

Influence of resource distribution and abundance on the population structure and dynamics of *Parnassius apollo*

Marianne S. Fred

*Integrative Ecology Unit
Faculty of Biosciences
Department of Biological and Environmental Sciences
University of Helsinki
Finland*

Academic dissertation

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Author's address

Department of Biological and Environmental Sciences
P.O. Box 65 (Viikinkaari 1)
FIN-00014 University of Helsinki
Finland

E-mail: marianne.fred@helsinki.fi

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- I** Brommer, J.E. and Fred, M.S. (1999) Movement of the Apollo butterfly (*Parnassius apollo*) related to host plant and nectar plant patches. *Ecological Entomology* 24;125–131.
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- II** Fred, M.S. and Brommer J.E. Resources, dispersal and spatial synchrony of *Parnassius apollo* in an archipelago population. Manuscript
- III** Fred, M.S. and Brommer, J.E. (2003) Influence of habitat quality and patch size on occupancy and persistence in two populations of the Apollo butterfly (*Parnassius apollo*). *Journal of insect conservation*, 7: 85–98.
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These are referred to by their Roman numerals.

Contributions

	I	II	III	IV	V	VI
Initial idea	MF, JB	MF	MF	MF	MF	MF
Material	MF, JB	MF	MF	MF	MF	MF
Model	–	–	–	JB	ROH	JB
Analyses	JB, MF	MF	MF	MF	MF	JB, MF
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MF: Marianne Fred¹, JB: Jon Brommer¹, ROH: Robert O'Hara².

¹Department of Biological and Environmental Sciences, PO Box 65 00014, University of Helsinki, Finland.

²Rolf Nevanlinna Institute, P.O. Box 4 00014, University of Helsinki, Finland

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Supervised by: Prof. Esa Ranta
University of Helsinki
Finland

Doc. Ippo Hanski
University of Helsinki
Finland

Reviewed by: Prof. Jorma Tahvanainen
University of Joensuu
Finland

Prof. Carol Boggs
University of Stanford
USA

Examined by: Prof. Jens Roland
University of Alberta
Canada

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“Butterflies? Pretty – but what are they good for?”
Butterfly-researcher Mike Singer’s grandmother

Summary

Introduction

The study of butterflies has long traditions. It has developed from an eminent hobby of early naturalists, to an important part of evolutionary and ecological biology. Still today studying butterflies has a stronghold among “amateurs”, and the data collected by these enthusiasts is often invaluable to any scientific study of butterflies. Ehrlich (2003) summarizes some of the main fields in which butterflies offer attractive model systems, and in which the study of butterflies has contributed greatly to our understanding of, as he writes, “How the world works”. Such fields are, for example, studies on adaptation and constraints in energy processing, how organisms orient themselves in the environment, population dynamics, metapopulation dynamics, hybridization as a speciation mechanism, coevolution, biodiversity, and climate change to name but a few (see Boggs, Watt and Ehrlich 2003). However, Ehrlich (2003) is especially concerned about the ongoing global destruction of ecosystems, and ecosystem processes. Butterflies have an important role to play as model systems for studies on conservation especially because (1) the phenetics and cladistics of major groups are reasonably well known, (2) most species have been described, and (3) larval host-plants have been identified and described for a large number of butterflies (Ehrlich 2003). Butterflies have also been shown to be useful umbrella species (Ehrlich 2003, Thomas 1995). However, what Ehrlich (2003) warrants from future studies are more coordinated efforts into studies on phenetics of pre-adult stages and the evaluation of larval host-plant and nectar source usage of populations.

Thomas (1995), mentions two causes of decline for butterflies across the Palearctic that have been identified as being responsible for major butterfly population changes, they are (1) habitat destruction (especially in semi-natural biotopes) and the decline of habitat quality, and (2) the too high isolation of suitable habitat that was generated through management, making colonization impossible during the time that the habitat remained suitable. Since then, the effect of habitat fragmentation and the following isolation of suitable habitat have received increased attention through the development of metapopulation theory. Butterflies have been extensively used as model systems since many occur as metapopulations either naturally or as a cause of habitat fragmentation (Thomas and Hanski 1997, Hanski and Thomas 1994, but see Harrison and Taylor 1997, Hanski 2003). Hanski (2003) gives a thorough summary of the biology of extinctions in metapopulations and shows results from the long term study of *Melitaea cinxia* on the Åland islands. Further, Hanski (2003) points out that habitat loss is such an obvious and important cause for extinction that from a conservation point of view one would not lose much by focusing on this factor alone.

In a recent paper, Dennis et al. (2003) advocate the use of a functional resource-based definition of habitat in butterfly biology. They argue that what

butterfly conservation needs is a definition of habitat based on species specific consumables and utilities, instead of the invariant habitat definition of “a patch”. They propose that habitat would be defined in terms of life-history requirements categorised over each life stage. Continuing along the same line of argument but from a life history point of view, Boggs (2003) describes the connection between the environment and the individuals that reside there by describing the way that variation in the environment can feed-back to the population level through resource allocation strategies realised by the individual. Boggs (2003) focuses on food resources, and how long- and short-term variation in these resources affects allocation and life-history variation. Gilbert and Singer (1973) showed that the spatial location of resources affects population structure in *Euphydryas editha*. They could show that dispersal, contrary to the perception at the time, was flexible within a species and could evolve to fit local or regional conditions. The conditions that formed dispersal were the spatial distribution of resources. It has later been shown by numerous studies that, in insects, the spatial location of resources in relation to each other affect life-history decisions such as ovipositing and host-plant preference (Murphy et al. 1984, Kareiva 1985, Grossmueller and Lederhouse 1987, Thomas and Singer 1987, Prokopy et al. 1996, Peterson 1997). Furthermore, these decisions are often mediated by dispersal, or the inverse, lack of dispersal.

Conservation biology of butterflies

A common feature of threatened European butterflies is that they occur in non-climax communities maintained by, for example, traditional systems of farming (van Swaay and Warren 1999, Thomas 1995). Half of the threatened butterfly species in Europe use grasslands. Other communities used by threatened butterflies are woodlands and scrubs (22%), heath, bogs and fens (12%). These are all communities that have changed and disappeared to a large extent, due to the rapid economic development of the twentieth century (van Swaay and Warren 1999). The largest threats to butterflies in Europe today are the loss of habitat and the degradation of habitat quality. In particular, agricultural improvements, building activities, an increasing use of herbicides and pesticides and changes in habitat management cause a reduction in size of breeding habitats (van Swaay and Warren 1999). Needless to say, these are factors affecting a much larger part of the flora and fauna than just butterflies. However, since butterflies are probably the best studied insect group they could also serve as umbrella species for other less-studied groups of organisms (Thomas 1995).

In terms of conservation biology, Thomas (1994) listed three specific features of insects: (1) many insects occupy very narrow ecological niches within a habitat. Especially the immature stages can have very particular demands on their environment (Thomas *et al.* 2001, Thomas 1995). For many butterflies, such demands can be a larval host-plant – sometimes restricted to a particular developmental stage – areas with a suitable micro-climate, adult resources (such as nectaring plants), and dung or mineral bearing soils (Shreeve 1992, Murphy *et al.* 1990). In addition, the presence of other animal species may be required. For example, members of the Lycaenidae are associ-

ated with certain species of ants (New *et al.* 1995, Thomas 1995). (2) A relatively small habitat area (as compared to habitat areas supporting vertebrate populations) can sometimes support insects. However, because of the particular demands insects have on their environment, habitat is more prone to become unsuitable due to natural succession. (3) The particular demands of insects on their habitat in combination with most insects' limited dispersal abilities and their incapability to colonise suitable areas (sometimes only some hundreds of meters from an established population) make them an especially vulnerable group.

Conservation biology of the Apollo butterfly

In the red data book of European butterflies, the status of the Apollo butterfly (*Parnassius apollo*) is listed as decreasing in twelve out of twenty-eight countries and the species is considered extinct in three countries (van Swaay and Warren 1999). Only five countries report that the Apollo populations are stable. In Finland, *P. apollo* began declining after peak abundances in the 1930s (Mikkola 1979) and today *P. apollo* has its stronghold in the south western archipelago and on the Åland islands (Huldén *et al.* 2000). Single adult individuals of *P. apollo* are sometimes sighted outside this range (Repo and Kullberg 1996, 1997, 1998). However, there is no evidence of the establishment of new breeding populations, because there are no reports on larvae. Hence it is unlikely that *P. apollo* is experiencing a range expansion.

The decline of many butterflies coincides with the development of industry and changes in agricultural practise. Pollution by heavy metals is viewed as a factor contributing to the historical decline and currently observed lack of re-establishment of *P. apollo* (Nakonieczny *et al.* 1996, Bengtsson *et al.* 1989, Nieminen *et al.* 2001). The "heavy metal hypothesis" states that heavy metals (especially Cd) are harmful for the development of *P. apollo* larvae. Furthermore, according to this hypothesis, the historical decline of *P. apollo* was caused by increased heavy metal pollution and current populations are restricted in their ability to regain their former distribution due to higher heavy metal concentrations outside their current range (Nieminen *et al.* 2001). Inside the current range, calcareous rock or salt from the sea are thought to buffer high heavy metal concentrations in the soil (Nuorteva 1999, Nieminen *et al.* 2001).

Conservation measures for Apollo

The conservation efforts taken to preserve *P. apollo* in Europe vary between most of its distribution. The most common conservation measures are the legal protection of the species (19 out of 28 countries), and legal protection of important habitat (13/28 countries) (van Swaay and Warren 1999). Only three countries have special habitat management procedures to benefit Apollo, and only one country monitors all populations on a regular basis, whereas five countries have occasional monitoring of part of the populations. Conservation measures taken in Finland to protect the species are the legal protection of the species and occasional surveys of part of the populations (van Swaay and

Warren 1999). Since the publication of the European red data book on butterflies in 1999, ecological research on the requirements of the species have also been conducted in Finland in addition to the five countries listed in the red data book. Thus there is room for improvement on the conservation measures taken to protect *P. apollo* in Finland. Especially the management of populations in agricultural environments can be improved, because these populations are also under the greatest threat of extinction.

Management plans vary according to the particular conditions in different populations. For example, in the Jura Mountains in southern Germany, the Apollo occurs on calcareous and chalk grasslands (Dolek and Geyer 2002). The decline of this habitat type has been severe during the last century, and remaining habitat has been degraded by scrub invasion (Dolek and Geyer 2002). Dolek and Geyer (2002), describe a conservation programme with a complex sheep grazing scheme, which includes the grazing of areas with different time intervals. In the study, the conservation of *P. apollo* in particular has been enhanced by including goats into the sheep herds. The goats are browsers and they are more effective at keeping the steep slopes where the host-plant for Apollo grows, open. Furthermore, the grazing period is timed according to the life-cycle of Apollo so that the grazing starts when the larval period is over to avoid trampling of larvae, the animals are then moved to other pastures during the flight period as to avoid overgrazing of nectar plants, finally the animals are moved back again when the flight period is over. The management concerns large areas and many species are benefited by preserving the grassland biotope. However, the conservation plan has had to deal with aspects ranging from ecological requirements of endangered species to socio-economical requirements of sheep farmers. Nevertheless, this conservation programme has been successful and provides many incentives to other conservation agencies working with conservation in agricultural environments.

Another country where *P. apollo* disappeared almost completely is Poland. In the Pieniny Mountains in southern Poland, the last surviving population was down to 20–30 individuals in the beginning of the 1990s (Adamski and Witkowski 1999). The habitat in which Apollo occurs here is open limestone slopes in early succession. Overgrowth by scrubs is also diminishing habitat quality here (Palik 1980). The conservation of the species in the Pieniny Mountains includes a reintroduction programme where the population is strengthened by bringing in individuals from areas previously belonging to the same continuous distribution (Witkowski and Adamski 1996). The small isolated population in the Pieniny Mountains showed signs of severe inbreeding (Adamski and Witkowski 1999, Witkowski and Adamski 1996). Since the captive breeding and reintroduction programme began, the populations have grown and started to show signs of recovery from inbreeding (Witkowski and Adamski 1996). In Finland, no management plans or programmes for preserving *P. apollo* have been developed.

Outline of the thesis

In my thesis I have studied how the environment in terms of resource abundance and the spatial distribution of resources affect different population pro-

cesses in *P. apollo*. I describe the population structure of the two populations (I, II), and the spatial synchrony of the population dynamics in one population (II). Furthermore, I show that the resources influence the dispersal (I, II), population sizes (IV), and patch occupancy and persistence (III). I have conducted a feeding experiment on larvae to study the effects of heavy metals on larval growth (V). I discuss the importance of my findings in explaining the reasons for the historical decline of Apollo, and its' current distribution (V). By modelling, the importance of the resource distribution for the population dynamics in the two populations was evaluated (III). I will also discuss the importance of resource distribution for the historical decline and current distribution of Apollo. I will conclude by discussing the relevance of my findings for the conservation of the species in Finland.

Material and Methods

The study areas

I have studied two Apollo populations. The populations are situated in Parainen and in the Hiittinen–Vänö archipelago in south western Finland. The Parainen population is situated on the coast – in the inner archipelago zone (Lindgren and Stjernberg 1986) – here termed the coastal population, and the Hiittinen–Vänö population in the outer archipelago zone, here termed the archipelago population. The coastal population is situated some 10 kilometres south of the town of Parainen, and the habitat is a characteristic coastal agricultural landscape with fields and mixed forest. The host-plant for Apollo in Finland is the perennial *Sedum telephium*, which typically grows in small groups on rocky outcrops. The only outcrops suitable for the butterfly are the outcrops that contain host-plants (host-plant patches). Entire outcrops are delineated as patches since adult butterflies readily survey and patrol entire patches, and are by no means restricted to the *S. telephium* stands. Outcrops are marked in grey on ordinary 1:20,000 maps. The habitat on the patches is rather dry, and vegetation is sparse, although some patches may be partly forested. The size of the patches ranges between 0.03 hectare to 16.46 hectares, with a mean of 1.31 ± 0.37 SE hectares. The entire coastal study area is 4.06 km². The archipelago population is situated some 50 kilometres south of the coastal population, in the outer archipelago zone (Lindgren and Stjernberg 1986). The classification of the zones is based on the ratio between open sea and land, the exposure of the land to waves and wind, the salinity of the water, and the soil type. The islands in the archipelago are analogous to the rocky outcrops on the coast, except that the islands are barren and the vegetation is mainly composed of grasses and shrubs, surrounded by big areas of mosses, lichens, and bare rock. Here, islands are delineated as patches, and similarly as in the coastal population, adult butterflies survey and patrol entire islands. The size of the patches in the archipelago ranges between 0.19 – 8.35 hectares, with a mean of 2.02 ± 0.09 SE hectares. The archipelago study system stretches over an area of 103 km², where a selection of islands has been studied. In both populations, the rocky outcrops or islands form a network of differently sized habitat patches.

The species

P. apollo is currently classified as a near threatened (NT) species in Finland (Rassi *et al.* 2001) and has been protected by law since 1976. The species began to decline drastically in the 1950s and 1960s, and now occurs only very locally along the south western coast of Finland and on the Åland islands (Huldén 2000). *P. apollo* is univoltine and over winters as a small larva within the egg (Richarz *et al.* 1989). The larvae hatch in May and pupate after three to four weeks, spinning a loose cocoon in the undergrowth. Adults emerge in June, males first, and the flight season lasts for some five weeks if the weather is warm and dry.

The yearly census

The larval data and data on host-plant abundance were gathered in 1996 and 1999 – 2003 from the coastal population and 1997 and 1999 – 2003 from the archipelago population. The patches in the two populations were surveyed once a year during the larval period. A patch was considered suitable for the species if host-plants occurred. Host-plant abundance was scored in four categories during the larval surveys (1 = 1–10 host-plants; 2 = 10–100 host-plants; 3 = 100–1,000 host-plants; 4 > 1,000 host-plants). The host-plants on the entire patch were counted for the score. The exception is the first census in 1996 in the coastal population where instead of counting host-plants we estimated the area they covered. Host-plant area has only been used in chapter I; in all other chapters categories of host-plant numbers have been used. To get an estimate of how many stems were on each patch in 1996, we took the median value of stems found on each patch during the surveys 1999–2002 (IV).

Apollo larvae occur singly in the vegetation. Their development is not synchronised and through most of the larval period, there are some individuals that still have not hatched from the egg and those that have already pupated. Both the egg and pupal stages are extremely difficult to survey in the field in these populations, although eggs can be surveyed in other populations due to a different ovipositing behaviour (Adamski, pers. communication). Nevertheless, already 0.5-cm long larvae can be seen, partly due to their bright colours and partly due to the characteristic grazing patterns they leave on the host-plant. Since the larvae hide in the undergrowth when they are not feeding, signs of grazing can be very helpful in indicating locations worth several visits if the species is not encountered at once. In the coastal population patch occupancy was scored due to low larval numbers. A patch was considered to be empty when no larvae were found during two visits, of which the last one had to be under optimal weather conditions. However, in the archipelago population where larval numbers are higher the larvae were counted. Empty patches were not visited again for a second time. The accuracy of the surveying methods were evaluated by removal counts (III). We performed the removal counts in two years during the larval period in May–June. The first year, twenty-two patches in each population were surveyed and in the second ten patches were surveyed on the coast and nine in the archipelago. On the first and the second survey of a patch, all observed larvae were collected and kept in plastic boxes on the patch where they were offered host-plant *ad libi-*

tum. In this way no larva was counted more than once. The boxes allowed for good ventilation and rainwater could run out. On the third survey, the larvae on the patch were counted, after which the larvae from the boxes were released back on their host-plant.

Mark Release Recapture studies

In the coastal population, MRR data was gathered from the entire study area. In 1996, the area was divided into three parts, and each part was surveyed every third day (I, IV). In 2002, the area was surveyed in two parts, one part per day. In both years the total study area was surveyed a total of eight times. The patch configuration in the coastal population changed somewhat between the years due to fluctuations in host-plant occurrence. Some patches became suitable after having been unsuitable, and some patches turned unsuitable after having been suitable (III) (Table 1).

In the archipelago, the set of islands for adult MRR studies were chosen based on high larval counts (III, IV). Movement data was collected during 1997, 1999, 2000 and 2002 by Mark-Release-Recapture (MRR) over several islands ($n_{1997} = 17$; $n_{1999} = 13$; $n_{2000} = 17$; $n_{2002} = 22$). The adult butterflies were caught by hand netting, and marked with a running number. The patches were surveyed in a similar fashion each time. The surveying regime was however, somewhat different between the years. In 1997, a core area of four islands was surveyed daily and in 1999 and 2000, the core area consisted of nine islands. An additional 13 islands in 1997, four islands in 1999 and eight islands in 2000 were surveyed a few times over the adult season. In 2002, twenty-two islands were surveyed over a period of three days. Thus, each patch was surveyed every third day, throughout the adult season. The MRR data was used to estimate population sizes using the Jolly Seber method (implemented in program JOLLY, 1988 version from J.E. Hines, US Fish and Wildlife Service, Laurel, Maryland). Isolation measures were calculated to incorporate the pair wise distances between all the patches where MRR was performed.

Studies on the ovipositing behaviour

Studies on the ovipositing behaviour were carried out in the archipelago population in 2000 (III). Individual females were followed and all the places where a female alighted oviposited, fed, or rested were marked in the terrain with numbered plates. The routes were then drawn in on a map of the patch. A detailed map around each oviposited egg was drawn, such that the egg was placed in the middle of a quadrat with one-meter sides and the contents of the quadrat were drawn. The distance to the nearest host-plant was also measured. To evaluate the site selection of ovipositing females, we selected random points over the entire patch. Detailed maps around the random points were drawn, and the distance to the nearest host-plant was measured in a similar fashion as described for the ovipositing sites.

Estimation of nectar resources

The amount of flowering nectar plants on the islands were counted every second day in the core area of 1999 and 2000, and on every second visit in 2002 (II, IV). The nectar plants on the islands that received only occasional visits in 1999 and 2000 were counted on all visits. In the coastal population the locations of nectar patches and the area covered by flowers was marked on a map and estimated by Map Info Professional 6.0. For an area to be considered as a nectar site, at least ten stems with large inflorescences had to be present in a group, or it had to be a smaller group of very large and conspicuous plants with several flowers such as *Cirsium vulgare*. In the coastal population, the main nectar flowers are different *Cirsium*-thistles, *Epilobium angustifolium*, and *Centaurea jacea*. Where it occurs, *Thymus serpyllum* attracts butterflies as well. In the archipelago population, the main nectar plant is *Valeriana officinalis*, but also thistles and *E. angustifolium* occur. *Veronica longifolia* occurs densely on some islands and is also used for nectaring.

Rearing of larvae for heavy-metal experiment

Twenty larvae were collected from the coastal population and forty larvae from the archipelago population. We collected larva of similar size that we estimated would still moult one more time before pupation. The larvae were kept individually under similar conditions, outdoors. The treatment group were fed host-plant collected from the former range of *P. apollo*. The site from the former range was selected to be as similar to the *P. apollo* populations as possible in terms of landscape and human population. The island of Skåldö was selected since it is within the former range of Apollo, not far from the existing populations geographically (40 – 50 km), and because it is an island in the inner archipelago zone (Lindgren and Stjernberg 1986). The control group were fed host-plants from their place of origin. We estimated the weight curve for the larvae, their food consumption and how effectively they could absorb their food by daily weighing of larvae, faeces, and the food. The larvae were kept until they eclosed as adult butterflies to allow sexing. After eclosing the butterflies were taken back to their patch of origin.

The influence of resources on population processes in *P. apollo*

The population structure of the two populations

Population structure can be defined by the degree of between-patch movement, and whether a patch can be described as a local population or as an aggregation of individuals depends on the between-patch dispersal rate (Harrison 1997, Sutcliffe et al. 1997). One rule of thumb is that if the average individual inhabits more than one patch in its lifetime, the population can be called “patchy” (Harrison and Taylor 1997), whereas in a metapopulation most individuals stay in their natal patch (Harrison 1991, 1994).

Table 1. A comparison of larval occupancy data across years in the coastal population. Mean area (ha \pm SE) of empty and occupied patches on the coast over six years. Numbers of patches (n) are shown in brackets. Turnover in occupancy shows the change in the number of patches occupied since the previous year. Turnover in suitability shows suitable patches that have turned unsuitable (-), or unsuitable patches that have become suitable (+), between survey years in terms of host-plant occurrence. The numbers of occupied patches within each suitability turnover group are shown in brackets.

	Area (ha)		Test			Turnover	
	Empty (n)	Occupied (n)	t	d.f.	P	Occupancy	Suitability
1996	0.5 \pm 0.1 (16)	1.9 \pm 0.6 (27)	2.25	27.6	0.033		
1999	0.8 \pm 0.2 (32)	2.1 \pm 0.9 (19)	1.45	20.1	0.164	-16 +6	-1 (1) +9 (2)
2000	0.6 \pm 0.2 (28)	2.1 \pm 0.7 (23)	2.09	24.5	0.048	-5 +8	-3 (0) +3 (2)
2001	0.4 \pm 0.1 (22)	1.7 \pm 0.6 (31)	2.34	31.7	0.026	-4 +13	-2 (1) +4 (1)
2002	0.6 \pm 0.2 (27)	1.9 \pm 0.7 (25)	-1.94	27.6	0.063	-11 +4	-2 (0) +1 (1)
2003	0.7 \pm 0.3 (21)	1.7 \pm 0.6 (28)	-1.47	39.0	0.148	-4 +9	-4 (0) +1 (0)

In the archipelago population almost 80% of adult *P. apollo* butterflies stay in their natal patch (II). Hence, this archipelago population could be described as a metapopulation formed by a network of islands linked by dispersal (Harrison and Taylor 1997). This stands in contrast to the coastal population, which has a patchy population structure with 48% (IV) to 73% of the recaptured adults changing patch (I). The difference in movement rates between these two populations probably stems from two factors. Firstly, movement across patches in the archipelago may be inhibited because patches are separated by sea, whereas all patches in the coastal population are on land (IV). Second, most patches in the coastal population do not contain nectar plants and adults therefore have to disperse away from their natal patch in order to find resources (I) (c.f. Gilbert and Singer 1973, Murphy et al. 1984).

Population dynamics and spatial synchrony

Both populations showed large fluctuations in patch occupancy and larval abundance (Table 1 and Table 2). For example, in the coastal population, the proportion of occupied patches changed between only 37% (19/51) occupied to 58% (31/53) occupied two years later. In addition, the suitability in terms of the occurrence of host-plant on the patches fluctuated between years (Table 1). The fluctuations in suitability were small and concerned patches poor in host-plant which had no host-plants at all in some years. In the archipelago population, the fluctuations in larval numbers were pronounced (Table 2). The larval numbers fluctuated between a total of 240 larvae over 71 islands (mean \pm SE = 3.4 \pm 0.5) in the lowest year to 762 larvae in total (mean \pm SE = 10.7 \pm 2.2) only two years later. In the archipelago, 46% (33/71) of the patches were empty in 2003 whereas only 28% (20/71) were empty in 2001 although the total and mean number of larvae per patch was similar (Table 2). Never-

Table 2. A comparison of larval occupancy data across years in the archipelago population. Data represent 71 islands. Mean area (ha \pm SE) of empty and occupied patches is given. Numbers of patches (n) are shown in brackets. It is tested whether the areas differ between occupancy categories. Under number of larvae, the sum (Σ) and mean number \pm SE of larvae on a patch is given. Turnover in patch occupancy is scored as the number of local extinctions (-) and local recolonisations (+).

	Area (ha)		Test	Number of larvae		
	Empty (n)	Occupied (n)	P	Σ	Mean \pm SE	Turnover
1999	1.5 \pm 0.2 (31)	2.4 \pm 0.3 (40)	0.025 ¹	240	3.4 \pm 0.5	
2000	1.7 \pm 0.3 (21)	2.2 \pm 0.2 (50)	0.217 ²	623	8.9 \pm 1.7	-5 +15
2001	1.1 \pm 0.1 (20)	2.4 \pm 0.3 (51)	0.001 ³	762	10.7 \pm 2.2	-9 +10
2002	1.7 \pm 0.3 (27)	2.2 \pm 0.3 (44)	0.225 ⁴	319	4.5 \pm 1.3	-12 +6
2003	1.5 \pm 0.2 (33)	2.5 \pm 0.3 (38)	0.006 ⁵	706	9.9 \pm 2.8	-14 +7

1 - d.f. = 69, t = -2.30

2 - d.f. = 69, t = -1.25

3 - d.f. = 68.8, t = -4.29

4 - d.f. = 69, t = -1.23

5 - d.f. = 69, t = -2.82

theless, the percentage of patches occupied in the archipelago in a bad year such as 2003 is still close to the highest percentage of patches occupied on the coast over the years (Table 1 and Table 2).

To what degree population dynamics are correlated spatially is partly determined by dispersal (Sutcliffe et al. 1996, Ranta et al. 1997, Koenig 1999 review). The more dispersal between the patches, the higher the spatial correlation of population dynamics is expected to be on a local scale (Sutcliffe et al. 1996). As Ranta et al. (1995) describe synchrony maintained by dispersal, dispersal rate is a function of distance and the further apart patches are the less correlated their population dynamics are expected to be. Sutcliffe et al. (1996) studied synchrony at a small spatial scale and found that dispersal capacity affected the strength and extent of synchrony in local population numbers. Furthermore, if dispersal is limited or if other local factors such as resource abundance affect local population numbers more strongly than dispersal, then more between patch variation in population numbers is expected, and thus between patch correlation is weaker. We have shown that in the archipelago population, the larval numbers counted during five years tend to be weakly synchronous, but the most apparent correlation in larval numbers are at short (<1500 m) spatial scales. In this population, local (island-specific) factors may be so heterogeneous that any effect of dispersal in linking populations is obscured in the census of the next generation. For example, local host-plant abundance (which varies four orders of a magnitude across islands) may affect larval survival (IV, III) and overrule the synchronising effect of dispersal. In addition, mobile species (such as *P. apollo*) may show low population synchrony because such species can track temporal changes in resource availability at the local, "between patch", scale (Sutcliffe et al 1996). The importance of factors such as local resource abundance for adult population sizes (IV), and the number of emigrants from a patch (II) will lessen the correlation between nearby islands.

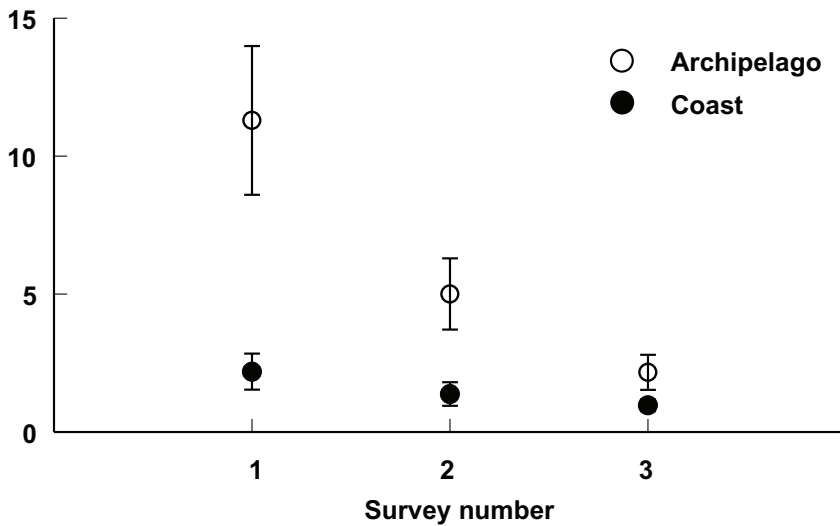


Figure 1. The mean number, \pm SE, of larvae encountered per visit to a patch during removal counts in 2000 and 2001. The number of patches was 32 for the coast and 33 for the archipelago population. Archipelago in open and coast in filled symbols.

The influence of resources on patch occupancy and persistence (III)

To validate our larval survey method we performed removal counts where larvae were counted and removed from a patch for three consecutive days. The removal counts in both populations showed a decline in number of larvae found at consecutive visits, although this was not so clear in the coastal population, where the overall larval numbers were very low (Fig. 1). In both populations, there was a strong correlation between the numbers of larvae found at the first visit and the number of larvae found in total, even if we excluded the empty patches from the analysis (Coastal population $r_p = 0.90$, $P < 0.001$, [$n = 22$]; Archipelago population $r_p = 0.98$, $P < 0.001$, [$n = 24$]). This correlation shows that the number of larvae found at the first visit indeed is indicative of the relative larval abundance on the patch (Fig. 2).

Patch occupancy in all our studies refers to larval occupancy. In the studies on patch occupancy by larvae we have studied factors that are related to the larvae directly. We have studied local factors on patch level leaving out any isolation measures since the larvae are non-dispersive, and leaving out nectar abundance since nectar is a resource only used by adults.

Patch occupancy per year in the coastal population is mostly affected by patch area and host-plant abundance on the patch. On the coast, large patches, and patches rich in host-plants are more often occupied than smaller patches and patches with less host-plants. In the archipelago population, the occupied patches have higher host-plant abundance than the empty patches. Further, larger patches have more host-plants. Host-plant abundance varies between years in both populations. In terms of long-term patch occupancy, here termed as patches being occupied for three years in a row, the most significant term is

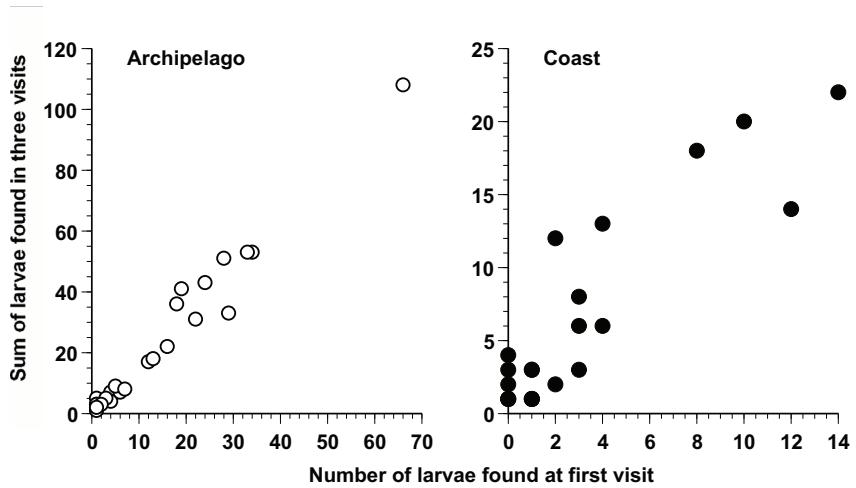


Figure 2. Correlation between the numbers of larvae found at the first of three consecutive visits against the total sum of larvae found during three visits. The archipelago population is shown in open circles and the coastal population in filled circles.

host-plant abundance. The probability of a patch being occupied for three consecutive years also increases with patch area. The host-plant abundance is higher in the archipelago population than in the coastal population (overall $\chi^2 = 9.12$; $df = 1$; $P = 0.003$), as well as the three-year patch occupancy (overall $\chi^2 = 5.13$; $df = 1$; $P = 0.02$). Thus, there is no difference in the probability of a patch being occupied for three years in a row between the populations. Instead, the higher number of patches being occupied for three years in a row in the archipelago stems from the higher host-plant abundance there.

The influence of resources on dispersal

The two populations of *Apollo* that we have studied differ considerably in their resource distribution. In the coastal population, the larval and adult resources are spatially segregated (see map in I) whereas in the archipelago they are not segregated as both resource types occur on the islands, but the amount of the two resources varies between islands. The *Apollo* is a highly active and relatively long lived species with adult life spans of several weeks. The adults are often seen feeding on nectar plants. Boggs and Ross (1993) found that the resources acquired through adult feeding of *Speyeria mormonia* mainly affected the fecundity in females. O'Brien et al. (2004) have shown that the importance of carbon derived from adult (nectar) feeding increases with the amount of immature eggs at eclosion and the earlier after eclosion the ovipositing is timed. At eclosion, not all eggs of *P. apollo* are mature (Weidemann 1995) and the mated, often newly emerged, female starts ovipositing soon after mating (M. Fred pers. obs.). The species is therefore expected to be dependent on nectar resources for maturing its eggs and increasing fecundity (Boggs 1997, 2003, O'Brien et al. 2004).

In both populations the dispersal between patches is influenced by the nectar distribution and the abundance of nectar resources. In the coastal population, 25% of all the movements recorded were between host-plant patches and nectar patches (I). More adults were also encountered on host-plant patches that were less isolated from surrounding nectar patches (I). In the archipelago population, the lower the nectar abundance was on a patch the more individuals emigrated from the patch. Furthermore, the less isolated a patch was from surrounding nectar sources, the more emigrants there were from that patch (II). Immigration however, was not influenced by either resource abundance on the receiving patches nor by any measure of isolation from resources on the surrounding patches. It seems that after leaving a patch, the behaviour of the dispersing individual becomes vagrant (II). The abundance and distribution of the host-plant did not affect dispersal in the archipelago population (II).

The influence of resources on the population size (IV)

Population sizes in this context refer to the estimated population sizes per patch in both populations, although the patches in the coastal population as such cannot be defined as populations in a strict sense because of a high movement rate between them (I, II).

The resources affecting the population sizes of both males and females in both populations were the nectar resources. The effect was through isolation of a host-plant patch from surrounding patches when the two resources, host-plant and nectar, were segregated spatially, or through the abundance of nectar plants on the patch when the two resources occurred together. The resource that affected the population size of only one of the sexes was the host-plant. Surprisingly, the males were affected by the host-plant abundance on the patch. Whereas the females were only affected by how isolated the patches, with host-plants, were from each other. There was no association between host-plants and the female population sizes.

Reasons for the decline and current status of *P. apollo* in Finland

Heavy metals (V)

To evaluate the effect of heavy metals on the development of *P. apollo* larvae, we conducted an experiment where larvae from two populations were fed either host-plants from their own population (control) or host-plants from a site within the former range of the Apollo butterfly (treatment). The heavy metal contents of the host-plants were higher in the plants from the current range of *P. apollo* than in the plants from the former range. Only fitness-enhancing effects on any of the measures concerning growth, food consumption or the length of the last instar could be detected in the larvae that were fed host-plants from outside *P. apollo*'s current range. Our feeding experiment clearly cannot establish a direct causal link between Cd concentration and larval per-

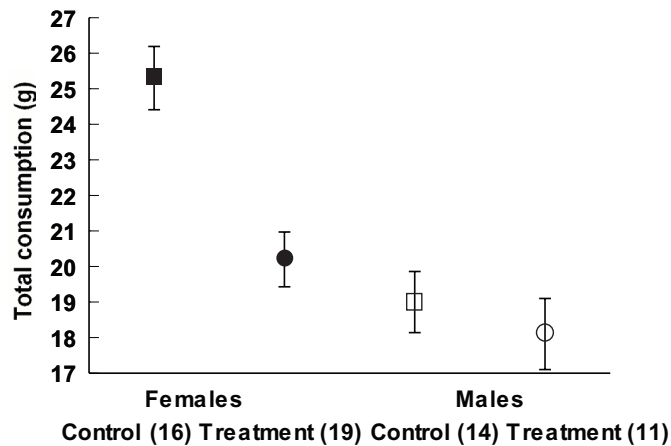


Figure 3. Least squares means and standard error of total consumption in the different sexes and treatment groups, adjusted for variation in the length of the larval period. The control groups are shown as squares and the treatment groups as circles. Females are indicated with filled symbols and males with open symbols. The number of individuals within each group is given between brackets.

formance, but our results are remarkably consistent with the notion that current Cd levels may repress certain aspects of larval development in *P. apollo*. Our results therefore at least partially support the “heavy-metal hypothesis”. Female larvae in the treatment group manage to grow similarly and reach the same final size as the female larvae in the control group on some 20% less food, which indicates a higher metabolic efficiency when Cd levels are low (Fig. 3). The same trend can be seen in male larvae (Fig. 3). Both sexes in the treatment group were able to complete their development in a shorter time without compromising their weight at pupation. Weight at pupation can be especially important for females, because weight at pupation is positively related to adult size and absolute fecundity (Boggs 1997, Spurgeon et al 1995, Ochiengodero 1992). For both sexes, a shorter developmental time in the conspicuous larval period can be beneficial in terms of avoiding predation and possibly parasites.

Nieminen et al. (2001) have suggested that the historical range contraction of *P. apollo* was partly due to an accumulation of heavy metals because of downfall from industrial and mining activities. Furthermore, recolonisation of current *P. apollo* populations back into its former habitat is thought to be hindered by a higher Cd concentration outside the species’ current range than inside (Nuorteva 1999, Nieminen et al. 2001). Nieminen et al. (2001) fed foreign host-plant with a high concentration of Cd to larvae from the same archipelago population as we have used. Nieminen et al. (2001) found that all larvae died when fed host-plants with a similar Cd concentration (4.3 – 4.4 mg/kg) that we found in the coastal population (4.4 mg/kg). Thus, even on a relatively small spatial scale within the current range of *P. apollo* (30 km), the Cd concentrations in one population (the coastal population) may be potentially lethal to larvae from another population (the archipelago population).

The fact that larvae from the coastal population can complete development on host-plant from their own population without any mortality, whereas larvae from the archipelago population suffer severe mortality on host-plant with such high concentrations of Cd (Nieminen et al. 2001) suggests that *P. apollo* from the coastal population have developed tolerance towards prevailing Cd levels. The historical increase in heavy metal concentrations in the landscape, which was intensified by acid rains that transform the metals into a soluble form (Nuorteva 1999), is a gradual process. Under such gradually increasing pollution, tolerance towards heavy metals is expected to evolve (Tyler et al. 1989, Lindqvist 1994, Ortel 1995, Nascarella et al. 2003). The possibility of the evolution of tolerance of *P. apollo* to Cd undermines the potential role that Cd has played in the historical range contraction of *P. apollo* populations. The variation in Cd levels within the current distribution of *P. apollo* and the apparently different tolerance of *P. apollo* towards Cd across existing populations make it unlikely that Cd played an important role in the historical contraction of *P. apollo* in Finland.

Habitat quality and the persistence of populations

From the point of view of an adult butterfly, there exists a potential allocation dilemma between meeting its own resource requirements and the requirements of its offspring in landscapes where adult and larval resources do not sufficiently overlap. For example, adult butterflies may aggregate at sites close to nectar sources which may be far from many sites where the larval host-plant occurs (Gilbert and Singer 1973, Murphy et al. 1984, Grossmueller and Lederhouse 1987, James et al. 2003, chapter I). Such behaviour may therefore affect the spatial distribution of larvae in the next generation (Lepidoptera: Murphy et al. 1984; other arthropods: Prokopy et al. 1996, Karban 1997). The spatial configuration of adult and larval resources in a landscape may hence have population-dynamical consequences. For example, host-plant stands close to nectar plants will contribute more to population dynamics than host-plant stands far away from nectar sources. Hence, a reduction in nectar plants or even a rapid change in the spatial location of nectar sources may affect the population. Understanding this phenomenon is therefore important for conservation, because the existence, amount and spatial location of nectar plants is in most modern agricultural landscapes solely determined by anthropogenic factors. The main challenge for documenting such a phenomenon is to separate the adult's behaviour from what affects the next generation. It is insufficient to document that adults distribute themselves in relation to adult resources without evidence that the adults' distribution actually affects the larval distribution the next year. In this respect, the distribution and behaviour of the ovipositing female forms the link between the spatial configuration of adult and larval resources and the distribution of the next generation.

The distribution of female adult *P. apollo* has consequences for the spatial distribution of the next generation. The number of females on a host-plant patch correlates strongly with the number of larvae on that patch in the next season. The nectar resource-oriented distribution of females may therefore place specific demands on the spatial configuration of resources in a habitat.

Host-plant patches that are attractive to females because of their proximity to nectar sources or high abundance of nectar sources on them also need to have adequate numbers of host-plants on them. Especially since *P. apollo* females in this population do not place the majority of their eggs close to a host-plant, higher abundance of the host-plant may indeed increase the survival of the larvae (III). In the archipelago population, there is indeed a residual effect of host-plant abundance on the number of larvae in the following season, which suggests that the host-plant abundance has a direct effect on the number of larvae present. Our studies show that patch occupancy in the archipelago is higher in patches with more host-plants and a larger patch area (III). If the survival of larvae is dependent on the host-plant abundance and not the direct ovipositing choice of the female, a conflict between the larvae and the ovipositing female is ameliorated. By selecting ovipositing sites with high host-plants abundance a female increases her offspring's survival chances, but availability of nectar plants increases the female's own fitness. In the archipelago, where the host-plant abundance is high, and nectar plants occur naturally on patches, the consequences of a conflict are probably not realised. However, as soon as rapid changes in the spatial configuration or abundance of either resource would occur, the population might have difficulty in tracking the changes in the location of nectar-plant patches. This scenario would apply especially to the coastal population, where the distribution of ovipositing females appears to be affected only by adult resource. However, the observed correlation between the distribution of nectar sources and adults, and between adult females and next season's larvae need not have population-dynamical consequences. Population level consequences of individual behaviour depend on how sensitive the population is to individual differences in behaviour (Sutherland 1996). For example, colonisation of an empty patch requires in principle but a single female to oviposit. Hence, our observation that females are on average less commonly found on host-plant patches far away from nectar-plant patches may not affect the population dynamics in a long-term sense. We have used a Bayesian modelling approach to evaluate the importance of the spatial distances between nectar-plant patches and host-plant patches for population dynamics in the two populations studied here. The model shows that the population dynamics of host-plant patches far away from nectar plant patches indeed are not different from those close to nectar-plant patches. However, the population dynamics in both populations are sensitive for the host-plant patches close to nectar-plant patches. A host-plant patch close to the surrounding nectar-plant patches will have a proportionally larger effect on the population dynamics than a host-plant patch further away. Hence, the dynamics across all patches in the population (but not the spatial distribution of larvae) is sensitive to (rapid) changes in the spatial location of nectar sources.

Thus far we have shown that the abundance and actual location of adult and larval resources with respect to each other affects (1) the location and population sizes of adult butterflies and (2) that the location of females in one season affects the larval abundance in the following season (3) there is an additional effect of host-plant abundance on the larval numbers that suggests a conflict between the ovipositing female and the survival of the larvae. Furthermore, we have shown by modelling that (4) the resource distribution indeed can have an affect on the population dynamics. The presence and persis-

tence of a *P. apollo* population is thus dependent on the presence of nectar plants and the host-plant, and the spatial location of these two in relation to each other is of crucial importance. Host-plant patches with relatively high host-plant abundance need to be interspersed with nectar bearing flowers.

Habitat change affecting the decline and current distribution of *P. apollo*

Nectar flowers in Finland today occur at the edge of fields, roads and railroads, under power lines, on wastelands and abandoned fields (Kuussaari et al. 2003). The natural habitat for nectar flowers however, is meadows. Meadows are one of the most threatened biotopes in Finland, and it has been estimated that less than 1% of the area covered by meadows only a hundred years ago remains (Salminen and Kekäläinen 2000, Vainio et al. 2001). The development during the last decades has been accelerating and today less than 10% of the area covered by meadows thirty years ago is left (Salminen and Kekäläinen 2000, Vainio et al. 2001). The development has been fastest in southern Finland (Pöyry et al. 2003). The intensification and increased effectiveness of agricultural practices is the reason behind the decline of the meadows (Alanen 1996, Pitkänen and Tiainen 2001). Although “modern” meadows such as power lines have proved to be important habitat for many specialist species, in the current situation they do not replace the meadows from a hundred years ago (Kuussaari et al. 2003). However, the realisation of their importance for meadow species, and the development of their management is a potential rescue for many species stumbling at the brink of extinction all over Europe. How the abundance and distribution of the other resource for *P. apollo*, *S. telephium*, has changed over the last century is not clear. It is by no means threatened by extinction, nor is the rocky habitat where it grows threatened. However, in some regional scale mappings conducted in 2003 in areas where *P. apollo* has occurred during the last century, we found that the host-plant abundance in general was low, and that the rocky outcrops were rather overgrown by forest (M.S Fred, W. Fortelius unpublished data). Overgrowing of rocky outcrops by forest is listed as one of the threats to *P. apollo* both nationally (Rassi et al. 2001) and internationally (van Swaay and Warren 1999), thus we feel that the pattern we have found is of a more general nature. The combination of the habitat specificity of *P. apollo* with respect to the spatial distribution of resources, and the profound large scale changes in its habitat over the last century is more than likely to be malignant. Whether the collapse in the distribution was brought on by these changes is difficult to assess afterwards, and possibly many factors acted in concert. However, the negative effect of habitat loss and degradation has been the demise of the majority of threatened butterflies across Europe and the same patterns can be seen in Finland (Thomas 1995, van Swaay and Warren 1999, Rassi et al. 2001). When discussing the current distribution of *P. apollo*, and the lack of re-colonisation into its previous range of distribution, habitat quality is a factor to take into account. The lack of nectar sources in the modern agricultural landscape, the overgrowth of rocky outcrops and the large grain of the agricultural landscape together make the habitat unsuitable for *P. apollo*. Even though all “ingredients” needed for a suitable landscape might be present at a large scale, it is the

small scale local spatial distribution of the resources that matter. To conclude, I find it unlikely that *P. apollo* will increase its range and become a common butterfly again, if the agricultural habitat within its former range is not managed differently than it is today.

Conclusions; implications for the conservation of *P. apollo*

Management

Our studies on the influence of resources on *P. apollo* give clear implications for habitat management. We have shown a connection between both larvae and adults to resources and further, that the spatial configuration of resources has implications for population dynamics. The Apollo butterfly is probably special in the sense that very crude measures of environmental factors are sufficient. In some species, it is even difficult to assess what a patch is because the requirements of the species are very complex and include measures on microclimate, the presence of other species such as particular ant species, the developmental phase of particular plants and sward height, to name but a few environmental factors that have been shown to be important in other species (New et al. 1995, Thomas 1995, Gutiérrez et al. 1999, Thomas et al. 2001). Furthermore, for Apollo patch suitability can be assessed by counting larvae, which in many other Lepidopteran species is not possible. Thus, the habitat requirements of Apollo can be identified and even quantified to some extent.

Habitat management implications that benefit the Apollo are (1) ensure the presence of nectar plants and the host-plant *S. telephium* (2) take care in creating enough small scale heterogeneity in the spatial location of both resources (3) retain from destroying any habitat (4) monitor the populations yearly. These management suggestions are especially applicable in the agricultural areas where Apollo occurs in Finland (Parainen and the Åland islands). The archipelago populations in Finland occur in areas largely unaltered by man. However special care in the archipelago has to be taken with (5) large scale habitat alteration on small islands and (6) introducing grazers.

To ensure the presence of nectar plants for *P. apollo* is relatively straightforward since the Apollo by no means constitutes a meadow specialist with very particular demands. On the contrary, the Apollo utilises species such as *Cirsium* thistles, *E. angustifolium* and *C. jacea* that readily grow on roadsides, abandoned fields, clear cuts, and under power lines. To ensure that the nectar flowers thrive, mowing abandoned fields yearly, or even biannually, would suffice. In our studies we have found roadsides, especially around smaller unpaved country roads and ditches to be very important nectar sites. However, the cutting of the roadsides should be postponed until end August when the flight season of Apollo is over. Apollo also uses rather small nectar areas that can be anything from a garden with flowers, a small untended area of a garden lot where weeds thrive to untended areas on the backyard that are sometimes cut to prevent forestation. All of these management actions in concert would ensure a sufficient amount of nectar for the Apollo in the few areas where it still occurs. Furthermore, it could even facilitate a spreading of the

species to nearby areas, provided that the host-plants occur there as well. The thriving of the host-plant can be enhanced by keeping rocky outcrops from getting overgrown by trees and shrubs. Most rocky outcrops on the mainland have some forest on them, but the forest is interspersed by bare rocky areas. It is these bare rocky areas where the host-plant grows that should be kept open. Since succession on the rocky outcrops is very slow the clearing and maintaining of the clearings would not require constant efforts. To maintain the small scale heterogeneity mostly has to be achieved by managing the nectar resources since the rocky outcrops are the only places where the host-plant grows. However, since the nectar plants grow along roads, ditches, abandoned fields, or in gardens it would only require that these areas be managed as described above, and there would be enough small scale heterogeneity. A particular threat towards the mainland population in our study is urbanisation. The area is situated close to one of Finland's major cities, Turku, and more and more people want to live on the country side while working in the city. So far, 16% (8/49) of the patches have been affected by building activity of some sort since 1996. What the impact of the building activities is, is difficult to assess, and is certainly dependent on the degree of habitat destruction involved. The degree of habitat destruction varies from complete destruction to no direct destruction. It is however difficult to assess whether the species is sensitive towards disturbance and trampling which perhaps are the most common direct effects of the building activities so far. The best way to stay informed about the state of the population is to monitor it yearly. Monitoring should be done during the larval period, when larvae should be counted on all suitable rocky outcrops in the area. Further, the amount of host-plant and nectar plants should be monitored together with changes in the environment such as building. As mentioned the coastal population in our studies is the only large population of *P. apollo* on the Finnish mainland, and I therefore find it has a high conservation value. It is therefore urgent that a management plan for this population is developed and put into action. The management plan can be fulfilled with rather small costs since some improvements would only include a different timing of procedures that are already carried out. Other improvements would only have to be carried out with long time intervals. The most challenging improvement would be to prevent further habitat loss due to building or other activities that destroy the habitat.

The management plans for the archipelago population are somewhat different because human activities have not altered this habitat and are not a threat at this moment either. However, building activities are continuing also in the archipelago but mostly at big islands and not at the shores where the host-plant grows. Finnish legislation is also protective about sea-shores and building on them or on small islands is strictly controlled. Thus, at the moment building activities are not a threat towards the Apollo in the outer archipelago zone. The nectar flowers in the outer archipelago zone grow on natural meadows that are not managed in any way. Succession in this part is very slow thus the host-plants are not threatened by trees or shrubs overgrowing the islands. The best management plans for the archipelago is thus to leave everything in the natural conditions that prevail now. Special care should be taken if grazers are introduced to the islands. On two of the islands sheep have been grazing for four summers. Since the islands are small and do not contain any large meadows, the sheep eat all plants available including nectar plants. Dur-

ing the years that the sheep have been present the number of nectar plants on these islands has been very low. The presence of sheep on two islands in the archipelago population is by no means a threat to the Apollo. However, introducing sheep to several of the small islands might affect the local populations. Nevertheless, it is doubtful if introducing sheep to the outer archipelago zone where succession is slow is valuable for the landscape. Meadows keep open naturally on the outer islands, as opposed to the larger islands closer to the mainland where grazers have kept the landscape open for hundreds of years. From a point of view of maintaining cultural landscapes by means of grazing, the larger islands are clearly benefited more.

Comparison of populations and including of all life-stages

Some further points for the conservation of *P. apollo*, and also more generally when planning conservation efforts, are to acknowledge the differences between populations and to include the particular demands of all life-stages. We have shown differences in the two populations we have studied, although the populations geographically are very close to each other. However, the landscapes where the populations occur are very different (I, II). We have found differences in the dispersal rates (II, VI), in the population structure (II), in the levels and tolerance of heavy metals (V), and factors affecting population sizes (IV) between the two populations. Furthermore, as mentioned above, also the threats in the two populations are very different. If we look at a pan-European scale, the overall threats towards the species are often connected to habitat loss but the conservation measures needed to correct the situation are often very different. Conservation measures range from adding goats to sheep flocks and changing the rotation schedule for different areas, to captive breeding programmes and the clearing of trees and shrubs. Thus although general points about the conservation of species, such as protecting the species and its habitat and monitoring the populations on a regular basis, are rather straightforward, the particular actions to be taken when preserving particular populations or distributions need to be based on more detailed data. An important part of the detailed data is the requirements of different life-stages. Especially in arthropods the life-stages differ profoundly from each other in morphology and physiology. Furthermore, the life-history decisions, and evolutionary consequences associated to them are very different. For example, food shortage in the larval phase has different consequences than food shortage in the adult phase in *Speyeria mormonia* (Boggs 2003). In the larval stage, food shortage led to lower adult body mass and reduced fecundity as a consequence of the lower body mass, although the relative fecundity (fecundity corrected for body mass) remained the same. The life span of adult females that had experienced restricted food conditions as larvae was also shorter. Food shortage in the adult stage led to reduced lifetime total fecundity in females because eggs were reabsorbed under stressful food conditions (Boggs and Ross 1993). The different effects of food shortage in the different life-stages are due to differences in the diet composition, and different energy requirements of egg production, growth, maintenance and other life-history components. Thus we need to identify the different requirements of all life-stages to get as complete a picture as possible of the species habitat prefer-

ence, not the least because the different life stages can have different effects on the population dynamics due to differences in their allocation strategies. We have shown that the adult female Apollo butterflies only orient themselves according to the resource they use themselves, whereas the larvae in the following year occur in areas with higher host-plant abundance within the area where the females have been (IV). However, in terms of resources each life-stage is distributed in accordance to the resource it utilises, thus including only one life-stage would give a limited and even erroneous picture of the requirements of the species. Furthermore, any population estimate connected to patch incidence would be misleading if not larval occurrence was considered, but the occurrence of adults on the patches. The occurrence of an adult on a patch does not describe the suitability of the patch for the species nor does it indicate a successful breeding attempt, especially in this mobile species.

The impact of this single study on the conservation of butterflies in general is most likely going to be small. Then again, very few small scale studies on a single species have a global impact on such a diverse discipline as conservation. However, it has been suggested that conservation efforts regarding butterflies should even be concentrated on the population level as a complement to preserving species through their entire distribution (Ehrlich and Murphy 1987, Thomas 1995, Ehrlich 2003). Since conservation in Europe still is country-specific, it has been proposed that the available resources be concentrated to conserving principal populations within strongholds rather than peripheral populations that are likely to go extinct, and stay that way (Thomas 1995, Hanski 2003). The greatest value of this study on *P. apollo* would indeed be if it were to be used for the conservation of Apollo populations in agricultural environments in Finland. The true value of the management implications suggested here can only be evaluated if they are put into practise. If indeed population decline could be reversed it could serve as an example, even on a larger scale. Other take home messages from this thesis that are of a more general nature are (1) the potential benefits of combining measures of habitat quality with a “metapopulation”-approach, (2) including all life-stages (or the ones that can be surveyed) into the study, and (3) comparing aspects of populations in different habitats. Hopefully, this thesis could inspire others to evaluate, and scrutinise these aspects in their work, and in so doing join this work to the long tradition of butterfly biology.

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My work with apollo started in 1996, and it was also my first encounter with doing science. Thinking back, it is always the field-work that comes to mind, especially the early days when accommodation sometimes meant sleeping in the back of the car, and eating at Hesburger in Parainen every day. Going out in the archipelago and getting sea-sick on the boat every day, learning how to get around, and being in the amazing archipelago environment that always had something new to offer. Doing this whole Ph.D.-project has been the sum of many people’s effort and good-will, for which I am very grateful. First of all I want to thank Tom Reuter who suggested that I could do something on apollo for my master-thesis. Without Tom’s suggestion and his generosity in providing the means for doing the field-work in Lofsdal, this project would never have seen the light. I am very thankful to the entire Reuter family that has been very supportive and always welcomed me as a sign of spring during the larval counts. I

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