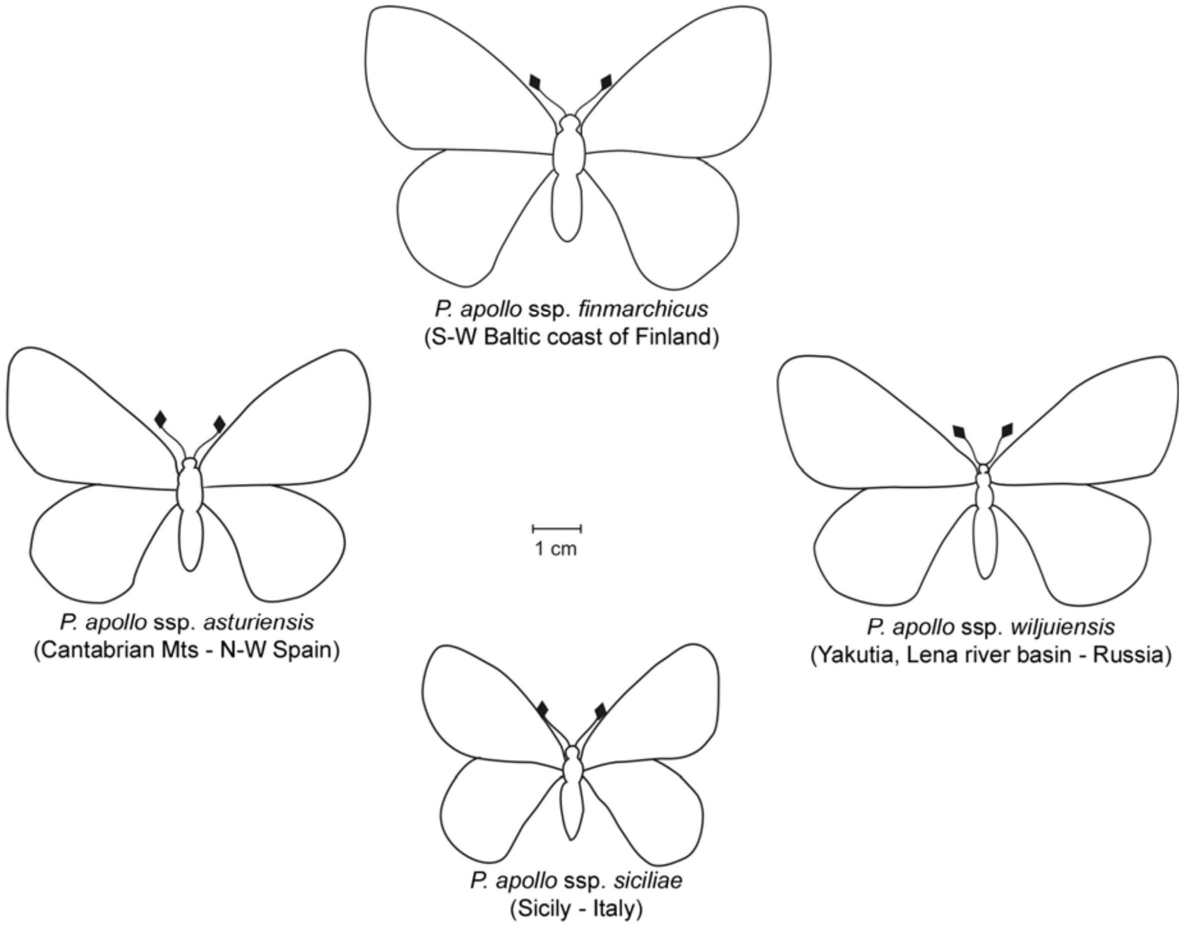


Fig. 2 Size comparison between Apollo males from outermost localities within Palearctic range of the species (after Möhn 2003).

sented by van Swaay and Warren (1999) in their 'Red Data Book of European Butterflies (Rhopalocera)' (**Table 3**).

Table 3 *Parnassius apollo* L. in Europe – present status (van Swaay and Warren 1999).

Status		Comments
Present distribution class	5-15%	Present abundance is regarded as the percentage of the total number of investigated grid squares, where the species is reported after 1980
Overall trend	decrease 20-50%	The change in distribution over the last 25 years
Threat status	VU	Vulnerable
Conservation status	SPEC 3	Species of European Conservation Concern – species with headquarters within and outside Europe, but threatened in Europe
Number of countries, where it is present	27 (30*)	Trend of population in the countries over the last 25 years: decrease - 11, stable - 5, increase - 0, unknown - 8, extinct - 3

* – according van Swaay *et al*. 2006

FOOD-PLANTS

Parnassius apollo has one generation in a year (univoltine species). First instar larvae develop during the summer but over-winter closed in the eggshell and hatch next year, usually early in March, often under snow cover. Like other species of the genus, Apollo is considered a stenophagous herbivore. Numerous observations – sometimes contradictory – on Apollo larvae feeding, point out various *Sedum* species as their food-plants (see e.g. Ackery 1975; Kreuzberg 1987). Compilation of available data is presented in **Table 4**. Their analysis leads to the conclusion that two species of *Sedum* are preferred by caterpillars: *S. telephium* (and its subspecies) and/or *S. album*. Hence, *P. apollo* larvae can be roughly classified into one of two trophic groups: 'telephiophagous' or 'albophgous' (for details see Nakonieczny and Kędziorski 2005). In fact larvae may taste and bite leaves of other species of Crassulaceae if they grow in their habitats. This refers mainly to the youngest instar, which may feed under snow cover on delicate rosettes of *Sempervivum arachnoideum*, *Jovibarba globifera* or *Rhodiola rosea* (Chrostowski 1957; Żukowski 1959b; Deschamps-Cottin *et al*. 1997). However, there are only a few solid data showing complete larval development on other stonecrop species than preferred ones (**Table 4**) (Deschamps-Cottin *et al*. 1997; Ronca 2006).

Sedum telephium differs from *S. album* in its morphology and habitat requirements. This perennial herb with large flattened leaves and tuberous roots grows preferably in open forest glades and lowland meadows, but is also quite abundant on mountain screes. It is widespread stonecrop from Central Europe to Japan (Stephenson 1994). In Europe it exists in four subspecies, two of which (ssp. *fabaria* and ssp. *maximum*) are found in western part of the continent (Webb 1993).

S. album is a very variable, perennial stonecrop but generally tiny, with small subterete leaves. It grows on rocks, screes and rocky mounds at various altitudes and in different soil conditions. This species is native to Europe (Webb 1993; Stephenson 1994). A brief comparison between these two species is given in **Table 5** and **Fig. 3**.

Geographical distribution of *S. telephium* and 'telephiophagous' apollo subspecies (Asia, eastern and central Europe, including the Carpathians and large parts of Scandinavian Peninsula) clearly indicate that this stonecrop was primary food-plant for *P. apollo* during its westward expansion from radiation centre (Slabý 1954; Kreuzberg 1987; Janzon 1990; Nakonieczny and Kędziorski 2005).

Table 4 *Parnassius apollo* larval food-plants named by various authors.

Primary food-plant	Subspecies of *P. apollo*	Distribution	Secondary food-plant	Reference
***Sedum telephium* group**				
S. telephium ssp. *telephium*	*apollo*	E Sweden		Janzon 1990
	finmarchicus	SW Finland and Åland Islands		Fred *et al.* 2006
	moscovitus	Central Russia Upland		Glassl 1993
	democratus	Volga Upland		Glassl 1993
	silesianus †	Silesia Upland		Fischer 1927
	not specified	French Alps and Pyrenees		Braconnot *et al.* 1993
S. telephium ssp. *fabaria*	*transsylvanicus*	E Carpathians (Romania)		Pekarsky 1953
	carpathicus	W Carpathians (Slovakia)		Pekarsky 1953
	candidus	W Carpathians – Tatras Mts (Slovakia, Poland)		Pekarsky 1953; Dąbrowski 1982-1984(86)
	djumbirensis, *liptuaensis*	NW Carpathians (Slovakia)		Slabý 1964
S. telephium ssp. *maximum*	*frankenbergeri*	W Carpathians – Pieniny Mts (Slovakia, Poland)	*S. acre* and *Sempervivum soboliferum* for youngest larvae	Żukowski 1959a, 1959b; Krzywicki 1963; Nakonieczny and Kędziorski 2005
	serpentinicus	E foreland of Alps	*S. album*	Glassl 1993
	not specified	The Massif Central (France)		Deschamps-Cottin *et al.* 1997
***Sedum album* group**				
S. album	*linnaei*	Gotland Island (Sweden)		Janzon 1990; Deschamps-Cottin *et al.* 1997
	not specified	French Alps, Pyrenees and the Massif Central – Causses (France)		Braconnot *et al.* 1993; Deschamps-Cottin *et al.* 1997
	interversus, *nitriensis* †, *sztrecsnoensis*, *liptauensis*, *djumbirensis*	W Carpathians – Low Tatras (south part, Slovakia)		Pekarsky 1953; Slabý 1964
	antiquus	SW Carpathians – Strážov Mts (Slovakia); Štramberk (introduced) (Czech Republic)		Kuśka and Lukášek 1993
	vinningensis	Mosel Valley (Germany)	*S. rupestre*	Glassl 1993
	siciliae	Sicily (Italy)	*S. amplexicaule*	Glassl 1993
Other *Sedum* sp. and other Crassulaceae				
S. sediforme	not specified	The Massif Central – Causses (France)		Braconnot *et al.* 1993
S. ochroleucum	not specified	The Massif Central – Causses (France)		Braconnot *et al.* 1993
S. ochroleucum ssp. *montanum*	not specified	French Alps and Pyrenees (France)		Deschamps-Cottin *et al.* 1997
S. amplexicaule	*filabricus*	S Spain, toward east from Sierra Nevada	*S. album*, *S. acre*	Glassl 1993
	pumilus	Calabry (S Italy)		Glassl 1993
	nevadensis	Sierra Nevada (Spain)	*Sempervivum nevadense*	Gómariz Cerezo 1993
	not specified	Sierra de Guadarrama	*S. pedicellatum*, *S. forsteranum*	Ronca 2006
Rhodiola rosea	*jotunensis*	Scandinavian Mts		Glassl 1993
	not specified	Central Russia Upland		Kreuzberg 1987
	not specified	Mercantour (France)		Braconnot *et al.* 1993
Sempervivum arachnoideum	not specified	Mercantour, French Alps and Pyrenees (France)		Braconnot *et al.* 1993; Deschamps-Cottin *et al.* 1997

† – extinct;
Outside Europe *P. apollo* larvae feed on: *S. album* and *S. pallidum* – Uludağ-Bursa, Turkey (Kovanci *et al.* 1999); *S. berunii* – Tian-Shan: Kirgisskii mountain range; *S. ewersii* – Tian-Shan: Kirgisskii, Tereski Alatau; central Altai: Aigulakskii mountain range; *S. hybridum* – Tian-Shan: Ketmen, Zailiiskii Alatau, Kungei Alatau mountain range; *S. telephium* ssp. *telephium* – Western Siberia (Barabinskaya steppe) (Kreuzberg 1987).

It is reasonable to assume that majority of extinct Apollo subspecies from central Europe were 'telephiophagous', like some populations still inhabiting central France, that feed on *S. telephium* ssp. *maximum* (Descimon 1995; Deschamps-Cottin *et al*. 1997). Change of the food-plant into *S. album*, and possibly a few related species, must have happened during colonization of mountainous habitats in southern and western parts of the continent during glacial and interglacial periods (Pax 1915; Pekarsky 1953, 1954; Slabý 1954; Żukowski 1959a; Krzywicki 1963). Hence, Apollo subspecies from the Alps, western Carpathians and southern areas of the species range in Europe belong almost exclusively to 'albophagous' trophic group (Moser and Oertli 1980; Descimon 1995; Deschamps-Cottin *et al*. 1997; Ronca 2006).

Feeding on *S. album* seems to have some disadvantages to Apollo larvae in comparison with *S. telephium*, since 'telephiophagous' subpecies are generally larger than 'albophagous' forms, particularly these from southern Europe (Greece, Calabria, Sicily and Spain) (**Fig. 2**) (Glassl 1993; Möhn 2003; Turlin and Manil 2005). Moreover, 'albophagous' forms from Germany and France develop better when fed on *S. telephium* (Nikusch 1991; Deschamps-Cottin *et al*. 1997). On contrary, 'telephiophagous' *P. apollo* ssp. *frankenbergeri* from the Pieniny Mts does not manage well on *S. album* (Nakonieczny and Kędziorski 2005). Among possible reasons for such 'trophic asymmetry' there may be: 1) much smaller energy and nutrient contents of *S. album* tissues (due to small size of the plant), and 2) greater amounts of secondary metabolites that may increase costs of their detoxication and/or decrease nutrients assimilation by the larvae. Both species contain various phenolic compounds (**Table 5**) that may inhibit digestion of dietary proteins in larval gut (see e.g. review by Swain 1977). Recently we have determined proteases and glycosidases activities profile in the last instar larvae of typical 'telephiophagous' *P. apollo* ssp. *frankenbergeri* (Nakonieczny *et al*. 2006, 2007). Lack of similar data for 'albophagous' larvae unable compa-

Table 5 Comparison of two main food-plants of *P. apollo* larvae (Webb 1993; Stephenson 1994).

	Sedum telephium	***Sedum album***
General description	Tall herbaceous plant, up to 80 cm high	Very variable tiny plant, about 12-20 cm high
Leaves	Flat, suborbicular to narrowly oblong, 2-8 cm long	Subterete or slightly flattened, blunt, 0.4-2 cm long
Geographical range	Native to Central Europe and whole Asia, including Japan	Indigenous to Europe[1], extending to North Africa and West Asia
Habitats	Lowland meadow margins[2]; forest glades and alluvial meadows[3]	Screes, rocks, and rocky mounds at wide range of altitudes, and great variety of soils and humidity conditions
Metabolism[4]	Unchanged in dry conditions; mainly C3 type	Enhanced in dry conditions - shift from C3 to CAM[5]
Secondary compounds[6]	Flavonoids, flavonol glycosides, coumarins, phenolic compounds (including phenolic acids, mainly gallic acid)	
	-	Condensed tannins (proanthocyanidins)

[1] – Except Ireland and Iceland
[2] – *S. telephium* ssp. *telephium*
[3] – *S. telephium* ssp. *maximum*
[4] – Measured by specific activity of phosphoenolopyruvate-carboxylase (EC 4.1.1.31) (Pilon-Smith *et al.* 1991)
[5] – Crassulacean Acid Metabolism
[6] – Available data suggest rather quantitative than qualitative differences in contents of these metabolites in compared species (see 't Hart *et al.* 1999 for discussion of this subject).

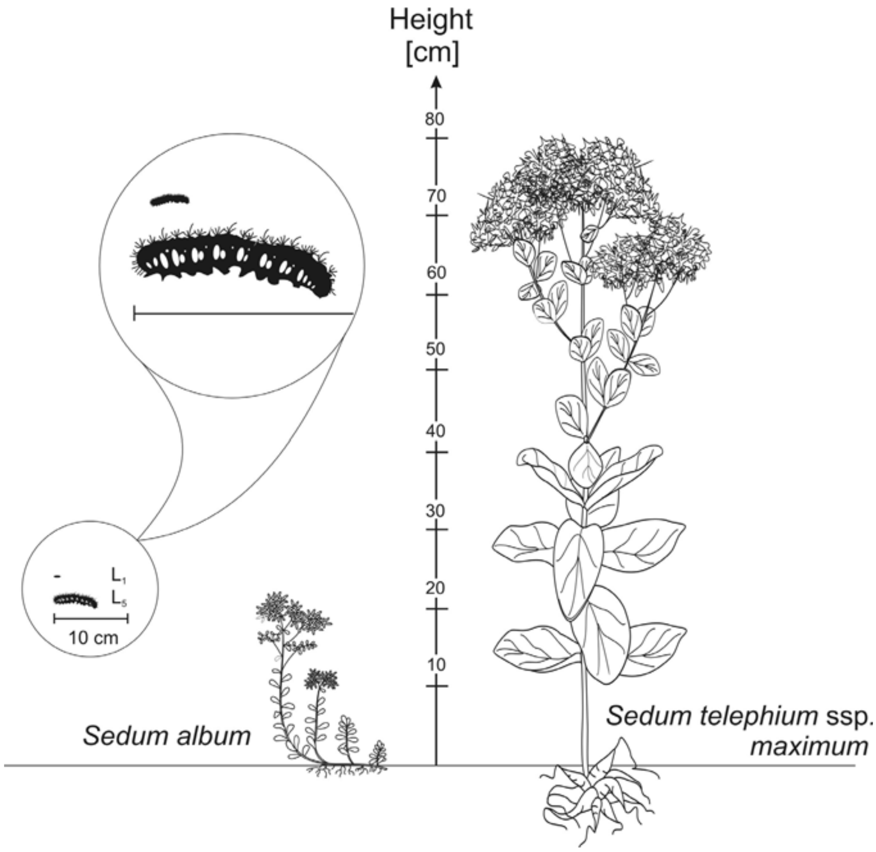


Fig. 3 Size comparison between Apollo larvae and their main food plants: *Sedum album* and *S. telephium*.

rison of feeding and digestion strategies between these two trophic groups at biochemical level. Observations done by Moser and Oertli (1980) have shown, that changed photoperiod and temperature during *S. album* cultivation made the plants unsuitable for the larvae what resulted in their high mortality. Bachereau *et al*. (1998) provided evidence, that UV radiation, present at high altitudes, caused elevation of phenolic compounds contents in *S. album*. We did not find similar data for *S. telephium* but its habitats are less exposed to deleterious UV spectrum.

Undoubtedly, the interaction between Apollo larvae and their food-plant is far more complex. The fourth and fifth instar larvae of *P. apollo* spp. *frankenbergeri* that live on scree, feed mostly alone on a given sprout, and usually eat only small amounts of the total leaves biomass (approximately a dozen or so percent, no more than 30%), then move to the next plant (inset in **Plate 1C**). In natural conditions larvae feed on plants that are in the phase of intensive vegetative growth. Due to substantial increase of leaf biomass, total loss of leaf surface in fully grown sprouts in generative phase is about 2-3% (**Fig. 4**) (Wala 1995; Adamski *et al*. 2000). In semi-natural colony or in the laboratory condition, when a few larvae simultaneously feed on the same plant we observed consumption of all leaves (**Plate 1C**). This suggests that some kind of plant response to the insects feeding is encountered at least in natural conditions.

Feeding on *S. telephium* may be somewhat problematic to youngest larvae due to disproportion in size between the insect and the plant. Only small buds shooting from soil are accessible to minute, first instar larvae. This explains observed strict synchronization of larval hatching and development with the plant phenology, as well as broader preferences for food-plants. As the larvae grow they can easily walk and feed on the growing plant (Żukowski 1959b; Wala 1995; Deschamps-Cottin *et al*. 1997). In this respect sprouts of *S. album* are more easily accessible both to young and older larvae of 'albophagous' subspecies (**Figs. 3, 4; Plate 1D**).

Broader food-plant preferences of 'albophagous' *P. apollo* from southern Europe than 'telephiophagous' ones may be due to morphological and biochemical similarity of selected stonecrops, that occur simultaneously in Apollo biotopes (Nakonieczny and Kędziorski 2005). This was well documented in the Sierra de Guadarrama in Spain (Ronca

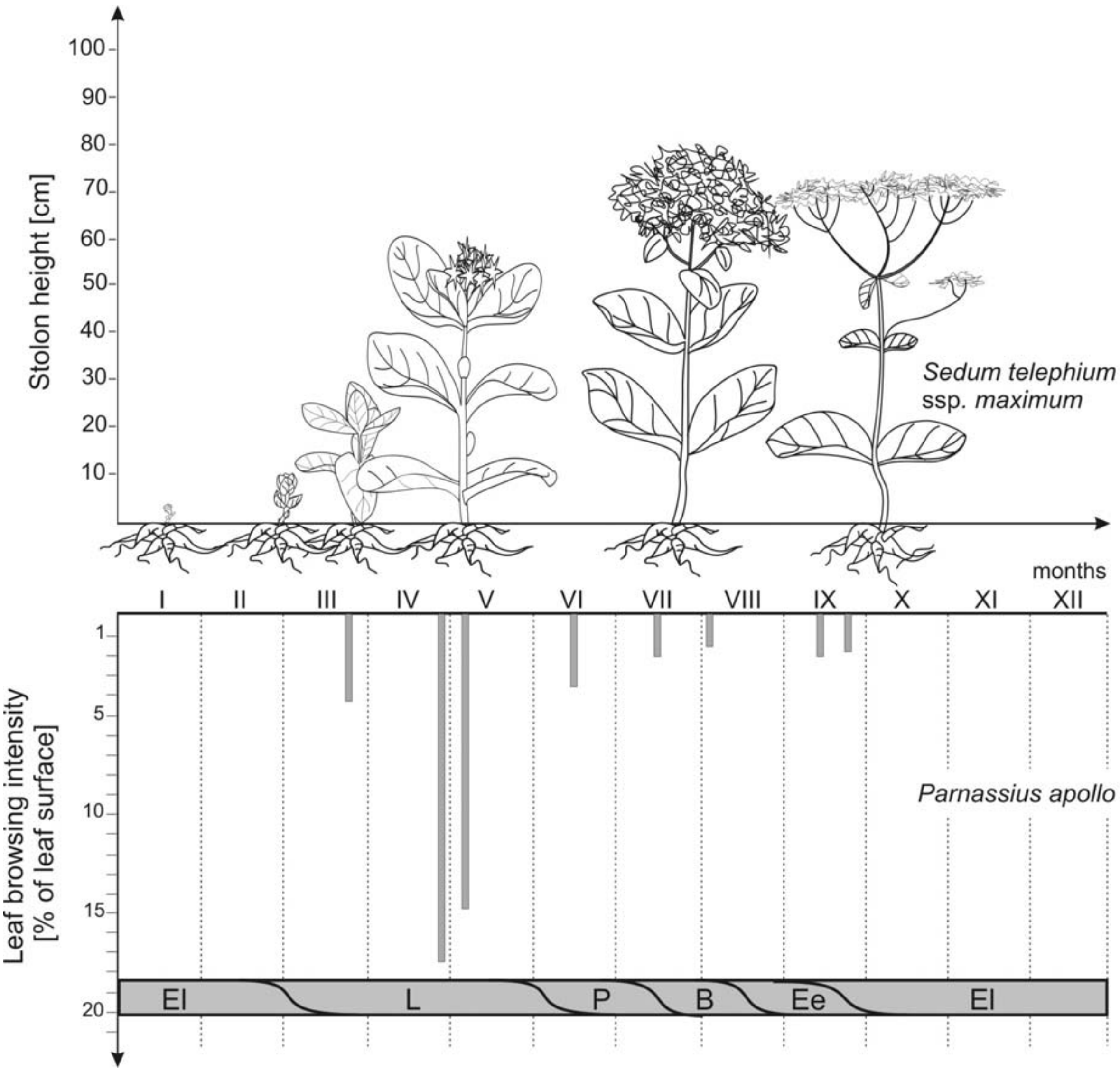


Fig. 4 Phenology of *Parnassius apollo* ssp. *frankenbegeri* and its food plant *Sedum telephium* ssp. *maximum* in Pieniny National Park (Western Carpathians, Poland). (Modified after Wala 1995 and Adamski *et al*. 2000). Abbreviations: El – first instar larvae enclosed in eggshell; L – larvae; P – pupae; B – butterflies; Ee – eggs with developing embryos.

2006).

Adult Apollo butterflies feed on nectar obtained from various plants available in their areas (**Table 6**). In searching for food, the insects, particularly males, may cover more than a few kilometres (Descimon 1995; Fred and Brommer 2003). As typical heliobionts they prefer sunny, open hillsides or meadows; even partly cloudy sky may decrease their activity. Insufficient amount of available nectar (that may results from drought episodes or small number of flowers) decrease female fecundity and shorten their lifespan. Hence, butterfly number and their flight activity depend on size of their habitats and abundance of nectar plants (Descimon 1995; Descimon *et al*. 2001; Fred and Brommer 2003). Adamski (1999) showed that flight pattern of male butterflies searching for females may depend also on population size – in abundant population, random-flight pattern prevailed over scanning-flight pattern that was more frequent in a deme.

VANISHING OF *PARNASSIUS APOLLO* IN EUROPE – REGIONAL PERSPECTIVE

Various publications concerning distribution of protected butterflies in Europe are based on political division and boundaries, and on national checklists of all identified species. In 'The Lepidoptera of Europe – a distributional checklist', published in 1996, *Parnassius apollo* was listed in 20 countries. The authors of 'Red Data Book of European Butterflies (Rhopalocera)', released 3 years later, took into account break-up of the Soviet Union and Yugoslavia. Hence, 27 countries with confirmed occurrence of *P. apollo*, distribution class, and general trend of the populations' size were mentioned in their publication (Karsholt and Razowski 1996; van Swaay and Warren 1999). In recent paper three more countries were added to the list (van Swaay *et al*. 2006). According to these authors distribution of Apollo in Europe decreased, in general, by 20-50% within the last 25 years. When the countries are grouped in geographical regions it becomes evident that the most threatened subspecies and forms are these from low altitudes in east and central Europe, while forms inhabiting high parts of the Alps and other, mostly south European, high mountain ranges, are still large and strong (**Tables 7, 8**) (Descimon 1995; van Swaay and Warren 1999). This observation indicates regional-specific or even site-specific threats and suggests that each protective activity should take into account specific local situation. In this section we provide an overview of condition of Apollo subspecies and populations in particular geographic regions of Europe.

We adopted borders of Europe after Kudrna (1986), so Turkey is excluded from our analysis, because of the fact that all of its Apollo populations live in the Asian part of the country. Due to a similar reason the Caucasian subspecies were also excluded, despite the fact that two Apollo subspecies inhabit northern slopes of this mountain chain (**Fig. 5**).

Table 6 Identified nectar plants of *Parnassius apollo* butterflies.

Nectar plants	Distribution	References
Scandinavia		
Asteraceae: *Centaurea jacea, Cirsium* sp., *Cirsium vulgare* Lamiaceae: *Thymus serpyllum* Onagraceae: *Epilobium angustifolium* Scrophulariaceae: *Veronica longifolia* Valerianaceae: *Valeriana officinals*	SW coast of Finland and Åland Islands (Finland)	Fred *et al.* 2006
Lowlands and Uplands of Central and West Europe:		
Asteraceae: *Centaurea* sp. Dipsacaceae: *Knautia* sp.	The Massif Central (France)	Descimon 1995
The Carpathians:		
Asteraceae: *Carduus* sp., *Centaurea scabiosa*, C. (*Jacea*) sp., *Colymbada* sp., *Chrysanthemum* sp., *Cirsium eriophorum*, *Cirsium eristales*, *Cirsium* sp., *Eupatorium cannabinum* Dipsacaceae: *Dipsacus* sp., *Knautia* sp.	W Carpathians – Pieniny Mts (Poland, Slovakia) and Moravian – Silesian Beskids (Czech Republic)	Żukowski 1959b; Kuśka and Lukášek 1993; Žlkovanová *et al*. 2004
South-European Peninsulas		
Asteraceae: *Carduus carpetanus*, *Jurinea humilis* Campanulaceae: *Jasione montana* Fabaceae: *Anthyllis lotoides* Lamiaceae: *Thymus brakteata* Plumbaginaceae: *Armeria arenaria*	Central Spain	Baz 2002

Scandinavia (N, S, FIN)*

This region is quite well studied and regular monitoring of Apollo populations has been carried out for several years. These data showed 15-25% decline in Sweden and Finland and about 50% in Norway, but this situation is not considered as severe threat (van Swaay and Warren 1999). Monitoring of two populations of *P. apollo* ssp. *jotunensis* inhabiting the Scandinavian Mts was carried out in the previous decade. It revealed about 900 individuals in each, and their size slightly increased during the monitored period (Aagaard *et al*. 1997). Populations of subspecies *norvegicus* seem to be more threatened. Their abundance has decreased since the beginning of the last century and in the 1970s became extinct at the coastal districts of south Norway (Gogstad 2000).

Since the 1950s the size and area of Apollo populations have decreased also in Sweden (Janzon 1990). This particularly concerned spp. *apollo*, inhabiting biotopes on granite bedrocks and resulted in division of formerly continuous area in the southern part of the country into the east coast and the west coast sub-areas. The population occupying the latter is severely threatened; although a slight overall increase in abundance in the 1980s, in comparison with previous decade, was observed, in some localities it even died out (e.g. Vänern lake area). On contrary, a large population of ssp. *linnaei* still exists in open sites on calcareous bedrocks of Gotland Island (Bengtsson *et al*. 1989; Janzon 1990). According to recent estimations situation of Swedish Apollo populations is stable (CITES 2002).

Glassl (1993) listed three Apollo subspecies within present Finland territory: ssp. *fennoscandicus*, ssp. *finmarchicus* and ssp. *carelius* (the latter described from border Republic of Karelia). Another one (ssp. *hoglandicus*) was described from Gogland Island, now belonging to Russia. The Apollo populations in Finland, that were large in the beginning of the last century, underwent changes in abundance during subsequent decades: they severely decreased in size by the 1930s, then, in the 1930s and 1940s, they expanded and became more abundant, particularly at the southern coast. Rapid decline occurred again in the 1970s and resulted in vanishing of Apollo in many localities except from the south-west coast and a few small, isolated inland areas (Mikkola 1979). Recent monitoring of Apollo in Finland revealed only one existing subspecies (*P. apollo* ssp. *fennoscandicus*) in the south-west coast and the Åland Islands (Fred 2004; Fred and Brommer 2005).

Apollo presence in Denmark is doubtful. Karsholt and Razowski (1996) listed the country in their distributional checklist, but there is lack of convincing data that whenever this species permanently colonized any habitats there. Instead, it is possible that some immigrants from near populations inhabiting the south coast of Sweden and/or Norway occasionally reached Danish territory.

The East European Plain (RUS, LV, BY)

This area was undoubtedly widely inhabited by Apollo in the past. Pekarsky (1954) and later Antonowa (1985) schematically depicted wide continuous stripe, occupied by the species, stretching latitudinally westward from the southern part of the Ural Mts towards Belarus territory, and towards Ladoga Lake and Karelia in the north, reaching the Northern European Lowlands, occupied by the Finnish Apollo populations. Within this large area, three Apollo subspecies (ssp. *moscovitus*, ssp. *democratus*, and ssp. *uralensis*) still exist, but areas occupied by their populations decreased significantly in recent decades (Glassl 1993; Kudrna 2002). The threats were more severe in the western part of the East European Plain than in the eastern one. Hence, populations of ssp. *moscovitus* from the Central Russia Upland become extinct in the highest degree. Recent data show their extinction in Belarus. Apollo described in Latvia is also considered extinct (van Swaay and Warren 1999; CITES 2002).

Situation of Apollo in the eastern part of the territory is much better than in the west: subspecies from the Volga Upland (ssp. *democratus*) still exist in numerous localities and abundant populations of ssp. *uralensis* occur at the Ural Mts and the Timan region (Utkin 2000; Kudrna 2002).

The Lowlands and Uplands of Central and West Europe (PL, CZ, D, F)

This area forms a long belt of lowlands in its northern part, and belt of uplands and old mountain formations in the southern part. The lowlands adjoin to the Baltic and North Sea and stretch from the East European Plain to the Bay of Biscay in the west. The uplands and mountain formations border in the south with large and younger mountain chains: The Carpathians and The Alps.

Available historical data and records led us to conclusion that in the past Apollo inhabited in Europe wide belt of lowland and upland habitats stretching in east-west direction from the Ural Mountains to the Atlantic coast in France. In the 18th century it was found occasionally in the Great Poland Lowland, more frequently in Warsaw environs at the Mazovian Lowland (Nizina Mazowiecka) and quite frequently in the Lesser Polish Upland (Wyżyna Małopolska) (vicinities of Cracow). Within a few next decades it became extinct there (Perthées 1778-1800 (after Witkowski 2004); Romaniszyn and Schille 1929; Witkowski 1986). The same happened to populations in Courland (today Latvia territory) and Sambia (today Kaliningrad district) (Rehenkampff 1937; Pekarsky 1954).

* Abbreviations of the countries are given in **Table 7**.

Table 7 Relative distribution of *Parnassius apollo* in European countries, grouped into geographic regions (van Swaay and Warren 1999, modified).

Region	Bio-geographic region*	Country	Distribution class**
Scandinavia	Alpine (Skands) (N), Boreal (FIN, N, S)	Norway (N)	> 15%
		Sweden (with Gotland) (S)	5-15%
		Finland (FIN)	1-5%
The East European Plain	Alpine (Urals) (RUS); Boreal (BY, LV, RUS); Continental (BY, RUS); Steppic (RUS)	Russia (European part) (RUS)	1-5%
		Belarus (BY) †	< 1%
		Latvia (LV) †	< 1%
Lowlands and Uplands of Central and West Europe	Continental (CZ, D, F, PL); Mediterranean (F)	France (F)	> 15%***
		Czech Republic (reintroduced) (CZ)	< 1%
		Germany (D)	< 1%***
		Poland (PL) †	< 1%
The Carpathians	Alpine (Carpathians) (CZ, PL, RO, SK, UA)	Slovakia (SK)	1-5%
		Czech Republic (CZ) †	< 1%
		Poland (PL)	< 1%
		Romania (RO)	< 1%
		Ukraine (UA) †	< 1%
The Alps	Alpine (Alps) (A, CH, D, F, FL, I, SLO)	France (F)	> 15%
		Italy (I)	> 15%
		Austria (A)	5-15%
		Slovenia (SLO)	5-15%
		Switzerland (CH)	5-15%
		Liechtenstein (FL)	1-5%
		Germany (D)	< 1%
South-European Peninsulas: • Iberian • Apennine • Balkan	Alpine (Pyrenees) (AND, F, SP); Alpine (Apennines) (I); Alpine (Dinaric) (AL, BIH, FYROM, HR, YU); Alpine (Balkans, Rhodopes) (BG); Mediterranean (I, GR, SP)	Andorra (AND)	> 15%
		France (F)	> 15%***
		Italy (I)	> 15%***
		Spain (SP)	> 15%
		Bosnia and Herzegovina (BIH)	5-15%
		Bulgaria (BG)	5-15%
		FYR of Macedonia (FYROM)	5-15%
		Greece (GR)	5-15%
		Yugoslavia (YU)	5-15%
		Albania (AL)	1-5%
		Croatia (HR)	1-5%

* – the bio-geographic regions used are the official delineations used in the Habitats Directive and for the EMERALD Network set up under the Bern Convention;
** – surface of *P. apollo* distribution to surface of country ratio, according to van Swaay and Warren 1999;
*** – including the Alps;
† – extinct at present in the region.

Table 8 General trends in *Parnassius apollo* abundance in Europe (Turkey included).

Trend class	Number of countries (%) (van Swaay and Warren 1999)*	Number of Prime Butterfly Areas (van Swaay and Warren 2006)**
Extinct	3 (10.7%)	-
Decrease:	12 (42.9%)	26 (21%)
75-100%	3 (10.7%)	-
50-75%	2 (7.1%)	-
25-50%	3 (10.7%)	-
15-25%	4 (14.4%)	-
Stable	5 (17.8%)	74 (59.7%)
Increase	-	1 (0.8%)
Unknown	8 (28.6%)	23 (18.5%)

* – the trend reflects change in species distribution over the last 25 years in particular countries (comparison of the abundance around 1975 versus 1999);
** – the trend for *P. apollo* present in 124 Prime Butterfly Areas (out of 431 Prime Butterfly Areas in Europe).

Further evidence of wide Apollo distribution in lowlands of Europe comes from Great Britain, where *P. apollo* was never a native species. Despite this, more than 20 confirmed records of this species were done in south of England and Scotland during two last centuries. The last published observation was done in 1986. These were most probably individuals from German (ascribed to ssp. *melliculus*) and Norwegian populations respectively (Emmet and Heath 1989).

During the first half of the last century Apollo became extinct in many of its upland and mountainous areas as well. Three subspecies, described from the Sudetes Mts (Sudety) and its foreland (ssp. *silesianus* from the Krucze Mts, ssp. *albus* from Śnieżnik Mt. and Kłodzko Basin, and ssp. *frieburgiensis* from the river Bystrzyca valley) died out at the turn of the 20th century (Rebel and Rogenhofer 1893; Pax 1915; Rebel 1919).

In the 19th century numerous and abundant populations of nine Apollo subspecies native to Czech inhabited biotopes dispersed all over the country, including foothills of the Krkonoše Mts (Krkonoše), the České Středohoři Highlands, the Šumawa Mts and the Jesenik Mts, the Javorniky Mts and Moravian Karst (Konvička and Fric 2002). Now there is only one site in Štramberk, inhabited by *P. apollo* ssp. *antiquus* from Velký Manín canyon in the Strážov (Strážovské) Hills (west Slovakia). Native ssp. *strambergensis* died out, so replacement were done and foreign subspecies was introduced in 1986 (Lukášek 1995).

Some populations from uplands in Germany shared similar fate. For example *P. apollo* ssp. *posthumus* that once inhabited Vogtland in the east of the country became extinct during the first half of the century. In the 1970s populations of *P. apollo* ssp. *suevicus* that were large at the turn of the 20th century, died out in all biotopes situated in The Black Forest (Schwarzwald). A decade later, it became extinct, except for one site, in the Swabian Alb (Schwäbische Alb). During construction of national road existing Apollo biotope was unintentionally enlarged. This enabled survival of the local population (Nikusch 1991; Glassl 1993).

The condition of Apollo populations in Bavaria (ssp.

Fig. 5 Schematic drawing of actual *Parnassius apollo* distribution in Europe. (Data compiled from various sources; European borders adopted after Kudrna (1986), modified).

melliculus from the Frankonian Jura (Frankische Alb) is much better, most probably due to the protection programme launched by scientists from Bavaria (Geyer and Dolek 1995). Out of all Apollo populations inhabiting lowland, upland and low mountain areas in Germany, only ssp. *vinningensis* from the river Moselle valley (Mosels Tal) in Rhineland-Palatinate is not threatened with extinction now. This is also due to the accomplishment of prolonged, years-lasting protection programme (Löser and Rehnelt 1983; Kinkler *et al*. 1987). Recent analysis of *P*. *apollo* distribution in Germany, calculated in 10 km squares of UTM grid with imposed field data, revealed a decrease from 139 to 38 squares, where Apollo was found, between 1979 and 1999 (Kinkler *et al*. 1987; CITES 2002).

Available data show that Apollo in France is found in areas covering more than 15% of the country area, and the populations' size is considered stable (van Swaay and Warren 1999). Effective monitoring system carried out in recent decades revealed that apart from the Alps and the Pyrenees (which are discussed below) Apollo inhabited mountainous biotopes above 1,000 m a.s.l. (e.g. Puy de Dôme and peaks of massifs of Cantal and Sancy) and exposed rocks at lower altitudes (e.g. the Plateau of Millevaches, rocky banks of the Loire river, the hillsides of massifs of Cantal and Sancy) (Descimon 1995; Descimon *et al*. 2005). Since the 1960s, *P. apollo* has been rapidly disappearing: in the Vosges Mts (Les Vosges). It became extinct within the next decade (in 1976), and populations from the Jura Folds (Le Jura) and an Alpine front decreased in size, and their areas were split into smaller patches. In the 1980s Apollo rapidly declined from lower sandy rocks massifs in Forez, Vivrais, Lozère and hillsides of Puy de Dôme (Descimon 1995).

The populations at lower altitudes of the Massif Central (Le Massif central) shared similar fate: *P*. *apollo* ssp. *cebennicus* from the Causse du Larzac and the Causse Noir in the south Mediterranean habitat of the Massif Central died out in 1989-1990 due to weather anomaly (Descimon 1995; Descimon *et al*. 2005). On contrary, at high altitudes of the Massif Central still there are quite favourable biotopes for Apollo and populations are abundant (Descimon 1995).

The Carpathians (CZ, SK, PL, UA, RO)

Considerable Apollo variability was stated in this region, particularly in the north-west part of the arch as it was already mentioned (see **Box 1**). Most of its populations, belonging to 14 subspecies, occupied areas within present Slovakia territory (Glassl 1993). Capdeville (1980) stated that distinction of so many subspecies is unjustified and combined all of them into three subspecies: ssp. *carpathicus*, ssp. *sztrecsnoensis* and ssp. *antiquus*. During the last century majority of existing Slovakian populations severely decreased in size or become extinct. This happened to ssp. *interversus* from the White Carpathians and Jesenik district – it no longer exists in biotopes on Czech side of the mountains (Konvička and Fric 2002), but survived in eastern habitats in Slovakia. Recent Apollo inventory revealed that out of about 28 formerly identified populations in Slovakia, only 13 still exist (CITES 2002). These are populations, usually found at higher altitudes in the northern part of the country: ssp *interversus* (the White Carpathians), ssp. *antiquus* (the Strážov (Strážovské) Hills), ssp. *sztrecsnoensis*, ssp. *djumbirensis* and ssp. *zelnyi* (the Little and Great Fatra), ssp. *frankenbergeri* (the Pieniny Mts), ssp. *carpathicus* (the Low Tatras), ssp. *candidus* and ssp. *liptauensis*) (the High Tatras). Subspecies that occupied habitats at lower altitudes as well as the southern and eastern parts of the country died out, irrespectively whether they were 'albophagous' or 'telephiophagous'. This happened to ssp. *nitriensis* (occurring to the east from Nitra), ssp. *rosnaviensis*, (found in Rožňava vicinities) and ssp. *braniskoi* (from the Levoča (Levočske) Mts) (Krzywicki 1963; Glassl 1993; Žlkovanová *et al*. 2004). Another extinct form (ssp. *cominius*) was described from the limestone Bükk Mountains (internal part of the Western Carpathians, Hungary) (Glassl 1993).

P. apollo ssp. *carpathicus* once occurred in long belt that included the middle-east part of Slovakia, and the Eastern Beskids (Beskid Wschodni) at the borderline between Ukraine, Slovakia and Poland (Glassl 1993). Last observations of the butterflies were done in the 1960s in the Bieszczady Mts. During a few next decades it became extinct in the eastern parts of its area (Chrostowski 1959; Bielewicz 1973; Witkowski 1986; Žlkovanová *et al*. 2004) (see also map in **Box 1**).

Within the Polish part of the Carpathians there is only one stable and abundant (ca. 1,000 individuals) population of *P. apollo* ssp. *frankenbergeri* in the Pieniny Mts. However, its good condition is solely the result of a special establishment plan (see section 'Protection of *Parnassius apollo* – directions and measures'). Another form (ssp. *niesiolowski*) has occurred in many valleys in the Western Tatras in the early 1950s. Twenty years later, it was found only in two of them: Chochołowska Valley and Kościeliska Valley (Dąbrowski 1980, 1981; Buszko 1997). There are some recent personal observations of butterflies on the Polish side of the mountains, made by the staff of Tatra National Park, but it is not sure, whether these were native individuals or occasional migrants from Tichá Valley on the other side of the massif in Slovakia (Pawłowski 2005).

There are preserved museum specimens and confirmed records of ssp. *sicinus* and ssp. *vistulicus* from Cieszyn Silesia at the Carpathians foreland (Glassl 1993), but these forms died out in the first half of the last century.

P. apollo ssp. *transsylvanicus* was widely distributed in the Ukrainian Carpathians (Ukrains'ki Karpaty). Recent inventory confirmed its extinction in Ukrainian part of its former range (Popov 2006).

In the Romanian part of this massif, the subspecies was recently confirmed in Kupás valley near Lacul Rosu (Varga *et al*. 2005). According to Glassl (1993) there were other Apollo populations in Romanian part of the Bukovina Mts (ssp. *rosenius*), in the Western Romanian Carpathians (ssp. *jaraensis*) and in the Transylvanian Plateau (ssp. *ruthenicus*). Despite thorough search we failed to find any data concerning current distribution and size of Apollo populations in this country. van Swaay and Warren (1999) classified them to the severely decreasing trend class 'decreased by 50-75%'.

The Alps (A, SLO, D, FL, CH, I, F)

The greatest number of Apollo populations of all described regions inhabited this mountain chain in the past. According to Glassl (1993) 79 subspecies were identified in the Eastern and Western Alps. In only one region (Trident in Italy) there were found 20 subspecies (Sala and Bollino 1997). There are still stable and abundant populations in high-altitude biotopes in Swiss, Italian and French parts of the Alps (Descimon 1995; van Swaay and Warren 1999; Balletto *et al*. 2005). According to Descimon (1995), in France they may count between 1,000 and above 3,000 individuals.

Centre Suisse de Cartographie de la Faune (CSCF) provides detailed historical and recent information on Apollo distribution in the country. These data leave no doubts that this butterfly is in decline in the country. In 1900, it was present in 595 5 × 5 km grid squares, but in 2000 – only in 237 squares. Five years later, it was confirmed in sites covered by 83 squares of the grid (CSCF 2007).

Only a few Apollo populations in Slovenia are considered stable and large, although there are 32 UTM 10 × 10 km grid squares in which the species was found (CITES 2002). It was observed in grazed grasslands e.g. on the foothills of the Dinaric Alps and the Polovnik Mts, near the river Soca and in Nanos-plateau outside the Alps territory (Varga *et al*. 2005).

Nevertheless, a decrease has been observed in numerous alpine areas, particularly at lower altitudes. In the 1960s, severe fall of the number of Apollo individuals was observed in Austria. In the above-mentioned countries, apart from abundant populations, there are other that markedly decreased in size or disappeared during a few past decades. Then, in overall view, Apollo has been declining in Austria, Slovenia, France and Switzerland – at lower altitudes it became extinct (Descimon 1995; CITES 2002; CONVENTION 2006; CSCF 2007). We did not find any data on recent changes in Apollo populations inhabiting alpine biotopes in Germany.

In the light of presented data the statement included in Red Data Book that Apollo populations from the Alps are stable and abundant (van Swaay and Warren 1999) seems to be over-optimistic.

The South-European Peninsulas

The Iberian Peninsula (SP, F, AND)

Twenty three Apollo subspecies were described in Spain, another two in French part of the Pyrenees. Spanish populations occupy mountainous areas in the northern, central and eastern parts of the country (Glassl 1993). Recent inventory showed occurrence of *P. apollo* in 295 UTM 10 × 10 km grid squares (CITES 2002). Like in the Alps, there are strong and abundant populations in northern, mountainous areas (the Pyrenees and the Cantabrian Mts) (Tarrier 1994 (1995); Ronca 2006). On the French side of the Pyrenees, there are also abundant populations (up to 3,000 individuals) of ssp. *chrysophorus*, ssp. *portensis*, ssp. *pyrenaicus* and ssp. *ossalensis* (Descimon 1995). However, many populations, particularly from central and southern localities, are considered endangered. *P. apollo* ssp. *ascalerae* and ssp. *wyatti* from the Sierra de Guadarrama has declined remarkably. Another form – *P. apollo* ssp. *nevadensis* from the Sierra Nevada – is even in worse condition, and occurring southernmost ssp. *gadorensis* from the Sierra de Gádor can be considered almost extinct (Tarrier 1994 (1995); Ronca 2006). van Swaay and Warren (1999) classified general trend of Apollo populations dynamic in the country as '15-25% decrease'.

The Apennine Peninsula (I)

Along the mountain chain of the Apennines Mts (Apennini) nine Apollo subspecies were identified, and another one in the northern part of Sicily (ssp. *siciliae*) (Glassl 1993). Populations that occur in the Tuscan-Emilian Apennines (Apennino Tosco-Emiliano) and the Abruzzo Apennine (Apennino Abruzzese) are still abundant but ssp. *pumilus* from the Calabria Apennine (Apennino Calabrese) is considered seriously threatened. Recent data showed occurrence of this subspecies in two isolated outermost localities of its former range. Native to Sicily ssp. *siciliae* was found only in Le Madonie massif. It became extinct from Etna massif, where once it was quite abundant (CITES 2002; Balletto *et al*. 2005).

The Balkan Peninsula (HR, BIH, FYROM, YU, AL, BG, GR)

This is the least examined European region in regard of recent Apollo distribution. According to Glassl (1993) there were 14 subspecies inhabiting this region. Three subspecies from Greece probably exist in stable populations, particularly ssp. *graecus* from the central part of the country (van Swaay and Warren 1999; CITES 2002). Considered as extinct ssp. *atrides* from the Peloponnese was rediscovered in 1983 (Casale and Cecchin 1990).

Once frequent in Bulgaria – it inhabited all mountain ranges in the country (Buresch and Arndt 1926; Glassl 1993) – now it is still found in 63 UTM 10 × 10 km grid squares, mainly at high altitudes in the West Rhodopes (Zapadni Rodopi): Černatica, The Pirin Mts (Pirin) and the Rila Mts (Rila). There are also some strong populations along the western border of the country. Populations of ssp. *hermiston* that once widely occupied the Balkans (Balkany) in the central part of the country now is limited only to the highest localities within the range (e.g. Stara Planina). It also became extinct at high altitude habitats in Vitosha Mt. (Vitosa), near Sofia (CITES 2002; PBA-Bulgaria 2007).

Abundant and stable Apollo populations occur probably also in Albania and the Former Yugoslav Republic of Macedonia (38 UTM grid squares) (CITES 2002). Out of six described Apollo subspecies from Serbia, Bosnia and Herzegovina, and Croatia (Glassl 1993), there are confirmed reports only from present territory of Croatia. Populations still inhabit the Dinaric Alps along Bosnia and Herzegovina border (ssp. *hercegovinensis*), Velebit (ssp. *liburnicus*) and Gorski Kotar (ssp. *leimdoerferi*) (Pleše 2005; CONVENTION 2006). Scarcity of data is undoubtedly due to recent ethnic conflicts in this region (van Swaay 2003).

This review of known regional distribution and extinction of *P. apollo* in Europe allowed us to identify areas of particular threat for the species (that may be called 'red spots') as well as areas with very little actual data (that may be described as 'white spots'). Majority of low-altitude localities in Finland, middle, west and south Europe should be considered as 'red spots'. Former localities on the Balkan Peninsula (except from Greece and Bulgaria), Romania and Russia need investigations ('white spots').

Available historical and recent data led us to conclusion that *P. apollo* is the most rapidly decreasing butterfly species over the largest territory examined so far.

MAJOR CAUSES OF APOLLO DECLINE AND EXTINCTION

Observations of *P. apollo* extinction in Europe allowed identifying numerous causes, which can be classified into one of three major categories (Kudrna 1986; Witkowski and Adamski 1996; New 1997; van Swaay and Warren 1999).

1) Natural factors that include long-term climatic changes, habitat succession, and short-term weather anomalies.
2) Anthropogenic factors that include broad impact of industrialization (increased pollution, direct damages to habitats and the insects), and butterfly over-collecting.
3) Intrapopulation factors that include negative processes in small population.

There are many excellent and detailed reviews concerning causes of extinction of numerous butterflies in their biotopes in Europe, as well as in other parts of the world (e.g. Collins and Morris 1985; Kudrna 1995; New 1997). For *P. apollo* the most comprehensive elaboration of this kind was made by IUCN as a compilation of reports prepared by group of national experts (van Swaay and Warren 1999) (**Table 9**). Every identified threatening factor was given an average grade of threat on 1-3 scale (1 – low, 2 – medium, 3 – high threat). However, there are also some other influential factors, that were not included in the IUCN report (Witkowski and Adamski 1996; New 1997).

It is evident from the table that besides threatening factors, directly influencing larvae or imagoes of *P. apollo*, some of them have indirect negative impact via the food-plants or biotope structure (Kudrna 1986; Witkowski and Adamski 1996; New 1997). Moreover, it should be noticed that particular factors have very often region-specific or even site-specific importance, and any attempts of their general quantitative descriptions are biased. Other difficulties for such descriptions result from insufficient data about local threats, and various criteria that were used in particular countries. For example, relatively ample and reliable data collected in Scandinavia and central and west Europe (e.g. in France) make a contrast with insufficient data from the Balkan Peninsula and Russia.

In the following paragraphs, we described majority of identified factors in these categories, going from general to local ones.

Table 9 Relative negative impact of various factors on *Parnassius apollo* populations in Europe.

Type of factor	Average grade of threat*
Natural:	
Fires	3.0
Natural forest and shrubs succession	2.5
Weather catastrophes	3-2**
Isolation and fragmentation of habitat	2.3
Afforestation of non-woodland habitat	2.2
Land claims/coastal development	1.8
Natural ecological changes (including ecotones)	1.8
Decrease of host-plant population	2-1**
Climatic change	1.4
Predation by birds	1.0
Parasites, pathogens, predators, competitors	1**
Anthropogenic:	
Overgrazing	2.5
Afforestation and expansion of introduced ecotypes of spruce (including spruce self-sowing)	3-2**
Agricultural improvements	2.4
Recreational pressure or disturbance	2.1
Felling/destruction of woodland	2.1
Waste disposal sites	2.0
Mining (including limestone)	2.0
Building of vineyards	2.0
Traffic/railway	2.0
Collecting	1.9
Industrial pollution (heavy metals, pesticides, biochemical changes in host-plant under anthropogenic stress)	1.9
Abandonment and change of woodland management	1.7
Built development	1.6
Agricultural abandonment and changing management	1.6
Mistakes in conservation programme	2-1**
Intrapopulation:	
Genetic erosion	3-1**
Natural demographic processes (genetic drift, sex ratio, spatial distribution)	3-1**
Negative growth rate and loss of dispersal ability	2-1**

* – according to van Swaay and Warren 1999; 1 – low; 2 – medium; 3 – high.
** – impact on population according to Witkowski and Adamski 1996.

Natural factors

Long-term climatic changes

Comparison of historic data with present Apollo distribution in Europe lead to conclusion that transient climate cooling, during so called small glaciation episode in the 16-17th centuries, was undoubtedly beneficial for this species. It probably slowed down forest succession and enabled butterfly expansion at lower altitudes. Recently confirmed global warming may have the adverse effect on various populations over the whole continent. It has been documented, that 35% of temperate butterflies in Europe contracted northward by 35-50 km during a few last decades. *P. apollo* also seems to be sensitive to temperature, because it retracted northwards both in northern and southern boundaries of its range (Parmesan *et al.* 1999). More severe Apollo decline in lowland habitats and its survival at higher altitudes correspond with this trend. It was recently documented in southern France, where Apollo survived only in biotopes above 850 m a.s.l. (Descimon 1995; Descimon *et al*. 2005; Parmesan 2006). Phenological shift resulting in earlier hatching of the larvae, observed among French populations of *P. apollo* (Briançon region in the Alps), may be another response to the rise of environmental temperature. In biotopes above 1,900 m a.s.l. adults nowadays appear about a month earlier than in the 1960s (Descimon *et al*. 2005).

Weather anomalies

Weather anomalies may be detrimental to Apollo, particularly when its populations are less abundant (Żukowski 1959b; Krzywicki 1963; Descimon 1995). It was well documented in the Pieniny Mts. In 1957 early and warm spring was followed by a very cold and rainy period with occasional snowfall. It lasted almost a month from the end of June till the end of July. Apollo males emerge from pupa earlier than females, so males that appeared in June could not mate because there were no females yet. When they eventually appeared, after cold weather episode, only a small number of them were fertilized by the few males that survived (Żukowski 1959b). The snowfall episode occurred again in June of 1961 and these two events became population bottleneck (Palik 1981).

At the end of the 1980s Apollo populations died out in Causse du Larzac in the southern part of Central Massif (France) as a result of 'false spring' in winter, followed by returning cold. About ten years later the same happened to population from Vaucluse massif (Descimon 1995; Descimon *et al*. 2005).

Apollo larvae are well adapted to low ambient temperature even if it falls below 0°C – dark colouration of their cuticle allows them to warm up quickly in the sun and feed. This is particularly important in mountain biotopes where maximal daily temperature during the development of younger larval instars seldom exceeds 15°C (Richarz *et al*. 1989). However they are susceptible to high humidity. During cold rainy days larvae stop feeding and almost completely cease their locomotion activity. Hence, periods of heavy rainfalls particularly when accompanied by low ambient temperature significantly slow down larvae development and increase their mortality (Żukowski 1959b; Elmquist 1998; Descimon *et al*. 2005).

Cold and rainy days in June or July decrease intensity of feeding and flight activity of Apollo butterflies. This happens more frequently at higher latitudes and may have remarkable impact on successful mating and production of fertilized eggs (Żukowski 1959b; Krzywicki 1963; Descimon 1995).

On the other hand, high temperatures (above 40°C) may also have detrimental effects on successful completion of the Apollo life cycle. In such conditions last instar larvae readily develop opportunistic diseases resulting in high mortality (Descimon *et al*. 2005). The adult Apollo is a typical 'heliobiont' and prefers warm, sunny days without rainfalls for its normal activity. However drought episodes in the summer accelerate shedding blossom, and butterflies have to take a longer flight on forage for nectar plants (Żukowski 1959b; Descimon 1995; Baz 2002; Ronca 2006). It is conceivable that longer time spent on feeding activity may decrease reproductive success but we did not find confirming data.

Natural forest expansion

Forests are climax ecosystems in large areas of Europe, particularly in the middle and northern parts of the continent. *P. apollo*, like other Papilionidae, is rather a stenobiotic species that prefers sunny, open habitats among which there are abandoned grasslands and meadows in early successional stages (Kudrna 1986; Erhardt 1995). Major negative impacts of forest succession on Apollo populations include fragmentation of formerly large habitats, what also changes their spatial conditions, and decreases availability of foodplants for larvae and adults. Grassland and herb communities with *Sedum telephium* have undergone long-term forest succession over lowland and upland areas in Europe. Despite the fact that forest glades can be suitable habitats for *S. telephium*, this process decreased and eventually eliminated many inhabited and potential biotope areas for 'telephiophagous' forms of *P. apollo* (Palik 1980).

Succession has been observed in Apollo habitats also in the South-European Peninsulas, but due to lower latitudes, grasslands gradually have altered into shrub communities (Kudrna 1986; Munguira 1995; Ronca 2006). Grasslands in alpine and subalpine belts and some rocky biotopes are the least subjected to succession. Hence, natural succession appears to be more threatening for 'telephiophagous' forms of *P. apollo* than for the forms that feed primarily on *S. album*.

Forest or shrub succession have also been observed in many open areas where former livestock pasture was decreased or abandoned, and there were too little – if any – wild herbivores to prevent alterations of existing grassland or herb ecosystems (Dąbrowski 1981; Descimon 1995; Geyer and Dolek 2006).

Predators and parasites

Both larvae and adults of *P. apollo* have aposematic colours (see **Plate 1C, 1D**). However, neither larval nor adult foodplants contain toxic alkaloids. Instead, preferred *Sedum* species contain various phenolic compounds. Hence, this warning coloration seems to be an example of mimicry. In fact, there were observations in the 19th century in the Carpathians that flocks of jackdaws actively looked for Apollo larvae on the mountain screes (Chrostowski 1957), although some contradictory observations are known as well (Niesiołowski 1925).

When Apollo was abundant in the Carpathians its larvae were sometimes infected by parasitic wasp *Exochilum circumflexum*, and parasitic fly identified as *Denteramobia glabiventris* (Niesiołowski 1925). In rearing colony in the Pieniny Mts larvae of *P. apollo* were occasionally attacked by ants (Palik 1980; Witkowski *et al*. 1993). In Turkey Kovanci and co-workers (1999) found common extreme generalist European dipteran *Compsilura concinnata* as parasite of Apollo. Recent observations made by Fred and Brommer (2005) point out also parasitic wasp *Pimpla turionellae* that attacked Apollo pupae.

Currently, in the light of available data, it appears that predators and parasites have negligible – if any – impact on Apollo populations in Europe.

Fires

Fires are not common incidents in natural Apollo biotopes but can have ambiguous impact on its population. They can directly kill all developing stages, which cannot escape but on the other hand, forest fires or shrub fires may have beneficial effect if lead to alteration of forest ecosystem into grassland or xerothermic community that can be further inhabited by Apollo (Munguira 1995; New 1997).

Anthropogenic factors

Human activity exerts multiple impacts on Apollo. Recognized threats include habitat destruction, butterfly collecting, pollution, and tourism.

Habitat destruction

Loss of habitat is considered the most threatening factor for numerous animal species that are in decline (e.g. Kudrna 1986; Pullin 1995; New 1997). Also in the case of *P. apollo* many kinds of human activity (mainly forest management and intensive farming) led to severe shrinkage of its biotopes, both in number and in their size. Heavy deforestation in many regions throughout Europe during industrial revolution caused transient regional expansion of Apollo into new areas and growth of its populations in the second half of the 19th century (Żukowski 1959b) and even in the 20th century (the 1930s-1940s in Finland) (Mikkola 1979). However, later the trend has reversed and various afforestation programmes were implemented in some countries. At first, they had economic reasons, later, in the second half of the 20th century, they were driven mostly by some new ideas in nature protection (Kudrna 1986; Witkowski 1986).

In the course of afforestation, aimed at fast growth of the planted tree biomass, there were introduced tree ecotypes or species (mainly spruce and pine) foreign to particular biotopes. This introduction resulted in an increase in soil acidity and further expansion of these unnatural forests, mainly due to uncontrolled self-sowing of these tree ecotypes in open biotopes – compare photos in **Fig. 6,** see also **Plate 1E, 1F.** There were also obligations for local authorities, at least in Poland, to plant trees over the whole open wastelands that were not suitable for agricultural activity (Żukowski 1959b; Dąbrowski 1981; Witkowski *et al*. 1993). These measures undoubtedly resulted in fragmentation or shrinkage of formerly large Apollo biotopes (**Plate 1G**). In the Sierra de los Filabres (Sierra Nevada, Spain) many xerothermophilous and xerophilous grasslands were planted with American pine species (Kudrna 1986; Munguira 1995).

It may be seen a paradox, but passive protection of Apollo by establishing protected areas, where traditional farming (e.g. sheep grazing) was banned or very limited, led to forest succession and ultimately to extinction of the protected species (Bielewicz 1973; Dąbrowski 1981; Geyer and Dolek 2006).

Fragmentation and isolation of Apollo habitats due to forest succession and afforestation led to concomitant division of formerly large metapopulations into smaller groups. In some cases these groups were able to maintain their genetic variability through ‘corridors’, existing within the fragmented primary area, otherwise small isolated groups were doomed (Chetkiewicz *et al*. 2006; Fred and Brommer 2006; Geyer and Dolek 2006).

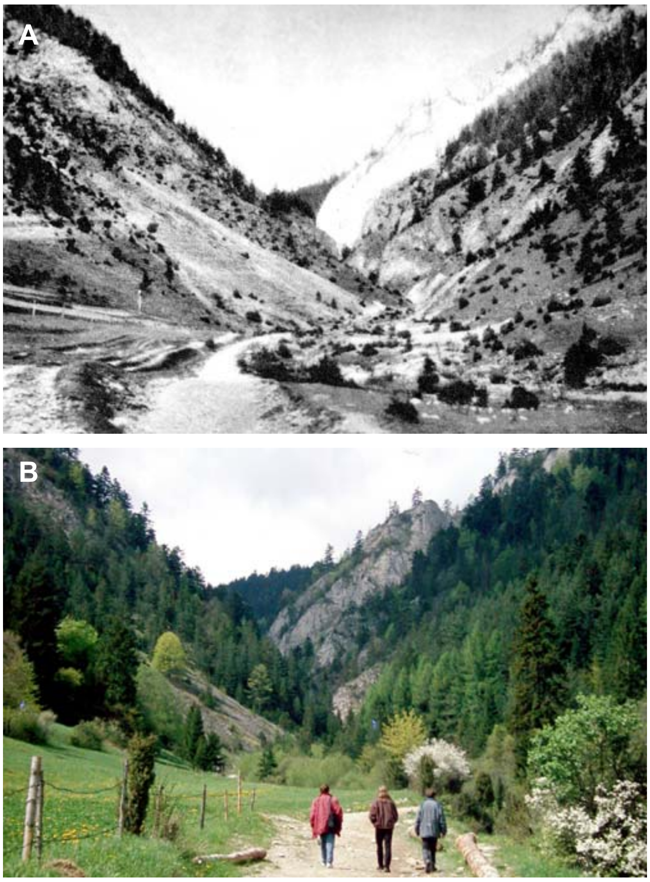


Fig. 6 Sobczański Gorge at Trzy Korony foothils (the Pieniny Mts). (**A**) Past view (the 1920s) (courtesy of K. Karwowski and Pieniny National Park archive); (**B**) Recent view (1995) from the same perspective as in A (photo: M. Nakonieczny).

Sheep or cattle grazing can help prevent habitat loss but overgrazing in mountain pastures above the forest belt has negative effects on Apollo populations. According to Dąbrowski (1981) extensive grazing had significant impact in regions of the middle and southern Europe, but nowadays it is almost insignificant.

Traditional vine growing on sunny hillsides in southern Europe may sometimes promote Apollo survival because there are favourable growth conditions for *S. album*. However, extensive cultivation, its mechanization and pesticide use has adverse effects on Apollo food plant. Abandoned vineyards due to enhanced soil fertility are prone to succession with shrubs that also drive out the stonecrop and may lead to Apollo extinction (Kinkler 1987; Richarz *et al.* 1989). Interesting study on Apollo survival in such areas was carried out by lepidopterologists from North Rhine-Westphalia (Nordrhein-Westfalen) (Kinkler *et al*. 1987).

Profound land transformations usually have rapid and very devastating effects on Apollo habitats and its populations. They include opencast mines, quarries, road construction and settlement building to name the more important. However, Nikusch (1991) described an example from Baden-Württemberg in Germany that deforestation of the wide stripe along the built road and levelling works created suitable conditions for the stonecrop and Apollo inhabited later these sites. He did not provide relevant data, but heavy road traffic undoubtedly may cause increased mortality of the butterflies (Dąbrowski 1981). Abandoned drifts in closed quarries and mines that are at early stages of succession also may offer favourable conditions not only for Apollo, but also for the whole communities of thermophilic plants and insects (Geyer and Dolek 2006).

Among anthropogenic factors that lead to the habitat loss or decrease of its area suitable for the species there is also traditional grassland and meadows burning in the spring.

Butterfly collecting

Butterfly collecting negatively influenced many Apollo populations in the past and could lead to decline of those less abundant. Apollo undoubtedly can be described as ‘panoramic’ species that is easy to recognize and for its ‘aesthetic (decorative) value is a praised «must» to every collector, preferably in a long series of specimen’ (Kudrna 1986). Today, when the butterfly is protected by international law and its trade is restricted, collecting has only local and probably insignificant effect on existing populations (van Swaay and Warren 1999). Official CITES Report of the Working Group points out illegal trade in Germany and Slovakia, where specimens from the Carpathians are particularly wanted. In other countries specimens originating from special colonies, or from private collections dated back to the 19th century, may be a subject of trade or exchange. CITES Secretariat and UNEP-WCMC registry contains data about all legal transactions of living butterflies or collection specimens. According to this registry 357 Apollo imports, mainly from neighbouring countries, and 765 specimens and living insects exports were recorded in the period 1977-2000 (CITES 2002).

Pollution

The hypothesis that increased environmental pollution (e.g. by heavy metals) may be responsible for rapid Apollo decline in some regions of Europe in recent decades, was put forward only in the late 1980s (e.g. Bengtsson *et al*. 1989; Janzon 1990). Main assumption is that increased emissions of CO_2, NO_x and SO_2 into the atmosphere lead to acid rains over large areas of the continent and subsequent soil acidification. Low pH may increase bioavailability of various toxic metals deposited in the soil (e.g. Al or Cd), hence facilitate their uptake by *Sedum* and then by the larvae. One can expect, that soils with good buffering capacities would release much less of the deposited metals into the biota than soils with low buffering capacity.

Indeed, some supporting evidences were gathered in Sweden. Bengtsson *et al*. (1989) have shown that Apollo disappeared from biotopes with crystalline, rocky substrates but persisted in regions with calcareous bedrocks. Janzon (1990) observed similar trend when compared mainland populations with that from nearby Gotland Island. Limestone acts as pH buffer then can protect Apollo food-plant against both acid precipitation and metal pollution.

Measurements of various metals content in the livelong orpine leaves and sprouts did not provide convincing evidence that heavy metals could play an important role in Apollo decline. In fact, *S. telephium* cumulates higher amounts of metals (Al, Fe, Cd, Zn, Pb) present in the soil in comparison with other plants growing in the same site (Nuorteva *et al*. 1993; Nakonieczny *et al*. 1996; Kędziorski and Nakonieczny 2000b). Finnish studies also revealed that average metal levels in the livelong orpine sprouts were higher in localities where *P. apollo* had disappeared than in areas where it survived, although significant differences were stated only for Al and Fe. The highest bioconcentration factor (BCF) stated for Cd (2.59) suggests that high level of this metal in the soil may be a real threat for Apollo larvae via their food-plant (Nuorteva 1990; Nuorteva *et al*. 1993; Nieminen *et al*. 2001). Feeding the larvae with 'foreign' plants, collected in former Apollo habitats resulted in slowing down their development and increased mortality (Bengtsson *et al*. 1989; Nieminen *et al*. 2001).

Recently Fred and Brommer (2005) have shown that larvae from the coastal population, fed on *Sedum* with higher Cd and Zn content (4.4 and 170 ppm dry weight respectively), had a higher asymptotic weight than the archipelago larvae (1.9 ppm Cd and 100 ppm Zn). Studying correlation between acid rain and disappearance of Apollo populations from coastal areas in Norway Gogstad (2000) has shown lower pH values in *Sedum telephium* ssp. *maximum* in current Apollo locations than in the former ones. The plants also had higher buffer capacity. Unfortunately, measurements were done during summer, when larval development is almost completed, hence the reader may only guess from available data, that during period of intense feeding the buffer capacity of the food-plants is considerably lower, irrespectively of the place of their origin. These findings lead to conclusion that, in recent several years, acid rains and heavy metals were not responsible (may be with few exceptions) for decline of Apollo populations in Northern or central Europe.

Pollution by pesticides could also be harmful to Apollo but this threat was probably local and limited to vicinities of agricultural areas (Richarz *et al*. 1989; Erhardt 1995; Geyer and Dolek 2006). Nowadays it probably has no measurable impact on Apollo butterfly.

Despite the scarcity of solid data on pollution impact on Apollo decline in Europe, it is conceivable that in previous decades when pollution was much higher, its detrimental effects to Apollo populations could be significant.

Tourism

In the past site destruction by great number of tourists was sometimes observed, e.g. at Mont d'Or in the Massif Central (Napolitano *et al*. 1990). Nowadays, it does not seem to be a serious threatening factor to Apollo in Europe. Ski runs, due to sporting facilities situated above the forest belt in mountainous areas, may do some harm to Apollo food plant (*S. album*) during sporting events played in the spring, when a snow cover melts in the sun and does not protect the plants underneath (Erhardt 1995).

Intrapopulation factors

So far, studies concerning polymorphism within and among European Apollo butterfly populations used allozyme electrophoresis and they were carried out only in France (Napolitano *et al*. 1990; Descimon 1995; Descimon *et al*. 2001). On the basis of morphological characteristics and allozyme variations there were identified three large and distinct populations: one in the Pyrenees, the second in the Massif Central, and third in the Alps. However, biochemical polymorphism within these populations was very small, while biometric criteria allowed identification of some subspecies (Descimon 1995; Descimon *et al*. 2001).

Population dynamics in these large groups of *P. apollo* in France showed differences from classical metapopulation characteristics, so they were described as pulsating metapopulations. In such population fluctuations in abundance occur within the occupied range. Sub-populations extinction and withdrawal from some habitats into refuges can be followed by expansions of individuals from these refuges in more favourable periods of population growth. In fact, all the isolated populations showed very small degree of heterozygosity with lack of distinctive isozymes (Napolitano *et al*. 1990; Descimon 1995; Descimon *et al*. 2001). The authors conclude that such small genetic divergence among these populations reflects their recent spatial separation rather than different selective pressure.

Irrespective whether Apollo metapopulations in general are more classical or pulsating type it is obvious that their long-term survival requires connectivity of many smaller subpopulations. Progression of their spatial isolation and habitat destruction may irreversibly destroy structure of metapopulation. Small isolated groups are particularly vulnerable to genetic erosion and negative demographic trends. It was studied in the Pieniny Mts, where about 30 larvae that survived in the last locality were used for population recovery (Witkowski and Adamski 1996). Population bottlenecks increased the genetic drift and inbreeding in this small deme during the restitution programme. Pupae deformations and high mortality (above 50%), emergence of imagoes with underdeveloped or deformed wings could be ascribed to genetic erosion within the deme (Witkowski *et al*. 1993; Adamski and Witkowski 1999). Adult males displayed changed mate-searching behaviour that influenced sexual selection (Adamski 1999). These effects led to disappearance of natural migratory behaviour and negative population growth (Witkowski and Adamski 1999). Change of dispersal behaviour of adult individuals in dependence on the population size was documented also in French populations of Apollo by Descimon (1995).

Small *P. apollo* populations from the higher altitudes in the Alps in some cases may suffer from introgression of *P. phoebus* genes. Different habitat and phenology are insufficient pre-mating barriers to prevent inter-specific crosses and the hybrids are observed quite frequently in localities where habitats of these two species are closely interspersed and phenology is perturbed. It was also evidenced that hybrid males are highly fertile and can backcross with females of both species (Deschamps-Cottin *et al*. 2000; Descimon and Mallet 2007, and references therein).

PROTECTION OF *PARNASSIUS APOLLO* – DIRECTIONS AND MEASURES

Various actions, taken to protect Apollo in particular European countries (see **Table 10**), roughly fall into one of two main categories: 1) passive protection measures and 2) active protection measures.

Passive protection

The first legal protective measures aimed to prevent the Apollo decline due to overcollecting. In 1936 in Germany, an appropriate regulation was introduced and included *P. apollo* together with two other *Parnassius* species and *Iphiclides podalirius*, as the first protected insect species. Unfortunately, this protection did not include Apollo habitats (Kudrna 1986). Apollo was also the first invertebrate species entered into international CITES list to monitor and control its trade more effectively. These measures made it a

Table 10 *Parnassius apollo* conservation measures taken in European countries (van Swaay and Warren 1999).

Type of conservation measures	Countries
Legal protection of species (no capture, trade, etc.)	A, AL, AND, BIH, BY, CZ, D, E, F, FIN, FL, FYROM, HR, RO, RUS, SK, SLO, UA, YU
Legal protection of important butterfly habitats	A, AL, BIH, D, E, FYROM, HR, RO, RUS, SK, SLO, YU
Habitat management: there is special attention for the species	AL, D, SK
Ecological research on the requirements of the species has been conducted	D, E, RUS, SK
All populations are monitored on a regular basis (e.g. every 1-5 years)	SLO
At least part of the populations are monitored (e.g. every 1-5 years)	D, F, FIN, S, SK
Other measures taken (reintroduction in several localities)	CZ, LV

Table 11 Legislation measures protecting *Parnassius apollo*.

Document	Comments
Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) – Washington Convention	Included in Appendix II: – species which although not necessarily now threatened with extinction may become so unless trade in specimens of such species is subject to strict regulation in order to avoid utilization incompatible with their survival.
Convention on the Conservation of European Wildlife and Natural Habitats – Bern Convention	Included in Appendix II – strictly protected fauna species.
Council Directive of European Union (Habitats Directive 92/43/EEC of 21 May 1992) on the conservation of natural habitats and of wild fauna and flora	Included in Annex IV – Animal and plant species of Community interest in need of strict protection.
Council Regulation of European Union (CE 338/97 of 9 December 1996) protecting species of wild fauna and flora by regulating trade therein	Included in Annex A (an equivalent to CITES Appendix I).

well recognized world symbol of invertebrates' protection (New 1997; van Swaay and Warren 1999).

At present *P. apollo* is protected by the local or international law in Austria, Bulgaria, the Czech Republic, Germany, Greece, Italy, Liechtenstein, Poland, Slovakia, Slovenia, Spain, Sweden, Switzerland, the Former Yugoslav Republic of Macedonia and Yugoslavia. International regulations protect the butterfly in the Former Yugoslav Republic of Macedonia (the Bern Convention) and in Sweden, where Directive 43/92 EEC, commonly called the Habitats Directive remains in effect. The protection range of the particular regulations varies but usually involves ban on catching insects in the wild, killing them, poisoning, selling, buying and exporting, and also disturbing in their habitat. There are fines, sometimes quite high, for breaking these regulations. In majority of European countries, Apollo is listed in national Red Lists, Red Books and Catalogues of Endangered Species, or other similar documents. International legislative measures according to CITES (2002) and van Swaay and Warren (1999) are given in **Table 11**.

Active protection

Habitat preservation and Apollo monitoring

Passive protection itself cannot counteract the complexity of factors responsible for Apollo decline. In the 1970s in Poland experts report was prepared for Tatra National Park to define conditions necessary for sustaining the local Apollo population (Dąbrowski 1980, 1981). Until now there are not many examples of active protection of Apollo in Europe. In Bulgaria habitats are actively maintained but only these ones within existing nature reserves and national parks. 'Plan of Action' set up in the Czech Republic protects habitat for reintroduced population in Štramberk (see below). Habitats conservation and enlargement were also done in abandoned vineyards in the Moselle valley (Germany), in Pieniny National Parks in Poland and Slovakia. Protective measures in the Polish part of the Pieniny Mts were directly relevant to Apollo recovery plan launched in 1991 (see **Box 2**). Habitat preservation in the Slovakian part of the Pieniny Mts enabled further Program of Protection aimed at stability of local Apollo populations (CITES 2002; Žlkovanová *et al*. 2004; Konvička 2005).

Habitat preservation appears to be one of the most important tasks in any programme of active protection of *P. apollo*. It includes trees and shrubs removal from the sites inhabited by both larvae and adults, and estimation of food-plants resources within the site. Depleted resources have to be enlarged e.g. by planting. Food plants for larvae and adults should also be planted in the sites recovered or newly prepared for Apollo introduction and their population should be monitored, particularly after introduction of the insects (Wala 1995; Witkowski and Adamski 1996; Fred and Brommer 2003; Geyer and Dolek 2006). Fred and co-workers showed increase of Apollo population dynamic when larval and adult food plants patches were crossing in the same habitat – fecundity of the adults was greater than in sites where larval and adult food plants were spatially separated (Brommer and Fred 1999; Fred *et al*. 2006). Availability of food plants for all developmental stages of *P. apollo* in close vicinity from each other seems to be particularly important in the sites where formerly large metapopulations were fragmented and separated into smaller ones. In such populations any corridors enabling gene flow should have a beneficial effect on Apollo population (Matter and Rolland 2002; Chetkiewicz *et al*. 2006).

Preservation of habitat usually goes hand in hand with regular Apollo monitoring, assessing effectiveness of the protective actions. In fact, these measures can have much broader beneficial impact than the relative stability of Apollo population. Kudrna (1986) pointed out that active protection of Apollo habitat preserves the complex plant and animal communities living there, hence this butterfly becomes an 'umbrella species' for the whole ecological system.

Surprisingly, opening Apollo sites for tourists may also have a beneficial effect on the species. Special routes like 'Apolloweg' in Valwig in the Moselle valley, various exhibitions and printed leaflets may help the development of awareness that tiny living creatures also need protection and are worth of it (**Plate 1H**, **1I**).

Planned reintroduction and breeding colonies

The first attempts to introduce Apollo into sites, where previously it occurred, were done already in the end of the 19^{th} century. German entomologists tried to do so in a few localities situated in the Karkonosze Mts and its foothills, and in Cieszyn Silesia (Śląsk Cieszyński). Later Chrostowski, then Palik tried to introduce Apollo into new habitats in the Carpathians. All the attempts eventually failed (see **Table 12**) probably due to 'incompatibility' between selected Apollo subspecies and the food plant growing on the site, or due to insufficient food resources. There could be other reasons of failure: inappropriate site selection; impact of threatening factors that was not eliminated or diminished; release of mated females (that most often escaped from habitat) instead of larvae (Witkowski 1989). As Descimon (1995) briefly pointed out – 'reintroductions are conceivable, but will be successful only if seriously designed'.

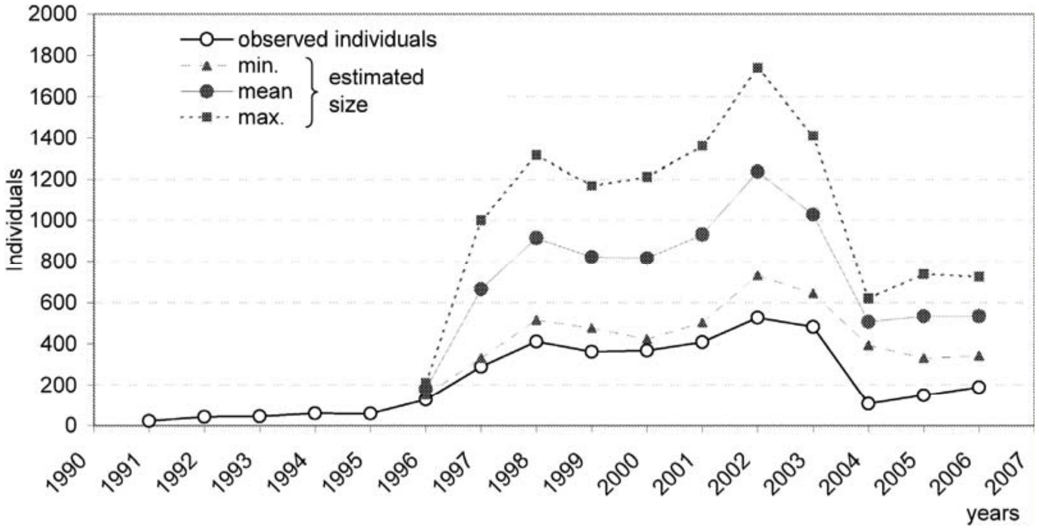
More recent efforts of planned introduction appear to be

BOX 2. RECOVERY PLAN FOR *PARNASSIUS APOLLO* IN THE PIENINY NATIONAL PARK (1991-2006).

In 1991 only one site at Trzy Korony (BrE: Three Crowns massif) with about 30 butterflies was identified in Pieniny National Park (**Plate 1E, H**). This was the last chance to launch a programme aiming at restitution of *P. apollo* ssp. *frankenbergeri* in its former habitats. It was cooperative effort that involved staff from Pieniny National Park in Poland (Pieniński Park Narodowy – PPN), the Institute of Environment Protection of Polish Academy of Science in Cracow, and Pieniny National Park in Slovakia (Pieninský Národný Park – PIENAP). Financial support for the project came from the Polish governmental departments and from National Environment Protection and Water Management Fund. There were three major tasks to do: 1) setting up breeding colony in semi-natural conditions (for preserving and gradually expanding the size of 'wild' population by releasing the bred larvae and butterflies); 2) restoring the sites once inhabited by Apollo (by removal of growing trees and bushes and creation of proper conditions for the larvae and butterflies released into the wild) (**Plate 1E**, **1F**); 3) enlarging food-plant resources in the habitats planned for its re-introduction (**Plate 1G**). Later, the Little Pieniny Mts (Małe Pieniny), situated outside Pieniny National Park area, were also included into this restitution plan.

Since the beginning, population was continuously monitored (with the use of capture-recapture method) and data on its abundance and eventual migrations of the butterflies were gathered. However, despite a slow increase in population size, inbreeding resulted in genetic degeneration of the individuals. To enrich the genetic pool of the deme, females from the colony were fertilized by wild males from Haligovske Rocks (Haligovske Skaly) in Slovakian part of the Pieniny range. Such 'enrichment' was repeated several times in consecutive years. Current observations confirm that butterflies fly between the habitats that used to be isolated, and between the restored sites (e.g. shown on the **Plate 1E-1G**).

Recent estimates show that about 800-1,000 butterflies live in Pieniny National Park every year. In 2004, a significant decrease in the population size was observed, probably due to cold weather and long rainfall periods during the caterpillars' intense feeding and growth phase. The count of the individuals done in 2005 and 2006 indicate that the population size increased again (see figure below).



Observed and estimated abundance of adults of *Parnassius apollo* ssp. *frankenbergeri* in natural biotopes of Polish Pieniny Mts during restitution programme 1991-2006. Data obtained from yearly monitoring reports, prepared for Pieniny National Park by Adamski P, Kosior A, Olejniczak P, Witkowski Z (1996-2006), and from Witkowski and Adamski (1996).

successful (**Table 12**). Albophagous *P. apollo* ssp. *antiquus* from Slovakia was introduced into habitats formerly occupied by ssp. *strambergensis* (also albophagous) in Štramberk environs in the Czech Republic (Lukášek 1995). Other successful measures include reinforcements done in Moselle valley (Kinkel *et al*. 1987; Richarz *et al*. 1989) and in the Pieniny Mts (Witkowski 2004). Recently intensive works are carried out on habitats recovery in Bavaria (the Frankonian Jura) as a part of Apollo establishment programme (Geyer and Dolek 2006).

Recent trends underline the importance of native individuals use in re-establishment programmes. Since many Apollo populations are in decline, one should seriously consider establishing of semi-natural or artificial colony in the site of planned introduction (Żukowski 1959b; Palik 1980; Descimon 1995). Efficacy of this method was confirmed during the Apollo reinforcement programme in the Pieniny Mts. Breeding a semi-natural colony was set up in 1991 just in the beginning of the programme and every year provided larvae and individuals that were gradually released into the enlarged habitats. The insects are raised through the whole life cycle in large glass insectaries. The bottom is covered with soil layer taken from natural Apollo habitats with planted livelong orpine and a few other crassulacean species, and some mosses. This provides the food and shelter for the hatched young and growing larvae. The larvae are exposed to all weather conditions just like insects in the wild, except for heavy rain episodes, when the insectaries are covered by glass lids. Older larvae that have higher consumption rate are fed on freshly cut livelong orpine sprouts growing within or outside Pieniny National Park. Adult males are released into the screes but females are exposed to males in their natural habitat, and after mating taken back to the colony to lay eggs for the next generation. Adults kept in the colony are fed on nectar plants collected in the field and females are offered a natural substrate to lay eggs. Since the beginning all these duties have been managed by one man, Tadeusz Oleś who gained great experience that allowed him to eliminate most of factors with possibly detrimental effect on Apollo developmental stages.

There are some limitations in captive Apollo breeding. The phenological synchronization of Apollo development with vegetative phase of the larval food plant allows breeding successfully only one generation per year. Shortening diapause of the first instar larvae resulted in great mortality of the hatched individuals that had to feed on fully-grown plants in a generative phase of their life cycle (Wala 1995; Geyer and Dolek 2006). Plants growing in changed photoperiod or temperature conditions were unpalatable to larvae – they vomited or had diarrhoea and eventually died (Moser and Oertli 1980; Ekkehard 1986; Richarz *et al*. 1989). We made similar observations when we offered cut sprouts kept in water for more than one day to the last instar larvae. We also do not know of any successful attempts to feed Apollo larvae on artificial or semi-artificial diet.

A survey of available data revealed that a similar breeding colony was set up in the Pieniny Mts in Slovakia. There are also registered breeding facilities in Spain, and in Sweden *P. apollo* is bred legally by a few enthusiasts (CITES

Table 12 Establishment efforts for *Parnassius apollo* undertaken in Europe.

Date	Leader	Place	Type of acitvity*	Source of insects and food-plant	Result	References
19th century	Silesian entomologists	The Sudetes (Poland) – Wałbrzych Mts, Kłodzko Basin, Śnieżnik Kłodzki Mt., Sobótka Mt., Silesian Stronie town	I	Unspecified	failure	Pax 1921 (see Witkowski 1989)
19th century	Silesian entomologists	The Sudetes (Poland) – Krucza Skała Mt. near Lubawka	I	Individuals from Tirol	failure	Marschner 1932 (see Witkowski 1989)
1880s	The Silesian Society of Insect Research	Lower Silesia (Poland) – environs of the Książ castle	I	*P. apollo* from Swabia and *S. album*	failure	Niepelt 1912; Pax 1915; Ruediger 1926 (see Witkowski 1989)
1912	W. Kuhnau – chairman of the Silesian Society of Insect Research	The Sudetes (Poland) – Karkonosze Mts	I	*P. apollo* ssp. *melliculus* from Regensburg and *S. album* and *S. telephium*	failure (extinct in 1927)	Wolf 1927 (see Witkowski 1989)
1912	W. Niepelt	The Sudetes (Poland) – Wałbrzych Mts	RI	*P. apollo* ssp. *melliculus* from Regensburg and *S. album* and *S. telephium*	failure	Witkowski 1989
1948	M. Chrostowski	The Carpathians: Low Beskids (Poland) – vicinity of Biecz town	I	*P. apollo* from Pieniny Mts and *S. maximum*	failure	Witkowski 1989
1980	E. Palik	The Carpathians (Poland)	E	Unknown	failure	Witkowski 1989
1986 - 1993	J. Lukášek and J. Ašmer (Univ. Ostrava and Czech Union of Nature Protection	The Carpathians: Moravian – Silesian Beskids (Czech Republic) – Štramberk	I	*P. apollo* ssp. *antiquus* from Velký Manín canyon in the Strážovské Hills (Slovakia) and *S. album*	success	Kuśka and Lukášek 1993; Lukášek 1995
1991-2001 and 2002-now	Z. Witkowski and Scientific Board of Pieniny National Park	The Carpathians (Poland) – Pieniny Mts National Park	RF	Native population of *P. apollo* ssp. *frankenbergeri* and *S. telephium* ssp. *maximum* from Pieniny	success	CONVENTION 2006
1994	J. Budzik	The Sudetes (Poland) – Kruczy Kamień reserve	I	*P. apollo* ssp. *frankenbergeri* × *P. apollo* ssp. *melliculus* and *S. telephium*	failure	Buszko 1997
after 1995	-	The Massif Central (France) – Puy-de-Dôme Mt.	RE	*P. apollo* ssp. *arvernensis* from Chaudefour Valley	success	Descimon 1995; Descimon *et al.* 2005
from 1977	Working Group 'Rettet den Moselapollo'	Mosel Valley	RF	Native population of *P. apollo* ssp. *vinningensis* and *S. album*	success	Kinkler *et al.* 1987; Richarz *et al.* 1989
1990-now	A. Geyer and M. Dolek – Büro für ökologische Forschung und Planung	Franconian Jura (Germany) – Altmühltal Naturpark	E	Habitats of native population of *P. apollo* and *S. album*	-	Geyer and Dolek 2006
1997-now	Project 'Apollo' – Department of Nature Protection	Whole Slovakia	E	Habitats of native population of *P. apollo* and *S. album*, *S. telephium* ssp. *maximum*	-	Žlkovanová *et al.* 2004

*- according to New 1997:
- Re-establishment [RE] – release and encouragement of a species in an area where formerly occurred but is now extinct;
- Introduction [I] – attempting to establish a species in an area to where it is not known to occur or to have occurred previously;
- Reintroduction [R] – an attempt to establish a species in an area to which it has been introduced but where that introduction has not succeeded;
- Reinforcement [RF] – attempting to increase population size by releasing additional individuals into the population;
- Translocation [T] – the transfer of individuals from endangered site to a protected or neutral one;
- Establishment [E] – neutral term used to denote any artificial or intentional attempt to increase numbers by transfer of individuals.

2002).

Described measures should counteract or eliminate at least major threats of anthropogenic origin that caused Apollo decline in a particular site. Hence, identification of specific local threats and their relative contribution to population decline should precede any further protective measures. Various directions for Apollo conservation in Europe were summarized in **Table 13**. However, it is unquestionable that only a large and stable population can withstand some negative influences both of anthropogenic and natural origin. The latter may be particularly problematic due to their large-scale effects. A population that is strong enough can survive unexpected weather anomaly when it rarely happens. Frequent events of this kind or long-term climatic trend may require human interventions to maintain remaining variability of this scenic butterfly. These emphasize the importance of setting-up natural or semi-natural breeding colonies of local Apollo populations. Particularly helpful in this respect could be commercial or public 'Butterfly gardens' with only low additional costs incurred. In a broader perspective, any efforts leading to the decrease in the greenhouse effect are beneficial for this and numerous other insect species (Parmesan *et al*. 1999).

Table 13 Directions for Apollo conservation proposed by national compilers (van Swaay and Warren 1999, modified).

Begin or improve monitoring
Legally protect habitats
Carry out ecological research on species requirements
Implement reintroduction programmes
Restrict recreational activities
Implement extensive grazing
Avoid overgrazing
Avoid natural afforestation
Improve habitat management
Stop development of mountain areas with sensitive populations
Enforce measures prescribed by law

Descimon (1995) calls for ecological studies that allow better understanding the mechanisms of Apollo adaptation into changing environment. We postulate that physiological, biochemical and genetic investigations are also necessary

Table 14 Selected web pages as a source of valuable information on Apollo butterfly in Europe (in alphabetical order).

Page title	WWW address	Comments
Apollo butterfly	http://goodnightstories.com/wildlife/insects/card50.htm	For laymen, short but competent information about Apollo.
Artenhilfsprogramm Apollofalter	http://www.geyer-und-dolek.de/apollo.htm	Exhaustive description of Apollo biology and establishment programme in Naturpark Altmühltal in Bavaria.
Artrópodos protegidos en Aragón (III): *Parnassius apollo* L. 1758 y *P. mnemosyne* L. 1758 (Lepidoptera: Papilionidae), Antonio Torralba Burrial	http://scriptusnaturae.8m.com/Articulos/1998Onso17710.htm	Exhaustive information about Apollo biology and protection measures with special emphasis put on Spain; includes many Spanish references.
Butterflies of Norway, *Parnassius apollo*	http://www.nagypal.net/norge/apollo.htm	Concise but almost complete information about two Apollo subspecies from Norway, including informative photos and long list of references.
Centre Suisse de Cartographie de la Faune (CSCF & KARCH & CCO & KOF)	http://lepus.unine.ch/carto/identify.asp	Useful database on Apollo (and many other species) historical and present distribution in Switzerland; map grid resolution: 5 × 5 km).
Database: Butterflies of Poland, Buszko Jarosław, Kartanas Edmund	http://motyle.biol.uni.torun.pl/atl/t4.htm	short info with photos about Apollo – in Polish.
Der Apollofalter, gehalten am Studientag 1993; von Florian Michahelles und Holger Frank	http://www.cip.ifi.lmu.de/~michahel/RefServ/apollo.htm	Concise text about *P. apollo* in Germany.
Der Apollofalter (*Parnassius apollo* L. 1758), (Rote Liste Bayerns: Gefährdungsgrad 2)	http://www.bundnaturschutz-eichstaett.de/schmetterlingsforum/papollo.htm	*P. apollo* ssp. *melliculus* from Bavaria – its biology and habitat; include beautiful photos.
Der Mosel-Apollofalter: Vorkommen, Gefährdung und heutiger Schutz, von Helmut Kinkler	http://www.nabu.de/nh/200/mosel200.htm	Concise info about biology and protection of *P. apollo* ssp. *vinningensis* in Moselle Valley.
Druhová ochrana živočíchov, Ochrana jasoňa červenookého na Slovensku	http://www.sazp.sk/slovak/periodika/chus/35/13.htm	History of Apollo protection in Slovakia with detailed description of the ongoing 'Project Apollo'.
Familia Papiliónidos; *Parnassius apollo* subsp. *Nevadensis*, Apolo o pavon diuno, Merche S. Calle y Juan Enrique Gómez	http://waste.ideal.es/parnassius.htm	Short info with photos about Apollo from Sierra Nevada in Spain.
Land Salzburg, Apollo (*Parnassius apollo*)	http://www.salzburg.gv.at/apollo.htm	Official site of Salzburg state government (Austria) with short info about Apollo.
Lepidoptera and some other life forms, *Parnassius* Latreille, 1804	http://www.funet.fi/pub/sci/bio/life/insecta/lepidoptera/ditrysia/papilionoidea/papilionidae/parnassiinae/parnassius/index.html#apollo	On this page devoted exclusively to *Parnassius* one can find plenty of data about Apollo zoogeography and systematics, as well as numerous photos and external links to relevant pages.
Naturhistoriska riksmuseet	http://www2.nrm.se/en/svenska_fjarilar/p/parnassius_apollo.html	Map of Apollo distribution in Sweden, and some photos.
Niepylak apollo (*Parnassius apollo*)	http://www.zzw-niedzica.com.pl/niepylak.htm	Biology, distribution and reintroduction of Apollo in the Pieniny National Park – in Polish.
Parnassiinae – Jasone	http://www.motyle.sk/papi/2319_apollo.htm	Excellent photos of Apollo from Slovakia, and some basic info about the species.
Parnassius apollo 2000, 2001, 2002, 2003	http://www.medri.hr/~dwolfl/apolon/apolon.htm	Exact chronology of Apollo development in 2000-2003 with many video, photo and audio materials; very interesting site but difficult to navigation – in Croatian.
Parnassius apollo (Linnaeus 1758); Apollo	http://www.perhostutkijainseura.fi/historia/papilionidae/par-apollo.htm	All about Apollo in Finland plus photos, phenology charts and maps showing its decline in the country; list of relevant references also provided – the page is in Finnish.
Parnassius of the world	http://www.geocities.com/tgorw_sm/gw1.html?20068	Short info on Apollo in Scandinavia with informative visualisation of distribution change in Sweden and Norway.
Polish Red Book of Animals, Invertebrates, *Parnassius apollo*, niepylak apollo, Apollo Butterfly	http://www.iop.krakow.pl/pckz/opis.asp?id=82&je=pl	Exhaustive description of Apollo biology, decline and historical distribution in Poland – in Polish.
Prime butterfly areas – Bulgaria	http://www.netempire.biz/butterfly_areas_bg/species/09_apollo.htm	Detailed list of all Apollo sites in Bulgaria and their map with overlaid UTM grid.
Protected insect species in Finland	http://www.funet.fi/pub/sci/bio/life/protected.html	Amounts of fines for illegal catchments of Apollo and other insects in Finland.
Rapport d'études de l'OPIE, vol. 1, janvier 1995, La conservation des *Parnassius* en France, aspects zoogéographiques, écologiques, démographiques et génétiques, par Henri Descimon	http://www.inra.fr/internet/Hebergement/OPIE-Insectes/re-parnass.htm	Very good and informative report summarizing knowledge on Apollo, particularly in France; included also maps and few photos.
Swallowtails - Papilionidae: Apollo - *Parnassius apollo* (Linnaeus 1758)	http://www.toyen.uio.no/norlep/english/papilionidae/apollo.html	Short but informative info about Apollo in Norway with list of useful references.
Ukrainian Butterflies from 'ALEXANOR'	http://www.alexanor.uzhgorod.ua/ALEPRO00.HTM	Exhaustive description of long-term monitoring project of Lepidoptera populations of West Ukraine, provided by Sergey G. Popov; confirm Apollo extinction in the East Carpathians within Ukrainian borders.

for adequate protective measures for this species. International Research Programme, e.g. within 'Framework Programme 7' of EU, combining experience of specialists working in the field seems to be the best possible option for developing long-term and effective strategies ensuring Apollo survival in Europe.

CONCLUSIONS – PROTECT OR LET IT DIE?

The question posed in the title seems to get positive answer. Recent meetings of experts within Animals Committee of CITES or within Bern Convention considered present status of *P. apollo* in the world and various issues of its protection (CITES 2002; CONVENTION 2006). As already mentioned in the previous section a growing number and variety of measures concerning protection of Apollo have been undertaken. The reasons lying behind them were postulated by various authors and can be listed as follows (Kudrna 1986; Kędziorski and Nakonieczny 2000a).

1. It is one of the biggest European butterflies, easy to recognize in its habitat.
2. It is now recognized as symbol of endangered terrestrial invertebrates.
3. It may function as so called 'umbrella species'; it means that protection of that kind of species protects a wide range of co-existing species in the same habitat, which may be lesser-known and difficult to protect.
4. For the same reason *P. apollo* may be a good 'indicator species' which status provides information on the overall condition of the ecosystem; especially it seems to be a sensitive indicator of environmental quality in monitoring of endangered xerothermic biotopes.
5. It displays high intra-species variability due to distribution of its population in isolated habitats.
6. It may serve as a 'flagship species' which appeals to the public and has other features that make it suitable for communicating conservation concerns.

Growing interest in *Parnassius apollo* is also reflected by a considerable amount of relevant internet information. One of the most popular web searching services returns about 69,000 WWW pages and 1530 of them contains 'Parnassius apollo' in the title. They contain nearly 1,000 images (mainly colourful photos) and about 13,800 PDF documents. 'Scirrus for science' returns 886 documents, including 27 journal results, 9 preferred web results and 850 other web results. In **Table 14** we enclose list of these web pages that we found as particularly reliable and useful source of recent information on Apollo butterfly in Europe.

Thousands of web pages contain little information on Apollo but they refer to local collections of images, presentations, sometimes include reports and descriptions of small-scale actions for protection of local environment. The pages are mastered not only by amateur entomologists but also by students of secondary schools. Thus, Apollo may become one of a few species that will commonly appear as a symbol in broader context of environmental issues. It may be particularly useful in education, turning pupils' attention to small living creatures that also deserve protection. This idea was obvious for native highlanders in the Tatras already in the 19th century. They extended existing regulations that protected marmots and chamois onto small 'Hapollok' implying that all species inhabiting the mountains constitute the one inseparable entity (Kawecki 1970).

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