Translocation of the endangered apollo butterfly *Parnassius apollo* in southern Finland

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SUMMARY

Translocation of individuals across a barrier which hampers natural colonisation is a potentially important, but debated, conservation tool for a variety of organisms in a world altered by anthropogenic influences. The apollo *Parnassius apollo* is an endangered butterfly whose distribution retracted dramatically during the 1900s across Europe. In Finland the apollo currently occupies only a fraction of the range of its suitable habitat and is apparently unable to re-colonise other areas. Using eggs collected from wild-caught females from the species' current Finnish stronghold, a population was reared in order to translocate larvae into an unoccupied, but highly suitable, part of the Finnish archipelago where the species historically occurred until its national decline in the 1950s. In 2009 a restricted number of larvae (1 larva/10 host plants) were released on 25 islands in the inner, middle and outer archipelago zones. In 2010, nine islands situated in all three archipelago zones were (re)stocked with a high density of larvae (1/host plant). In 2011, apollo larval populations were found only on islands in the outer archipelago zone, which were then restocked. The species remained present here in the following two years (2012, 2013) and was hence able to sustain multi-annual population establishment without restocking. Our findings demonstrate that empty suitable habitat may in reality consist of only a few sites where population establishment is possible. Hence, starting the introduction in many sites, which are putatively suitable based on biotic and abiotic criteria derived from species' existing populations, but then "zooming in" on a smaller set of promising sites showing evidence of successful establishment was key to the success of this translocation.

BACKGROUND

Moving living organisms from one locality to another (translocation, IUCN 2012) is one broad category of commonly-used conservation actions (Seddon *et al.* 2007). One example is the re-introduction of species in areas where populations went extinct in the past (Scott & Carpenter 1987, Griffith *et al.* 1989, Thomas *et al.* 2009, IUCN 2012). Assisted migration (Peters & Darling 1985, MacLachlan *et al.* 2007) or assisted colonisation (Hoegh-Guldberg *et al.* 2008) is another, heavily debated, form of translocation of species to suitable habitat beyond their natural range (Hewitt *et al.* 2011, IUCN 2012).

Translocations, in general, are poorly documented (Seddon *et al.* 2007). Assisted colonisation, in particular, is mostly debated or modelled, as opposed to studied empirically (Hewitt *et al.* 2011). This is unfortunate, because most translocation attempts fail or succeed only partially (Seddon *et al.* 2007, Chauvenet *et al.* 2013). Lack of clear *a priori* targets of translocations and *a posteriori* evaluation of their effectiveness currently hamper our understanding of why many translocation attempts fail (Chauvenet *et al.* 2013). Thus, there is a need for well-documented translocation experiments in conservation biology.

In this paper, we detail a translocation of the apollo butterfly *Parnassius apollo* in southern Finland. The apollo is a threatened species with European IUCN status "near threatened" (van Swaay *et al.* 2010) and it is listed in Appendix II by the Convention on International Trade in Endangered Species of Wild Fauna and Flora and in Annex IV of the European Union's Habitats Directive. Distribution decline during the twentieth century is the main reason for conservation concern for this species. In Finland, the species was found historically (approximately until the 1950s) throughout the southern and central part of the country, but has since retracted its national range to a narrow band of islands of the southwestern Finnish archipelago. In Finland apollos are assigned the IUCN status "endangered" (Rassi *et al.* 2010).

The current distribution of apollos in Finland is highly restricted in relation to its main host plant *Sedum telephium* (other *Sedum* species commonly eaten by the apollo occur rarely in Finland). This plant occurs widely throughout the southern half of the country, both on the mainland and in the archipelago. Although it is not clear why apollos have become locally extinct in many parts of Finland where their host plant remains extant, it is likely that changes in the landscape associated with the intensification of agriculture have reduced the suitability of habitat for apollos, especially on the mainland. The islands in the Finnish archipelago, however, present highly marginal and largely homogeneous habitat consisting of pre-Cambrian bedrock with vegetation growing in cracks and depressions in the rocks (Figure 1). Because this landscape is not suited for intense agriculture or forestry it has changed little, which is why apollos may be able to sustain populations here. Nevertheless, apollos do not occur throughout the whole archipelago belt. This is surprising because it is a large butterfly that can readily disperse between the islands that currently form its naturally fragmented environment (Fred & Brommer 2009).

Local extinction probability of apollo island populations is higher when the host-plant density is low (Fred & Brommer 2003), although the availability of nectar sources is also an important factor (Fred *et al.* 2006). Furthermore, apollo larvae

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ISSN 1758-2067

develop normally when fed *S. telephium* from an area outside their current distribution (Fred & Brommer 2005) and hence host plant "quality" is probably not hampering the species' ability to establish itself at new sites. However, host plant density is likely to be the main reason for apollos being unable to colonise currently unoccupied habitat. Female apollos oviposit their eggs singly and at random on the substrate of a habitat patch, which causes many larvae to hatch at considerable distances from the nearest host plant (Fred & Brommer 2010). Apollo larvae do not use visual or olfactory cues to find their host plant, and as a consequence larvae have a high probability of starving to death, except where host plants occur at high density (Fred & Brommer 2010). This low larval survival rate during patch colonisation therefore generates an Allee effect, where a small founding population of ovipositing females colonising new habitat cannot achieve sufficiently high population growth rate to allow establishment (Courchamp *et al.* 2008, Bonsall *et al.* 2014).

Therefore, we predict that a re-introduction of apollos in habitat they formerly occupied, through release of a large number of larvae placed directly on their host plant, should overcome the Allee effect. We here define establishment of a population as the unaided survival of the population for two consecutive years which equals two generations in the univoltine apollo.

ACTION

Rearing of the founding populations: Because the apollo is a threatened species it is not ethical to remove reproductive individuals from existing populations thereby degrading population viability. Instead, we opted to harvest a small proportion of eggs of females from a population living in a similar environment and to use these eggs as founders for rearing a captive apollo population under semi-natural conditions. The source of the reared population was a large apollo metapopulation in the middle and outer islands of the southern Finland archipelago (59°42'N, 22°30'E). In 2005, six mated females were collected from three islands and in 2006 six mated females were collected from four islands. The females were placed in white 10 L buckets with a mesh over the opening. Nectar flowers were offered to the females while they were in captivity. The buckets were placed on their side with the opening facing towards the sun. Female apollos in this population produce single eggs. The females primarily placed the eggs on the mesh and the eggs were collected daily into 1.5 ml Eppendorf tubes sealed with cotton wool. In total, these females produced 81 eggs in 2005 and 189 eggs in 2006. Females were kept in captivity until they had produced at least 10 eggs (which took about one to four days), after which they were returned to their population of origin.

Apollos overwinter as small larvae inside the eggs. Eggs were overwintered in the Eppendorf tubes at ambient winter temperatures inside a barn, protected from precipitation and away from direct sunlight. Moisture and fungus was a problem during overwintering. Therefore, in order to maximise overwinter egg survival, the Eppendorf tubes with eggs were placed inside a large box surrounded by silica crystals (commercially available cat litter) to reduce condensation of moisture in the Eppendorf tubes.

Eggs were taken out of their overwintering storage on 1 May. Once exposed to ambient light and temperature, most eggs hatched within 24 h. Some larvae had hatched already sometime during the overwintering period and these larvae became active within minutes to a few hours in the sunlight. Larvae were kept in family groups in plastic containers with the bottom covered by commercially available wood chips used for pet rodents and covered by a mesh. Host plants *S. telephium* were picked from nearby mainland locations and fresh stems were provided as larval food daily. Once pupated, each individual was transferred to a plastic container (diameter 20 cm, height 8 cm) covered by a mesh. After eclosion, each individual was sexed and marked by writing a unique code with a felt-tip pen on its wing.

Individuals were then placed in mating cages, constructed using a wooden frame of approximately 1.5 m x 1.5 m x 2.0 m covered by a mesh on all sides except for a plastic bottom. Water and nectar plants were provided inside the mating cages. The cages were sprayed with water regularly during sunny and warm weather to avoid dehydration. To avoid inbreeding, males and females of the same family group were placed in separate mating cages. However, due to logistical limitations involved in rearing multiple generations, as well as occasional errors in sexing newly eclosed apollo butterflies, matings between distant relatives (e.g. individual with a shared grandparent) did occur, as well as the occasional mating between close relatives.

The identity of individuals mating was recorded, and mated females were placed individually in a 25 cm x 30 cm x 30 cm wooden box covered with a mesh on the front and back sides. Male apollos place a mating plug (sphragis) over the females' genitals after mating. Mated females can hence be recognised confidently. By 2009 the size of the reared population was sufficiently large to allow their introduction into the wild. The average population inbreeding coefficient was then 0.05 (calculated using Pedigree Viewer, Kinghorn & Kinghorn 2010). Thus, individuals released in the wild were mildly inbred.

Selection of suitable sites and release of reared apollo larvae: The archipelago of southern Finland is divided into three zones (inner, middle and outer), which differ in biotic and abiotic characteristics. The inner archipelago consists of both small and large forested islands which are relatively close to each other and hence sheltered from wind and waves. In the middle archipelago, islands are small, and more exposed. Islands in the outer archipelago are surrounded by open sea and hence exposed. Typically, large parts of the outer islands consist of bare rock. Because the apollo falls under the Habitats Directive, introduction of a population was planned on already protected islands in the Tammisaari archipelago (approximately 60 km east of the source populations, 59°48N', 23°45'E), where there are three protected areas: Skärgårdsmiljöstiftelse r.f. (inner archipelago), Nothamns naturskyddsområde (middle and outer archipelago), Ekenäs Archipelago National Park (large area covering all archipelago zones). Based on their geographical location and available mapping of flora, a set of islands within these three protected areas were selected as suitable locations for release of apollos. The criteria for suitable islands were a high density of host plants, in sufficient numbers to sustain a population, and availability of nectar sources (flowers). Apollos occurred in this area until their national decline in the 1950s, although we lack records of their presence on the specific islands included in the translocation. There were no reports of apollos from these areas in the decades prior to this translocation. Part of the islands where the translocation was carried out was surveyed by the authors during summers prior to the start of the translocation effort and no apollos were encountered.

ISSN 1758-2067

We decided to start the translocation scheme over a wide range of suitable islands which met the criteria, and to concentrate effort in subsequent years on those islands where there were signs of success. Suitable islands had sunny and non-forested areas where the host plant grows (Figure 1). This kind of habitat typically occurs along the shoreline. Due to isostatic rebound and progressive island emergence, the further from the mainland an island is, the more exposed habitat there is relative to its size. Hence only the smallest islands in the inner archipelago have suitable open habitat, whereas even the largest islands in the outer areas have suitable open habitat. We wanted to keep the translocations within the protected areas and within the same geographical archipelago. In order to achieve this, the initial set of islands unavoidably consisted of more smaller inner islands than outer islands which are larger and further apart.

The first introduction of apollo larvae was in 2009. Prior to release, the number of *S. telephium* was counted on each island. *S. telephium* is a perennial plant which grows one or several long stems per plant, and can hence be counted relatively easily. One apollo larva for approximately every 10 host plants was introduced by placing them directly onto host plants growing in places which were sheltered, but not encroached by bushes or trees, at a safe distance from the sea and surrounded by other host and nectar plants. Releases were conducted under sunny and calm weather conditions. In total, apollo larvae were introduced on 24 islands in 2009 (Table 1).

In May 2010 all islands were surveyed to count the number of apollo larvae. The larvae are conspicuously coloured (orange and black). They occur singly, either on or just beside their host plants, and can be effectively censused (Fred & Brommer 2003). Because of the low establishment success (Table 1), further introductions were carried out in 2010 by placing approximately one larva per host plant on three large islands in the inner and middle archipelago zones. The 2010 release of larvae was only conducted on patches of *S. telephium* growing in the highest density and typically south-facing side of the islands. Thus, the number of larvae released on the island as a whole do not necessarily equate to the number of *S. telephium* plants on the island (Table 1). However, due to an insufficient number of larvae, it was only feasible to introduce apollo larvae on two islands in the outer archipelago zone in 2010 (Table 1). Because of the logistical difficulty in reaching one of the islands where larvae were released in the outer zone in 2009 (Skyffelskär), this locality was replaced by a different outer zone island (Västergadden) in 2010. Adults were surveyed in the summer of 2010 and 2011 by slowly walking transects over the islands multiple times during the flight season. Adult apollos are distinctive butterflies which can be easily recognised in flight. Some adult apollos were netted to confirm identification and immediately released. We here report whether adults were encountered or not. A census for apollo larvae was also conducted in May 2011. The last release of apollo larvae in 2011 primarily aimed to re-stock the populations on islands where wild apollo larvae were found in 2010.

Evaluating the establishment success of the translocation: From 2010 the translocation scheme converged on nine islands (indicated in bold in Table 1). Larval counts in spring and multiple adult transect surveys during summer were conducted on six of these islands where there was evidence of establishment in 2012. In 2013, all nine islands were surveyed in summer for adults. Successful establishment was defined as the presence of apollo adults at least two years after the last release of captive-reared larvae.

Figure 1. Picture showing habitat on the outer archipelago islands where re-introduction of apollos was successful. The host plant and other vegetation, including nectar plants, mainly grow in the cracks and shallows formed in the granite bedrock.

Ethical note: The non-destructive harvesting of eggs from wild female apollos for rearing was approved by the Environment Centre of Lounais-Suomi (LOS–2005–L–536–254). No female was damaged during the harvesting procedure, and only a part of each female's reproductive potential was harvested, after which the female was returned to her native population. The release of reared apollo larvae was approved by the Environment Centre of Uusimaa (UUS–2009–L–218–254). Apollos were introduced only on already protected islands, and permission for the translocation was obtained from the landowners prior to translocation. Permission to enter the protected areas and survey the islands was obtained from the landowners and relevant authorities. All rearing of apollos stopped after the last release of larvae in the wild in 2011.

CONSEQUENCES

We found clear contrasts between islands in their ability to sustain a released apollo population (Table 1). In particular, none of the 16 islands in the inner archipelago zone showed any evidence of the released apollos surviving over the winter. As no survey for adults was conducted in 2009, it was possible that development into the adult stage was problematic on these islands. Even when substantial numbers of apollo larvae were released on three inner archipelago islands in 2010, no adults were observed two months later. This latter aspect suggests that ordinary development of apollo larvae on these inner archipelago islands was not possible despite the high availability of their host plant.

Survival of the population over the winter 2009–2010 was observed in two of the six islands in the middle archipelago zone following introduction of larvae (Table 1). In addition, development of larvae to adults was also successful on three middle archipelago islands where apollo larvae were released. in 2010. Survival of the population over the winter 2010–2011 was observed on one of these islands (adults observed).

ISSN 1758-2067

Table 1. Translocation effort and population monitoring for each island in each year in the study. The number of released larvae ('Rel') on an island is provided for each year they were released. The number of larvae ('N_{larvae}') counted on the island (before the potential release of more larvae) is given and whether adults were observed during summer surveys ('Adults'). Absence of release or survey is indicated by '–'.

Island		*S. telephium*		2009	2010			2011			2012		2013
	Zone	No. plants	Area (ha)	Rel	N_{larvae}	Rel	Adults	N_{larvae}	Rel	Adults	N_{larvae}	Adults	Adults
Gräsgrundet	**Inner**	**374**	**0.18**	**51**	**0**	**161**	**no**	**0**	**0**	**no**	–	–	**no**
Kattklobben	Inner	10	0.61	0	0	–	–	–	–	–	–	–	–
Lilla Estskär	Inner	130	0.42	13	0	–	–	–	–	–	–	–	–
Lilla Halsholm	**Inner**	**378**	**0.16**	**38**	**0**	**61**	**no**	**0**	**0**	**no**	–	–	**no**
Mellersta Smultrongr.	Inner	169	0.16	22	0	–	–	–	–	–	–	–	–
Mellersta Viggklobben	Inner	125	0.06	25	0	–	–	–	–	–	–	–	–
Norra Halsholm	**Inner**	**682**	**0.23**	**92**	**0**	**227**	**no**	**0**	**0**	**no**	–	–	**no**
Rovan	Inner	44	0.45	7	0	–	–	–	–	–	–	–	–
Råklobben	Inner	28	0.08	10	0	–	–	–	–	–	–	–	–
Stora Sölvskär	Inner	462	7.63	59	0	–	–	–	–	–	–	–	–
Södra Smultrongrunden	Inner	638	0.10	115	0	–	–	–	–	–	–	–	–
Västra Hökholmarna	Inner	50	1.10	5	0	–	–	–	–	–	–	–	–
Västra Viggklobben	Inner	90	0.04	9	0	–	–	–	–	–	–	–	–
Äspskär	Inner	274	1.42	49	0	–	–	–	–	–	–	–	–
Ö om Stora Sölvskär	Inner	43	0.11	7	0	–	–	–	–	–	–	–	–
Östra Hökholmarna	Inner	10	0.51	1	0	–	–	–	–	–	–	–	–
Limpan	Middle	890	0.90	67	0	–	–	–	–	–	–	–	–
Prackharuna	Middle	799	2.00	79	0	–	–	–	–	–	–	–	–
Skadaharun	**Middle**	**1430**	**1.00**	**129**	**0**	**179**	**yes**	**0**	**0**	**yes**	**0**	**no**	**no**
Stenlandet	Middle	355	0.92	37	0	–	–	–	–	–	–	–	–
Tjuvskär	**Middle**	**1540**	**1.00**	**141**	**10**	**459**	**yes**	**0**	**0**	**no**	**0**	**no**	**no**
Viören	**Middle**	**1502**	**0.80**	**153**	**11**	**440**	**yes**	**0**	**0**	**no**	**0**	**no**	**no**
Hjortronskärsgrunden	Outer	1335	0.38	135	0	–	–	–	–	–	–	–	–
Skogsgadden	**Outer**	**928**	**2.30**	**88**	**28**	**593**	**yes**	**41**	**150**	**yes**	**39**	**yes**	**yes**
Skyffelskär	Outer	790	3.58	76	–	–	–	–	–	–	–	–	–
Västergadden	**Outer**	**1346**	**2.52**	**0**	–	**337**	**yes**	**16**	**80**	**yes**	**6**	**yes**	**yes**
Östergadden	**Outer**	**1336**	**2.53**	**0**	–	–	**no**	**0**	**192**	**yes**	**1**	**yes**	**yes**

However, two years after the last release in 2012, it was clear that establishment had not succeeded on these middle archipelago islands since no apollo larvae or adults were observed.

Islands in the outer archipelago zone showed a fairly consistent pattern of both successful over-winter survival and of successful development of released larvae into adults. One of the three outer archipelago islands where apollo larvae were released in 2009 showed no evidence of over-winter survival, and a second one proved to be too logistically challenging to work on and was taken out of the protocol. Nevertheless, release of apollo larvae on new outer archipelago islands in 2010 and 2011 strengthened the notion that success rate for establishment was high in outer archipelago islands. In the end, successful establishment was only observed on these three outer islands (Table 1).

Habitat: Analysis of existing apollo populations showed that islands with a higher overall density of host plant were less likely to suffer local extinction (Fred & Brommer 2003). We therefore anticipated that the density of *S. telephium* on the islands would be the main factor determining the success of establishing a translocated population. On the nine islands where repeated introduction events were tried (Table 1), the density of *S. telephium* plants was highest in the inner archipelago zone (where translocation failed) compared to the other zones (*S. telephium* plants per ha: inner 2469 ± 320 (S.E.), middle 1616 ± 164 (S.E.), outer 489 ± 52 (S.E.); ANOVA $F_{2,6} = 33.5$, $p < 0.001$). We therefore conclude that factors other than host-plant density determine the colonisation success of empty apparently suitable habitat by apollos.

DISCUSSION

Translocation is a conservation tool which is likely to increasingly be used, either for re-introduction of species in localities where they previously became extinct or to aid

ISSN 1758-2067

species in their colonisation of habitat made suitable due to climate warming. The latter type of translocations could be a promising conservation action for many Lepidoptera (Willis *et al* 2009). However, translocations are typically poorly documented, hampering assessment of viable translocation schemes (Chauvenet *et al.* 2013). Theoretical work underlines that even shallow gradients in extinction and colonisation probabilities over the landscape can result in sharp limits of a species' occurrence in that landscape, with suitable patches existing outside the species' present range (Holt & Keitt 2000). This pattern is evident for apollos in southern Finland. There were plenty of suitable habitat patches, on the basis of the density of the host plant, the main factor determining suitability in this species (Fred & Brommer 2003, 2005, Fred *et al.* 2006). There is no evidence that the apollos' host plant from areas outside its present Finnish range is of unsuitable quality, as evidenced, for example, by the fact that for this translocation we reared the species on host plants picked from the mainland (see also Fred & Brommer 2005). We hence expected that release of apollo larvae directly onto host plants growing on apparently suitable islands would allow population establishment. However, we found that only a restrictive subset of islands allowed establishment of a population (defined here as a population surviving two years without re-stocking). The islands where translocation was successful were all in the so-called outer archipelago zone, bordering the open sea, and this factor alone was the strongest determinant of population establishment. Host plant density, however, did not explain failure of population establishment, thereby suggesting that other factor(s) are limiting. We see two main implications of this work.

(1) Most translocation attempts fail or succeed only partially (Seddon *et al.* 2007, Chauvenet *et al.* 2013). Our findings suggest that even when analyses of abiotic and biotic factors which affect occurrence of an organism in extant populations predict that certain habitat is suitable, release of animals may not lead to successful population establishment. In our case, despite repeated trials, establishment by apollos was only observed in the subset of suitable islands located farthest from the mainland. An important practical consequence of this finding is that translocation efforts should include the possibility of variable outcome and be directed, whenever possible, to initially cover a wide variety of potentially suitable habitat. In our case, for example, we carried out introductions also in the middle and outer archipelago zones, despite the fact that *S. telephium* density (identified as the main habitat factor for apollos) was highest on the inner archipelago islands. Our results suggest translocation would have failed if we had solely concentrated on these islands.

(2) Our finding that successful establishment by apollos was restricted to only a subset of suitable islands provides an explanation for why the species has not been able to colonise by itself suitable habitat outside its present range. Even when substantial numbers of larvae (far exceeding the potential reproduction of a single female) are placed directly on host plants, population establishment still failed at the majority of sites. Thus, colonisation probability is very low, at least outside the species' present range. We can here only speculate over why this could be. For the inner archipelago islands, it seems that larvae could not develop to adults, at least in 2010. In addition, winter conditions on the islands may be important, as suggested by the apparent difficulty of populations surviving winter (especially the 2010-2011 winter). Populations on outer islands may experience an earlier onset of spring than populations on more inner islands. Sea ice forms later on outer islands and also disappears earlier. Outer islands may also be more exposed to wind, which may mean they are less covered by snow during winter. In addition, the assemblage of species in the community likely changes in islands closer to the mainland. Inner and middle archipelago islands may have a higher abundance of predators and parasites as well as indirect competitors compared to outer islands and this may reduce the probability of apollos colonising these islands. The currently occupied sites in the inner and middle zone of the south-western Finnish archipelago may, in fact, constitute population sinks (*sensu* Pulliam 1988). That is, the presence of apollos on these islands may be upheld only by dispersal from populations in the outer archipelago zone. In general, our findings on a species occupying a naturally fragmented habitat (archipelago of islands) may also apply to species living in anthropogenic fragmented habitat, where putatively suitable sites may, for unknown reasons, not allow population establishment.

Implications of this study for carrying out translocations: Careful follow-up of sites where individuals are released is needed, because successful multi-annual establishment is not guaranteed even if establishment one year after release is observed. For example, after releasing larvae in 2009, we observed over-winter survival in two islands in the middle archipelago zone. Despite this early success, establishment here did not occur in the longer term. A second implication of our work is that presumably good-quality habitat, as based on study of extant populations, may not allow establishment of translocated populations. Hence, a viable strategy is for translocation efforts to cover multiple years, and base decisions on where to release additional individual on evidence provided by the previous years' success and failures. By using this approach we were able to overcome the unexpected inability of apollos to establish a population on inner and middle archipelago islands. This design allowed us to start 'wide' (many sites with various characteristics) and then 'zoom in' on localities where the likely success of establishment appears to be high.

ACKNOWLEDGEMENTS

We thank Skärgårdsmiljöstiftelse r.f., Nothamns naturskyddsområde and the Ekenäs Archipelago National Park for permission to introduce *P. apollo* in these protected areas. The Academy of Finland and the Nessling Foundation supported this work (to MSF).

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ISSN 1758-2067