Laura Härkönen, Arja Kaitala

9 Host Dynamics and Ectoparasite Life Histories of Invasive And Non-Invasive Deer Ked Populations

9.1 Introduction to Ectoparasite Invasions

A considerable fraction of biological invasions, including terrestrial ectoparasites, is a consequence of human activity. The most important environment for arthropod ectoparasites is a vertebrate host — the host as an environment can be highly heterogeneous both quantitatively (abundance of host individuals) and qualitatively (different genotypes, host races, populations and species). Ectoparasites are vectors for harmful pathogens, whereas ectoparasite infestations as such rarely cause substantial fitness costs or health issues for their host (Lehane, 2005; Muirhead-Thomson, 1982). Accordingly, ectoparasites are often considered in the context of transmitting invasive pathogens (Lehane, 2005), whereas ectoparasite invasions among host populations, or invasive expansion of geographical range have received less attention (Pyšek *et al.*, 2008). However, understanding the natural history and evolutionary ecology of parasites should become a key part of public health planning (Renaud *et al.*, 2005). Here, we review the main factors behind the invasion of a blood-feeding fly, the deer ked (*Lipoptena cervi*; Hippoboscidae), in a host population coupled with substantial expansion of geographical distribution.

9.1.1 Host-parasite Interactions

Warm-blooded vertebrates provide a necessary habitat and resources for a variety of terrestrial ectoparasites. True ectoparasites, such as ticks (Parasitiformes: Acari), fleas (Siphonaptera), lice (Phthiraptera) and many louse flies (superfamily Hippoboscoidea: Diptera), are specialized in inhabiting the host surface for at least part of their life. During the obligate host-dependent stage(s) they consume host-derived resources (e.g. blood, secretions, keratin, skin cells; Lehane, 2005). Due to the tight host-dependency, factors related to host dynamics, i.e. spatio-temporal variation in host abundance, and co-evolutionary interactions, are the main factors driving ectoparasite invasions (Holt *et al.*, 2003; Meier *et al.*, 2014).

A typical relationship between an ectoparasite and its host is characterized by co-evolution. Ectoparasites adopt a variety of morphological, physiological, and behavioural adaptations to exploit hosts for living and reproduction. Hosts, in turn, evolve adaptations to regulate the number of parasites and their negative effects. They may either behaviourally avoid contact with ectoparasites, or use defensive mechanisms to prevent or minimize infections and/or the infection can be counteracted by the immune system (Agnew *et al.*, 2000; Poulin, 2007). The more competent the host defence systems, the fewer the chances for the ectoparasite to exploit the host and spread effectively in the host population. Accordingly, well-documented cases of invasions by terrestrial ectoparasites have been associated with hosts that have not yet evolved efficient defences against the invaders [e.g. the winter tick *Dermacentor albipictus* invasion of moose *Alces americanus* in Northern America (Samuel *et al.*, 2000) and the deer ked invasion of European moose *Alces alces* in Finland (Kaitala *et al.*, 2009)].

The geographical range size of ectoparasites is often smaller than the range(s) of its host(s) owing to narrower environmental tolerance of the parasite, and smaller range sizes are more frequently found among host-opportunistic than in host-specific ectoparasites (e.g. in fleas; Shenbrot *et al.*, 2007). Accordingly, the most efficient way for an ectoparasite to adapt to a host environment is to actively select only the most suitable hosts. However, several potential host species may be available in a given environment, and depending on the degree of host specificity, ectoparasites exhibit varying performances across the different hosts (Valimaki *et al.*, 2011). Host-specialist ectoparasites may use their host more efficiently, but a high degree of specialization often leads to low performance across the other potential host species (Poulin, 2007). On the contrary, a generalist parasite should invest in counter-adaptations against several host species. A lower degree of specificity often results in lower performance across all potential species, even on an optimal host species. However, ectoparasites may shift their host preferences according to local host availability (Shenbrot *et al.*, 2007), and an adaptation to geographically different host populations or species may be an important determinant of an ectoparasite's ability to invade new host species and areas (Härkönen *et al.*, 2015).

Ectoparasites may encounter novel, but potentially suitable host species when colonizing new geographical areas. A recently infected host is often poorly adapted to the novel parasite, either because it has not yet developed an immunological defence or because of fortuitous vulnerability, and hence there is potential for the parasite to spread rapidly in a new host population (Poulin, 2007). The overall performance of specialist ectoparasites on a novel host may remain low due to specialization in native hosts or because the resources derived from novel hosts are of lower quality than from native hosts (Gandon & van Zandt, 1998). The attempts to reproduce on low-quality hosts may be so frequent that the invasion process ceases. In other words, high abundance of low-quality novel hosts qualifies as an ecological trap for ectoparasites (Battin, 2004; Robertson & Hutto, 2006; Robertson *et al.*, 2013).

9.1.2 Invasion Process in Temperate Ectoparasites

Ectoparasites' ability to fly and migrate long distances is often negligible for active dispersal. Instead, the vertebrate host usually migrates long distances, and thus the hosts are efficient carriers of ectoparasite propagules into new areas. Colonization of new geographical areas is affected by the extent of propagule pressure, referring to the number of parasites carried by the host to new environments (Lockwood *et al.*, 2005). Thus, high host density and high ectoparasite prevalence on the hosts increase both propagule pressure and genetic diversity in the introduced founder population, and may hence facilitate the establishment of the ectoparasite population in a new area (Davis, 2009).

During transportation phase, temperate ectoparasites are protected from unfavourable external temperatures by the thermoregulatory abilities of their warm-blooded hosts (Wharton, 1999), but establishment in novel geographical areas depends on the survival of ectoparasites through the free-living stage(s) (Härkönen *et al.*, 2010; Khatchikian *et al.*, 2012). Since ectoparasites are rarely able to actively choose their environments, adaptations to the local abiotic (off-host) or biotic (host) environment are predicted to only occur when the dispersal rate of the parasite is very low (Kirkpatrick & Barton, 1997). Instead, many ectoparasites have adopted a plastic behaviour and life history that allows them to tolerate conditions in different off-host habitats (Gandon & van Zandt, 1998). When survival requires phenotypic plasticity, wide ecological requirements and high ecological tolerance, the same characteristics may facilitate the invasion process across different off-host environments (Agrawal *et al.*, 2001; Yeh & Price, 2004).

An essential requisite for persistence of an ectoparasite population in a new area is an individuals' ability to complete its life-cycle, i.e. ectoparasites must find a host from the new environment during the free-living infective stage. Most true ectoparasites exploit a *sit-and-wait* host-ambushing strategy instead of an active 'cruising' strategy, and thus the infection strongly depends on the probability of close host contact (Fenton & Rands, 2004). High local host density is particularly important for host-ambushing ectoparasites to increase the likelihood of host encounter. Host densities are likely to decline towards the host's distribution range edge, which could limit ectoparasites' range expansion by decreasing the probability of host encounter. In addition, since ectoparasites are often restricted to using the same host through the reproductive lifespan, a low number of infective-stage ectoparasites on an individual host animal reduces the probability of male-female pair formation and subsequent reproductive success (Gascoigne *et al.*, 2009; Kramer *et al.*, 2009). Thus, low ectoparasite density in recently colonized areas can prevent further spread of invasive species because of the Allee effect (Lewis & Kareiva, 1993; Tobin *et al.*, 2011).

Ectoparasite persistence in a given environment also depends on the interactions between individual life-history and the experienced abiotic environment (Härkönen *et al.*, 2010; Stearns & Hoekstra, 2005). Towards higher latitudes the severity of winter increases, and the length and temperature of the growth season decline (Bale & Haywards, 2010; Crozier, 2004a,b). Survival and development during off-host stages are dependent on seasonal temperature variation, and hence colder climate commonly increases winter mortality, prolongs the developmental period, and may thus limit range expansion of ectoparasites (Härkönen *et al.*, 2010). Timing of the infective stage is particularly important in the north, where the potential transmission period is often short due to earlier arrival of winter (Härkönen *et al.*, 2010; Samuel *et al.,* 2000). Thus, the prolonged development due to cold climate, and thereby delayed emergence of the infective stage, may lead to a mismatch with host availability and decrease the probability of host encounter.

In theory, when suitable hosts are numerously available beyond the distribution range limits and abiotic environmental factors do not restrict parasite numbers, ectoparasites may spread rapidly in a host population and across geographical areas in an invasive manner. However, due to geographical differences in absolute and relative densities of differently suitable host species, the ability of ectoparasites to survive and complete their life-cycle may vary markedly, resulting in population differences in invasion potential (Härkönen *et al.*, 2015). Particularly among host-specialist ectoparasites, relative rather than absolute density of primary host species is likely to determine the invasion potential of an ectoparasite.

9.2 Effects of Host Dynamics and Deer Ked Life Histories on Population Invasiveness

The blood-sucking deer ked (*Lipoptena cervi*, Hippoboscidae) is an Old World dipteran ectoparasite of European moose (*Alces alces*) and other boreal cervids (Cervidae). Its distribution extends from the British Isles through Europe and Russia to Northern China and the Korean peninsula (e.g. Haarløv, 1964; Sleeman, 1983; Kim *et al.*, 2010; Välimäki *et al.*, 2010). In addition, the deer ked was apparently introduced in North America in the late 1800s by an unknown European deer species, and currently infests native cervids of the North-eastern United States (Samuel *et al.*, 2012).

In Fennoscandia (Northern Europe), the deer ked has undergone significant geographical expansion in distribution during recent decades (Välimäki *et al.*, 2010; Figure 9.1). In addition, a moose has been found to host over 17,000 deer keds (Paakkonen *et al.*, 2010), demonstrating the intensity of fly infestation in recently colonised hosts. The contributing factors for the invasion potential of deer ked among the Fennoscandian cervid populations and their range expansion towards high latitudes have been studied intensively (Härkönen, 2012; Härkönen *et al.*, 2010, 2012; 2013; Kaitala *et al.*, 2009; Kaunisto, 2012; Kaunisto *et al.*, 2011, 2012; Madslien, 2013; Madslien *et al.*, 2012; Meier *et al.*, 2014; Nieminen *et al.* 2012, 2013; Paakkonen, 2012; Paakkonen *et al.*, 2010, 2012; Välimäki *et al.*, 2010, 2011). The importance of host dynamics and life-history attributes in deer ked invasion are reviewed here.

9.2.1 Invasion of Fennoscandian Cervids

The distribution of the deer ked in Fennoscandia is divided by the Baltic Sea into two distinct, western (Sweden and Norway) and eastern (Finland) ranges (Fig. 9.1.).

The deer ked is a host-ambushing ectoparasite and requires close contact with a potential host for infection. Thus, high abundance of suitable hosts is of particular importance for deer ked invasion. A relatively wide range of cervid species is available for the deer ked in Fennoscandia (Välimäki *et al.*, 2011). The European moose (*Alces alces*) is currently the only host species that promotes high reproductive success of the deer ked in both western and eastern parts of Fennoscandia (Välimäki *et al.*, 2011). Reproduction on roe deer (*Capreolus capreolus*) has proved to be successful only in the western range; in the eastern range, successful offspring production has been observed only once (Härkönen *et al.*, 2015). There is as yet no data on reproduction on less common cervids, such as the fallow deer (*Dama dama*) or the red deer (*Cervus elaphus*), in the western range. In the eastern range, deer ked reproduction — with low success — has been reported on reindeer subspecies [semi-domesticated reindeer (*Rangifer tarandus tarandus*; Kaunisto *et al.*, 2009) and wild forest reindeer (*R. t. fennicus*; Välimäki *et al.*, 2011). In the southern parts of eastern range, the white-tailed deer (*Odocoileus virginianus*) is relatively common in dense deer ked areas, but no evidence of infestation has been found (Välimäki *et al.*, 2011).

Abundances of many large vertebrates, including cervids, have been regulated by man, which has exerted immediate consequences on their parasite community and distribution (reviewed by Thomas *et al.*, 2009). Correspondingly, many Fennoscandian cervid species have undergone remarkable population declines during the last centuries due to human activities, such as hunting and forest management (Liberg *et al.*, 2010; Tiilikainen *et al.*, 2012). Today harvest policies and other management actions are similar in both the western and eastern parts of Fennoscandia (Luoma, 2002). In particular, moose and roe deer population sizes are maintained in artificially large numbers for recreational hunting purposes, facilitating outbreaks of deer ked (Meier *et al.*, 2014; Figure 9.2).

The deer ked was first reported by Carl Linneaus in Sweden, Western Fennoscandia (i.e. Scandinavian Peninsula; Linneaus, 1758). This western deer ked population originates from Central Europe, but its arrival time in Sweden is not exactly known. The colonization of the Scandinavian Peninsula has been poorly documented, but the deer ked has been resident in southern and central parts of Sweden since at least the 18th century (below the latitude of 62°N; Fig. 9.1). The abundances of the two main hosts in the western deer ked range, the moose and the roe deer, have varied independently from near extinction to very large numbers (Lavsund *et al.*, 2003; Liberg *et al.*, 2010). The Scandinavian roe deer was hunted nearly to extinction before the remnant population was declared protected in Southern Sweden around 1840. The roe deer quickly recovered and recolonized most of the Scandinavian Peninsula (Liberg *et al.*, 2010; Thulin, 2006). The Scandinavian moose population began to recover markedly later, around the 1930s. It is likely that the roe deer maintained the western deer ked population during the threatened moose extinction. Since then, the western range of the deer ked has remained relatively stable and the population is considered non-invasive (Välimäki *et al.*, 2010). However, a minor range expansion started in the 1980s when the deer ked spread westwards across the Norwegian border and invaded South-eastern Norway (Figure 9.1).

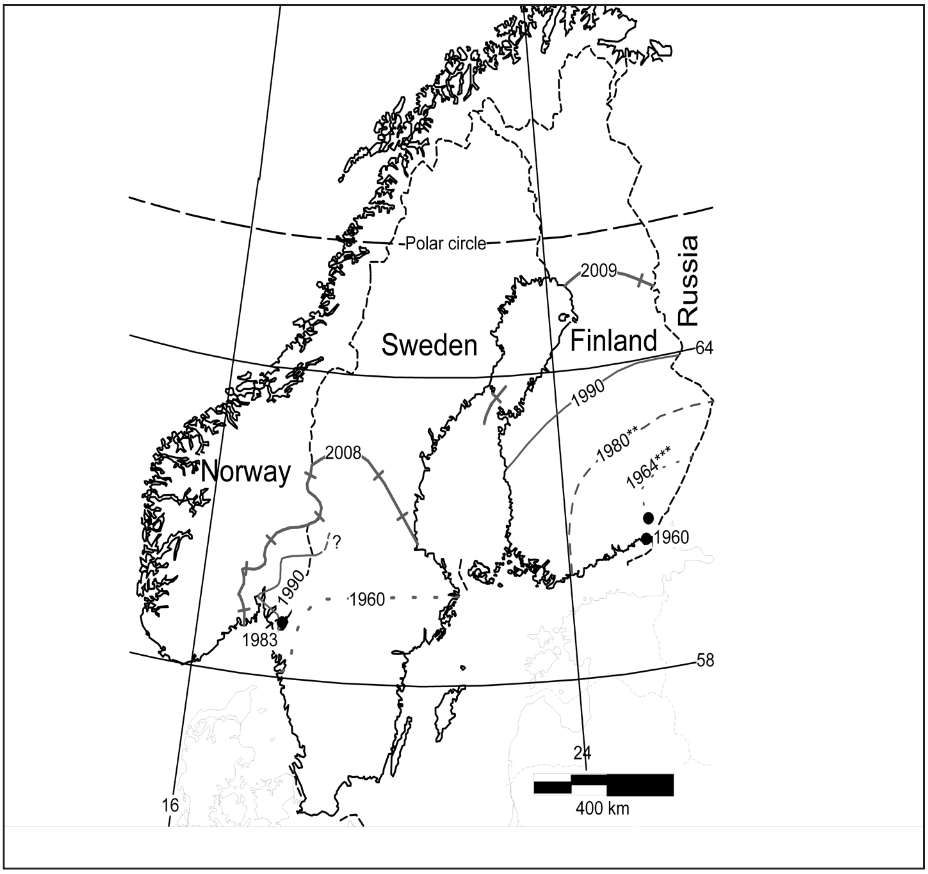

Fig. 9.1: Illustration of the bimodal distribution of the deer ked in Northern Europe from the early 1960s to the present. The first verified observations (in Norway and Finland) are indicated by black dots. The northern range limit is based on scarce observations of the northernmost individuals, which do not correspond the established range limit. The western and eastern deer ked populations likely separated thousands of years ago, but there are no genetic differences between the populations (Jaakola *et al.*, 2015). Reprinted from Välimäki *et al.* (2010), with kind permission from Springer Science and Business Media.

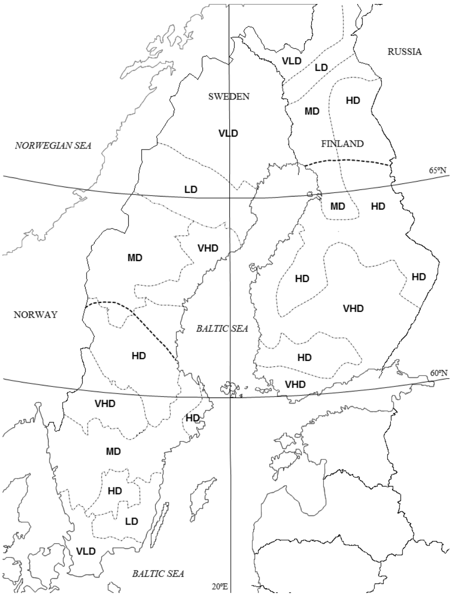

Fig. 9.2 (A): Current densities of the moose (VHD = very high density, HD = high density, MD = medium density, LD = low density, VLD = very low density) in Sweden (Kindberg *et al*., 2008) and Finland (FGFRI, 2011). The northernmost observations of the deer ked are presented as a black dashed line (according to Välimäki *et al*., 2010).

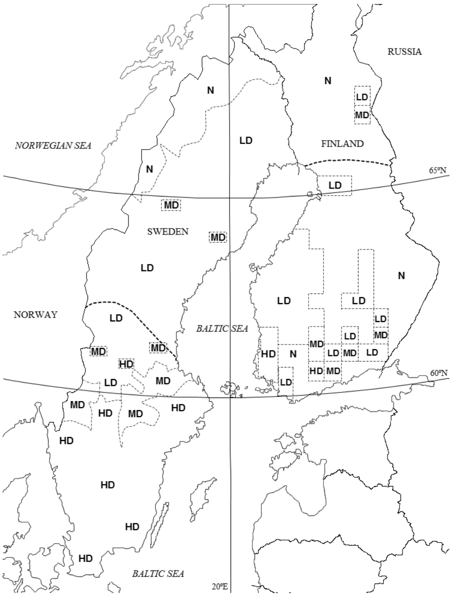

Fig. 9.2 (B): Current densities of the roe deer (HD = high density, MD = medium density, LD = low density, N = no observations) in Sweden (Liberg *et al*., 2010; harvesting numbers in 2004) and Finland (FGFRI, 2013; Snow-track counting). The northernmost observations of the deer ked are presented as a black dashed line (according to Välimäki *et al*., 2010)

The first records of the deer ked in Eastern Fennoscandia are from 1960 in Southeastern Finland, where it arrived from Russia (former U.S.S.R.; Hackman *et al*., 1983). Systematic moose management in Finland began in 1969–1971 when the nearly extinct moose was declared protected, after which moose numbers showed an exponential population increase (Luoma, 2002). Accordingly, the spread of the deer ked began from the latitude of 60°N in the 1970s, and during the following twenty years its range extended to western and central parts of Finland (Hackman, 1977). In other words, the spatial and temporal dynamics of the deer ked outbreak are closely associated with the extremely rapidly expanded distribution and increased densities of moose (Meier *et al*., 2014). The range expansion towards higher latitudes was rapid until the northern range limit was recently reached, along the latitude of 65°N where the southern border of reindeer herding territory is located (Välimäki *et al*., 2010). Altogether, the eastern range extended over five latitudes and two climatic zones in less than 50 generations (i.e. 50 years). Hence, the eastern deer ked population has been considered an invasive population.

Taken together, the western distribution has remained at markedly more southern latitudes for centuries compared to the distribution of eastern population. There are no definite figures of the present total number of moose in Sweden and Finland, but the harvest level and local surveys indicate that winter populations (post-harvest) are around 200,000 individuals in Sweden (2005) and 80–90,000 in Finland (2006) (Liberg *et al.*, 2010). In Sweden, the roe deer population has been estimated to consist of 400–500,000 individuals (post-harvest in 2005–2007; Liberg *et al.*, 2010). The present roe deer number in Finland is significantly lower, being approximately 15,000 individuals (Burbaité & Csányi, 2009). Moreover, these cervids are available for the deer ked beyond the current range limits (Figure 9.2) indicating that the latitudinal differences are not simply explained by abundance of suitable hosts. Instead, the differences in invasiveness of deer ked populations likely derive from co-evolutionary or environmental factors driving the population dynamics through off-host survival (Härkönen *et al.*, 2015).

9.2.2 Life-history Variation in the Deer Ked

9.2.2.1 Reproduction and off-host Survival

A cervid host offers a constantly favourable habitat for the deer ked – feeding, mating and reproduction occur on the host all year round (see Figure 9.3). The deer ked is a live-bearing, viviparous insect: the development of an embryo and egg-hatching occurs inside the female, where the larva is nourished through “milk glands” until it reaches the final instar. The mother gives birth to one pre-pupa at a time, which completes its pupation immediately after birth. The total offspring number of a female has been estimated as few dozen at maximum (Ivanov, 1981). The new-born pupae drop off from the host to undergo an obligate free-living period, including phases of diapause (i.e. winter dormancy that varies in its duration according to the birth date), pupal development, and host search as an adult (Härkönen & Kaitala, 2013).

Viviparous females provide a *safe harbor* for juvenile development, and by producing well-developed offspring, the survival prospects of each offspring are relatively high (Stearns, 1992). In the deer ked, offspring survival after birth correlates strongly with its size as large size increases physiological tolerance to environmental adversities and starvation resistance during the off-host period (Härkönen *et al.*, 2012, 2013). Offspring survival thus depends on the resources their mother transfers from the host’s blood during larval incubation, but offspring size also varies with respect to host condition (Härkönen *et al.*, 2013). When a host is in good condition, it may be able to increase its immunological resistance against parasites (Tschirren *et al.*, 2007). As the winter progresses, the condition of a moose declines, which increases the deer ked’s ability to exploit the host for offspring production — the offspring size, and thereby also off-host survival, increase steadily from autumn towards the spring and the end of the reproductive period (Härkönen *et al.*, 2012, 2013).

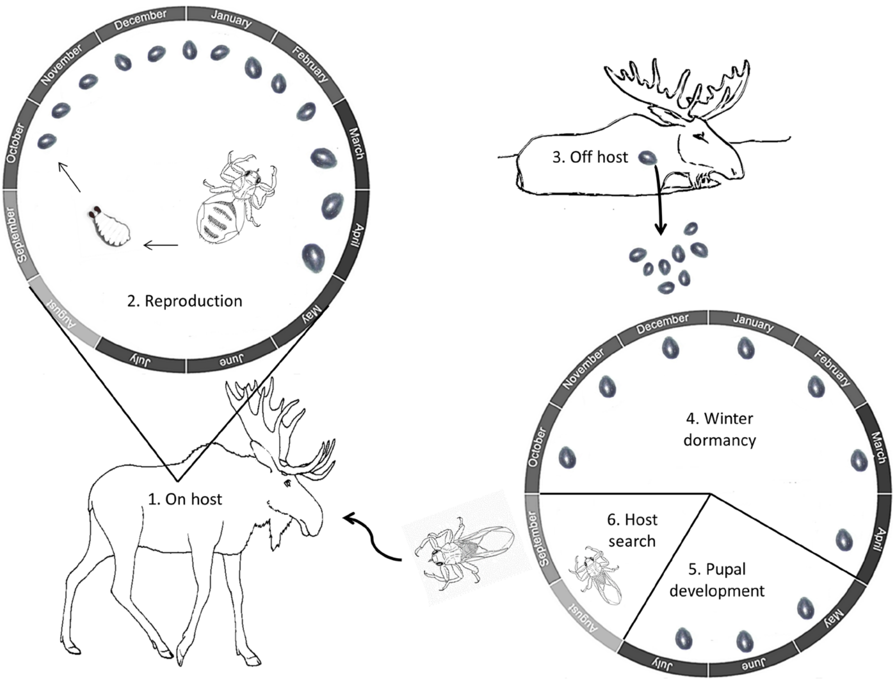

Fig. 9.3: Illustration of the deer ked life-cycle. (1) Once an adult finds and attaches on a host, it loses its wings, exploiting the same host until senescence. (2) Viviparous blood-sucking females give birth to one full-grown larva at a time. Offspring production starts in autumn and lasts at least until the following spring (even until July; Härkönen, 2012). (3) The larva pupates immediately after birth and the pupa falls off from the host, often on a host bedding site. (4) On the ground, the pupae first overwinter at diapause. (5) Once the temperature rises in the spring, diapause ends and pupal development begins. After approx. three months of development, adults emerge in high local synchrony. (6) The adults may ambush hosts until late autumn.

In addition to host-dependent offspring quality, off-host survival is directly affected by environmental harshness and the duration of the period outside the host. Due to viviparity, the period of offspring production is exceptionally long (Figure 9.3). In seasonally challenging environments, early-born small autumn pupae have a low survival probability due to higher risk of starvation during long winter dormancy (Härkönen *et al.* 2013). Since offspring are produced throughout winter months some of them will risk freezing, and thus the roles of cold tolerance and insulating snow cover for winter survival are of great importance in areas with frequent harsh frosts (Härkönen *et al.*, 2012). The newborn pupae are highly tolerant against short-term frosts when they drop off from the warm host: even without cold acclimation they survive briefly in temperature as low as -26°C by supercooling. An increase in offspring size enhances tolerance of pupae to long-term harsh frosts — especially large pupae can tolerate three days of direct exposure at -20°C but are likely to die if frost period is longer. Lateborn large pupae in spring overwinter only briefly and do not experience harsh winter conditions (frosts, lack of snow, predation) (Kaunisto, 2012), and are likely to survive until the infective stage (Härkönen *et al.*, 2012, 2013). Taken together, long reproductive period and production of large well-developed offspring increases the probability that some of the introduced propagules will experience favourable conditions in a novel off-host environment and survive long enough to find a host.

The deer ked adults emerge in late summer and search for a host through the autumn. A host-ambushing adult relies on very simple host location cues; it does not discriminate between potential hosts, instead attacking all large, dark, moving objects, including humans, dogs, cows, and horses (Kortet *et al.*, 2010). The adults are able to survive without feeding for a few months while sitting-and-waiting for a potential host to pass by. In addition to risk of starvation before host contact, arrival of winter may cease the host search period. However, the adult stage may briefly tolerate frost below -15°C and host search may continue as long as the daily temperatures remain high enough for flying (Härkönen *et al.*, 2012; Nieminen *et al.*, 2012). The ability to tolerate autumnal frosts may extend the host search time and thereby facilitate the range expansion northward.

9.2.2.2 Host-specific Life History Variation

Ectoparasite life histories at the margin distribution areas determine the invasion potential of a population, i.e. the ability to spread beyond established range limits (Bridle & Vines, 2006; Hill *et al.*, 2011; Sexton *et al.*, 2009). Large size and high physiological tolerance are generally among the best predictors of invasion success (Davis, 2009). Both these characteristics in the deer ked are closely associated with host-derived resources (Härkönen *et al.*, 2012). However, distinct co-evolutionary and invasion histories of the Fennoscandian populations have modified deer ked life history characteristics, and nowadays the local host species and populations differ in their quality for deer ked reproduction (Härkönen *et al.*, 2015).

The most important difference in deer ked characteristics between the noninvasive western and invasive eastern populations is body size. The pupae and adults in the invasive population may be as much as twice the size of the non-invasive population (Välimäki *et al.*, 2011). This difference has likely emerged as a result of long co-evolution with different hosts. For example, a positive relationship has been observed between ectoparasite size and host mass (Poulin, 1998). Large size and inability to infect multiple host species indicate that the invasive eastern population is well-adapted to exploit the largest cervid, i.e. the moose. Although the joint history of moose and the invasive deer ked in eastern Fennoscandia is short, the moose has already become the native host species in its origin areas in Eastern Europe and Russia (Ivanov, 1981). Co-occurrence of the western deer ked with roe deer goes back to Central Europe, where the deer ked has exploited medium- or small-sized cervids as its native hosts (Haarløv, 1964). Joint history with the moose is shorter as it presumably started when deer ked colonized Western Scandinavia. Simultaneous co-evolution with several cervids, and particularly with small-sized cervids, may have selected for small body size in the western deer ked population (Härkönen *et al*., 2015).

Reciprocal influence of the host resistance and the deer ked female's ability to invest resources in developing larva varies with respect to invasion histories and with different host species. In other words, variation in offspring size and cold tolerance indicate immediate host effects on off-host survival owing to local variation in host condition or quality (Härkönen *et al*., 2012, 2013). Within the well-established western range, offspring size, survival, and cold-hardening capacity are greater on pupae produced on roe deer than on moose in the same area, indicating a higher ability to exploit roe deer for reproduction. On the other hand, the moose differ in quality for reproduction between the eastern and western populations. We have observed production of offspring with markedly larger size, higher supercooling capacity and survival on moose in the invasive eastern than in the stable western population (Harkonen *et al*., 2015). Such differences in performance on the same host species in different geographical areas indicate that the invasive, moose-specialist deer ked exploits the moose more efficiently for offspring production. When parasites become locally adapted on one host species they often lose the ability to infect other hosts (Gandon & Van Zandt, 1998). Accordingly, the reproductive performance of the eastern population on any other local cervid species (roe deer, wild forest reindeer or semi-domesticated reindeer) is very low (Kaunisto *et al*., 2009; Kynkäänniemi *et al*., 2010; Välimäki *et al*., 2011). Interestingly, our preliminary findings suggest that the deer keds in the recently expanded western subpopulation in Norway exhibit a substantial increase in size and viability compared to the old, well-established core population in Sweden. The recently invaded moose population in Norway may still have low ability to resist the deer keds, and thus the deer keds may hold the potential to spread in that area owing to higher ability to survive in adverse off-host environments.

9.2.3 Current State of Deer Ked Invasion

The potential for further invasion of the deer ked would primarily depend on host availability and their movements and secondarily on off-host survival beyond the current range limits. In theory, both Fennoscandian deer ked populations have the potential to spread further north because a high number of cervids are also available far beyond the current northern range limits. Long distance migrations of cervids facilitate spreading of the deer ked to new areas. For example, moose are highly mobile and may move for hundreds of kilometres between seasonal ranges during the deer ked's reproductive life span (Heikkinen, 2000). However, current distribution limits correlate with the density of that host species on which the off-host survival probability is the highest. In the western deer ked range, the roe deer is currently the most abundant cervid species in the area (Liberg *et al*., 2010) — it is common in the southern and central parts of Scandinavia but rarer further north (Figure 9.2B).

Accordingly, the well-established deer ked range limit follows the high density roe deer distribution, rather than moose distribution which is high also beyond the current northern range limit. Correspondingly the invasive eastern population has followed spatio-temporal variation in moose densities. Northward range expansion has also exposed the semi-domesticated reindeer populations to a novel ectoparasite (Kynkäänniemi *et al.* 2010, 2014). Once the deer ked range extended to southern reindeer herding areas, where the densities of reindeer are tenfold compared to moose densities in the area, its invasion ceased. Along the current northern range limit, the deer ked has been reported to infect reindeer but the reproductive success is low (Kaunisto *et al.*, 2009; Kynkäänniemi *et al.*, 2010), suggesting that low quality hosts may function as an ecological trap for the deer ked, preventing further spread (Aikio & Kaitala, unpublished data). Taken together, instead of absolute density of the host species, the relative densities of different host species play an important role in deer ked invasion potential in the future.

The deer ked pupae dropping off from the host during seasonal migrations are effectively distributed over a wide range of habitats and climatic conditions. Due to viviparous production of large, high-quality offspring, the deer ked off-host stages are highly tolerant to northern adversities prevailing outside the host. However, in order to establish even further north, free-living stages should not only tolerate low temperatures but also adjust the life-cycle to shorten the growth season. Although the eastern invasive deer keds have better ability to survive in the north due to larger size and higher cold tolerance, off-host survival of the western deer keds does not differ so dramatically that it would consecutively explain their southern range limits. Under identical conditions, however, adults from the stable western population emerge markedly later than in the invasive eastern population (Välimäki *et al.*, 2011). Longer development time indicates that the emergence of the infective stage in the western population is adjusted to the relatively longer and warmer summer prevailing in Southern Fennoscandia and thus, there may be a mismatch between emergence time and ability to ambush hosts under colder northern climate conditions, and thereby a limit to northwards invasion. On the contrary, faster pupal development rate in the eastern range has facilitated rapid northwards invasion (Kaunisto *et al.*, 2011). Furthermore, a transplant experiment conducted using the invasive eastern population showed that the deer ked is able to complete its pupal development at the latitude of 70°N, i.e. 500 kilometres to north from the current range limit (65°N). Further northward invasion may still be unlikely because lower spring and summer temperatures restrict the parasite numbers substantially by decreasing pupal survival, delaying adult emergence, and shortening the time window for host search (Härkönen *et al.*, 2010).

9.2.3.1 Socio-economical Consequences of Deer Ked Invasion

The detrimental effects of deer ked on host health have been contradictory – severe alopecia has been associated with massive deer ked infestation in Norway (Madslien *et al.*, 2011) whereas no physiological effects, or only minor effects, have been reported in moose in Finland (Paakkonen *et al.*, 2012). However, the blood-feeding deer ked is a potential vector for transmitting various diseases (Rantanen *et al.*, 1982; Dehio *et al.*, 2004). The deer ked is known to harbour haemotrophic *Bartonella schoenbuchensis*. The same *Bartonella* species have been identified, with high prevalence, in moose in areas with deer ked infestation (Duodu *et al.*, 2013; Korhonen *et al.*, 2015). It is yet unknown whether chronic bacteremia with *Bartonella* has any impact on the health of the moose, or on other species that the deer ked may attack.

The outbreak of the deer ked has been accompanied by public health issues for humans, particularly in high density areas in southern and central parts of Finland. Due to simple host location cues, the deer ked often mistakenly attacks humans (Kortet *et al.*, 2010). The deer keds readily accept humans as a host, but they have never been reported to reproduce on humans. Instead, an increasing number of people are suffering from chronic, long lasting dermatitis associated with deer ked bites (Laukkanen *et al.*, 2005). The incidental infestation is a nuisance in that it affects participation in autumnal outdoor activities, such as hunting and berry picking (Härkönen *et al.*, 2009). Moreover, given that deer keds may take blood meals from humans, there is also substantial risk for occasional transmission of *B. schoenbuchensis* to humans, but its direct health risks for human have not yet been demonstrated (Dehio *et al.*, 2004; Duodu *et al.*, 2013; Korhonen *et al.*, 2015).

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In a nutshell

- A considerable fraction of biological invasions is a consequence of human activity. For terrestrial ectoparasites, those activities include artificial regulation of the numbers of host animals. Ectoparasites may spread in an invasive manner when suitable hosts are numerously available beyond the distribution range limits, and the abiotic environment does not restrict parasite numbers. However, management of invasive ectoparasites may be challenging because of host-parasite co-evolution and their interactions with the abiotic environment.

- Harvesting and regulation of cervid species have been a major determinant of deer ked invasion across Fennoscandia. In Finland, Eastern Fennoscandia, the invasion of blood-feeding deer ked of European moose has been intense once the host population recovered from over-harvesting. During the recent decades the geographical range expansion of the ectoparasite towards higher latitudes has also been rapid. In Sweden, Western Fennoscandia, the deer ked have alternately exploited two host species — the moose and roe deer — for centuries, and the ectoparasite population has been stable and remained at markedly lower latitudes. However, a small invasive frontier has recently emerged from the stable population after which the distribution expanded westwards to Norway.
- The deer ked life histories across Fennoscandia have been modified by co-evolutionary specialization on different local hosts. The invasive eastern deer ked only exploits moose efficiently, and females produce large and cold-tolerant offspring with high survival probability outside the host. High success on moose has been explained by short co-existence and specialization in only one host species. The stable western deer ked population has undergone long co-evolution with both moose and roe deer. At present, the western deer ked exploits the roe deer more efficiently than moose, but as a cost of having two main host species, particularly the offspring size, and consequently the off-host survival is lower than in the eastern population.
- In theory, both Fennoscandian deer ked populations have high invasion potential since current host abundances are high and also available beyond current range limits. However, the host effects on the deer ked life histories and off-host performance varies between the populations due to co-evolutionary interactions. Invasion of deer keds seems to be limited by high density of low-quality hosts. Thus it is the relative, not absolute, densities of the local host species which determines the population differences in invasion potential.

9.4 Bibliography

Agnew, P., Koella, J. C., Michalakis, Y. (2000). Host lifehistory responses to parasitism. Microbes and Infection, 2, 891-896.

Agrawal, A. A. (2001). Phenotypic plasticity in the interactions and evolution of species. Science, 294, 321-326.

Bale, J. S., Hayward, S. A. L. (2010). Insect overwintering in a changing climate. Journal of Experimental Biology, 213, 980-994.

Battin, J. (2004). When good animals love bad habitats: ecological traps and the conservation of animal populations. Conservation Biology, 18, 1482-1491.

Bridle, J. R., Vines, T. H. (2006). Limits to evolution at range margins: when and why does adaptation fail? Trends in Ecology and Evolution, 22, 140-147.

Burbaitė, L., Csányi, S. (2009). Roe deer population and harvest changes in Europe. Estonian Journal of Ecology, 58, 169-180.

Crozier, L. (2004a). Field transplants reveal summer constraints on a butterfly range expansion. Oecologia, 141, 148-157.

Crozier, L. (2004b). Warmer winters drive butterfly range expansion by increasing survivorship. Ecology, 85, 231-241.

Davis, M. A. (2009). Invasion Biology. New York, NY: Oxford University Press.

Dehio, C., Sauder, U., Hiestand, R. (2004). Isolation of *Bartonella schoenbuchensis* from *Lipoptena cervi*, a blood-sucking arthropod causing deer ked dermatitis. Journal of Clinical Microbiology, 42, 5320-5323.

Duodu, S., Harris, P. D., Hjelm, E., *et al.* (2013). Bartonella infections in deer keds (*Lipoptena cervi*) and moose (*Alces alces*) in Norway. Applied Environmental Microbiology, 79, 322-327.

Fenton, A., Rands, S. A. (2004). Optimal parasite infection strategies: A state-dependent approach. International Journal for Parasitology, 34, 813-821.

FGFRI (2011). Hirvi. Kannan koko ja vasatuotto vuonna 2011. [Finnish Game and Fisheries Research Institute. Moose: population size and calf production in 2011]. Retrieved from: http://www.rktl.fi/riista/hirvielaimet/hirvi/

FGFRI (2013). Lumijälkilaskenta: metsäkauris. [Finnish Game and Fisheries Research Institute. Snow track counts: European roe deer]. Retrieved from: http://www.rktl.fi/riista/pienriista/lumijalkilaskenta/metsakauris.html

Gandon, S., Van Zandt, P. A. (1998). Local adaptation and host-parasite interactions. Trends in Ecology and Evolution, 13, 1-3.

Gascoigne, J., Berec, L., Gregory, S., *et al.* (2009). Dangerously few liaisons: a review of mate-finding Allee effects. Population Ecology, 51, 355-372.

Haarløv, N. (1964). Life cycle and distribution pattern of *Lipoptena cervi* (L.) (Dipt., Hippobosc.) on Danish deer. Oikos, 15, 93-129.

Hackman, W. (1977). Hirven täikärpänen ja sen levittäytyminen Suomeen [Moose louse-fly and its immigration in Finland]. Luonnon Tutkija, 81, 75-77.

Hackman, W., Rantanen, T., & Vuojolahti, P. (1983). Immigration of *Lipoptena cervi* (Diptera, Hippoboscidae) in Finland, with notes on its biology and medical significance. Notulae Enlomologicae, 63, 53-59.

Härkönen, L. (2012). Seasonal variation in the life histories of a viviparous ectoparasite, the deer ked. Doctoral dissertation, University of Oulu, Oulu, Finland.

Härkönen, L., Kaitala, A. (2013). Months of asynchrony in offspring production but synchronous adult emergence: the role of diapause in an ectoparasite's life cycle. Environmental Entomology, 42, 1408-1414.

Härkönen, L., Härkönen, S., Kaitala, A., *et al.* (2010). Predicting range expansion of an ectoparasite – the effect of spring and summer temperatures on deer ked (*Lipoptena cervi*) performance along a latitudinal gradient. Ecography, 33, 906-912.

Härkönen, L., Kaitala, A., Kaunisto, S., *et al.* (2012). High cold tolerance through four seasons and all free-living stages in an ectoparasite. Parasitology, 139, 926-933.

Härkönen, L., Hurme, E., Kaitala, A. (2013). Unexpected seasonal variation in offspring size and performance of a viviparous ectoparasite. Parasitology, 140, 229-236.

Härkönen, L., Kaunisto, S., Månsson, J., Hurme, E. & Kaitala, A. 2015. Host-specific variation in off-host performance of a temperate ectoparasite. Biological Journal of Linnean Society, DOI: 10.1111/bij.12628 [Early view: Article first published online: 3 AUG 2015]

Härkönen, S., Laine, M., Vornanen, M., *et al.* (2009). Deer ked (*Lipoptena cervi*) dermatitis in humans – an increasing nuisance in Finland. Alces, 45, 73-79.

Härkönen, L., Kaunisto, S., Månsson, J., Hurme, E. & Kaitala, A. 2015. Host-specific variation in off-host performance of a temperate ectoparasite. Biological Journal of Linnean Society, DOI: 10.1111/bij.12628 [Early view: Article first published online: 3 AUG 2015]

Heikkinen, S. (2000). Hirven vuosi. Suomen Riista, 46, 82-91.

Hill, J. K., Griffiths, H. M., Thomas, C. D. (2011). Climate chance and evolutionary adaptation at species' range margins. Annual Review of Entomology, 56, 143-159.

Holt, R. D., Dobson, A. P., Begon, M., *et al.* (2003). Parasite establishment in host communities. Ecology Letters, 6, 837-842.

Ivanov, V. I. (1981). Spread of the deer ked *Lipoptena cervi* L. (Diptera, Hippoboscidae) in Belarus, its biology and deleterious effects [In Russian]. Doctoral dissertation, Veterinary Academy of Moscow, Moscow, Soviet Union.

Jaakola, M., Ojanen, M., Hurme, E., Mutanen, M., Wahlberg, N., Välimäki, & Kaitala, A. 2015. Morphological variation between populations of the expanding ectoparasitic deer ked *Lipoptena cervi* (Diptera: Hippoboscidae) in Fennoscandia. Biological Journal of the Linnean Society, 116, 432-448. DOI: 10.1111/bij.12587

Kaitala, A., Kortet, R., Härkönen, S., *et al.* (2009). Deer ked, an ectoparasite of moose in Finland: A brief review of its biology and invasion. Alces, 45, 85-88.

Kaunisto, S. (2012). An invasive ectoparasite of cervids, the deer ked: dispersion, cold tolerance and predation. Doctoral dissertation, University of Eastern Finland, Joensuu, Finland.

Kaunisto, S., Kortet, R., Härkönen, L., *et al.* (2009). New bedding site examination-based method to analyse deer ked (*Lipoptena cervi*) infection in cervids. Parasitology Research, 104, 919-925.

Kaunisto, S., Härkönen, L., Niemelä, P., *et al.* (2011). Northward invasion of the parasitic deer ked *(Lipoptena cervi*), is there geographical variation in pupal size and development duration? Parasitology, 138, 354-363.

Kaunisto, S., Välimäki, P., Kortet, R., *et al.* (2012). Avian predation on a parasitic fly of cervids during winter: Can host-related cues increase the predation risk? Biological Journal of the Linnean Society, 106, 275-286.

Khatchikian, C. E., Prusinski, M., Backenson, P. B., *et al.* (2012). Geographical and environmental factors driving the increase in the Lyme disease vector *Ixodes scapularis*. Ecosphere, 3, 1-18.

Kim, H. C., Chong, S. T., Chae, J.-S., *et al.* (2010). New record of *Lipoptena cervi* and updated checklist of the louse flies (Diptera: Hippoboscidae) of the Republic of Korea. *Journal* of Medical Entomology, 47, 1227-1230.

Kindberg, J., Holmqvist, N., Bergqvist, G. (2008). Årsrapport Viltövervakningen 2006/2007. Svenska Jägareförbundet. Viltforum, 2, 1-28.

Kirkpatrick, M., Barton, N. H. (1997). Evolution of a species' range. American Naturalist, 150, 1-23.

Korhonen, E. M., Pérez Vera, C., Pulliainen, a T., *et al.* (2015). Molecular detection of Bartonella spp. in deer ked pupae, adult keds and moose blood in Finland. Epidemiology and Infection, 143, 578-585.

Kortet, R., Härkönen, L., Hokkanen, P., *et al.* (2010). Experiments on the ectoparasitic deer ked that often attacks humans; preferences for body parts, colour and temperature. Bulletin of Entomological Research, 100, 279-285.

Kramer A. M., Dennis, B., Liebhold, A. M., *et al.* (2009). The evidence for Allee effects. Population Ecology, 51, 341-354.

Kynkäänniemi, S.-M., Kortet, R., Härkönen, L., *et al.* (2010). Threat of an invasive parasitic fly, the deer ked (*Lipoptena cervi*), to the reindeer (*Rangifer tarandus tarandus*): experimental infection and treatment. Annales Zoologici Fennici, 47, 28-36.

Kynkäänniemi, S.-M., Kettu, M., Kortet, R., *et al.* (2014). Acute impacts of the deer ked (*Lipoptena cervi*) infestation on reindeer (*Rangifer tarandus tarandus*) behaviour. Parasitology Research, 113, 1489-1497.

Laukkanen, A., Ruoppi, P., Mäki-Kiljunen, S. (2005). Deer ked-induced occupational allergic rhinoconjunctivitis. Annals of Allergy, Asthma and Immunology, 94, 604-608.

Lavsund, S., Nygrén, T., Solberg, E. (2003). Status of moose populations and challenges to moose management in Fennoscandia. Alces, 39, 109-130.

Lehane, M. J. (2005). The biology of blood-sucking insects. Cambridge, UK: Cambridge University Press.

Lewis, M. A., Kareiva, P. (1993). Allee dynamics and the spread of invading organisms. Theoretical Population Biology, 43, 141-158.

Liberg, O., Bergstrom, R., Kindberg, J., *et al*. (2010). Ungulates and their management in Sweden. In M. Apollonio, R. Andersen, & R. Putman (Eds.), European ungulates and their management in the 21st century (pp.37-70). Cambridge, UK: Cambridge University Press.

Linnaeus, C. (1758). Systema naturae per regna tria naturae: secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Stockholm (Holmiae), Sweden: Laurentii Salvii.

Lockwood, J. L., Cassey, P., Blackburn, T. (2005). The role of propagule pressure in explaining species invasions. Trends in Ecology and Evolution, 20, 223-228.

Luoma, A. (2002). Moose hunting in Finland – management of a heavily harvested population. Doctoral dissertation, University of Helsinki, Helsinki, Finland.

Madslien, K. (2013). Deer ked (*Lipoptena cervi*) and moose (*Alces alces*) in Norway – interactions between an invading ectoparasite, its host and the environment. Doctoral dissertation, Norwegian School of Veterinary Science, Oslo, Norway.

Madslien, K., Ytrehus, B., Vikøren, T., *et al.* (2011). Hair-loss epizootic in moose (*Alces alces*) associated with massive deer ked (*Lipoptena cervi*) infestation. Journal of Wildlife Diseases, 47, 893-906.

Madslien, K., Ytrehus, B., Viljugrein, H., *et al.* (2012). Factors affecting deer ked (Lipoptena cervi) prevalence and infestation intensity in moose (*Alces alces*) in Norway. Parasites and Vectors, 5, 251.

Meier, C., Bonte, D., Kaitala, A., *et al.* (2014). Invasion rate of deer ked depends on spatio-temporal variation in host density. Bulletin of Entomological Research, 104, 314-322.

Muirhead-Thomson, E. C. (1982). Behaviour patterns of blood-sucking flies. New York, NY: Pergamon Press.

Nieminen, P., Paakkonen, T., Eerilä, H., *et al.* (2012). Freezing tolerance and low molecular weight cryoprotectants in an invasive parasitic fly, the deer ked (*Lipoptena cervi*). Journal of Experimental Zoology Part A: Ecological Genetics and Physiology, 317, 1-8.

Nieminen, P., Paakkonen, T., Halonen, T., *et al.* (2013). Fatty acid modifications during autumnal cold-hardening in an obligatory ectoparasite, the deer ked (*Lipoptena cervi*). Journal of Insect Physiology, 59, 631-637.

Paakkonen, T. (2012). Ecophysiology of the deer ked (*Lipoptena cervi*) and its hosts. Doctoral dissertation, University of Eastern Finland, Joensuu, Finland.

Paakkonen, T., Mustonen, A.-M. Roininen, H., *et al.* (2010). Parasitism of the deer ked, *Lipoptena cervi*, on the moose, *Alces alces*, in eastern Finland. Medical and Veterinary Entomology, 24, 411-417.

Paakkonen, T., Mustonen, A.-M., Käkelä, R., *et al.* (2011). Experimental infection of the deer ked (*Lipoptena cervi*) has no negative effects on the physiology of the captive reindeer (*Rangifer tarandus tarandus*). Veterinary parasitology, 179, 180-188.

Paakkonen, T., Mustonen, A.-M., Käkelä, R., *et al.* (2012).The effects of an abundant ectoparasite, the deer ked (*Lipoptena cervi*), on the health of moose (*Alces alces*) in Finland. Parasitology Research, 111, 1223-1232.

Poulin, R. (1998). Host and environmental correlates of body size in ticks (Acari: Argasidae and Ixodidae). Canadian Journal of Zoology, 76, 925-930.

Poulin, R. (2007). Evolutionary ecology of parasites. Princeton NJ: Princeton University Press.

Pyšek, P., Richardson, D. M., Pergl, J., *et al.* (2008). Geographical and taxonomical biases in invasion ecology. Trends in Ecology and Evolution, 23, 237-244.

Rantanen, T., Reunala, T., Vuojolahti, P., *et al.* (1982). Persistent pruritic papules from deer ked bites. Acta Dermato-Venereologica, 62, 307-311.

Renaud, F., De Meeus, T., Read, A. F. (2005). Parasitism in man-made ecosystems. In F. Thomas, F. Renaud, & J.-F. Guegan (Eds), Parasitism and ecosystems (pp.155-170). Oxford UK: Oxford University Press.

Robertson, B. A., Hutto, R. L. (2006). A framework for under- standing ecological traps and an evaluation of existing evidence. Ecology, 87, 1075-1085.

Robertson, B. A., Rehage, J., Sih, A. (2013). Ecological novelty and the emergence of evolutionary traps. Trends in Ecology and Evolution, 28, 552-560.

Samuel, W. M., Mooring, M. S., Aalangdong, O. I. (2000). Adaptations of winter ticks to invade moose and moose to evade ticks. Alces, 36, 183-195.

Samuel, B., Madslien, K., Gonynor-McGuire, J. (2012). Review of deer ked (*Lipoptena cervi*) on moose in Scandinavia with implications for North America. Alces, 48, 27-33.

Sexton, J. P., McIntyre, P. J., Angert, A. L., *et al.* (2009). Evolution and ecology of species range limits. Annual Review of Ecology and Systematics, 40, 415-436.

Shenbrot, G., Krasnov, B., Lu, L. (2007). Geographical range size and host specificity in ectoparasites: a case study with *Amphipsylla* fleas and rodent hosts. Journal of Biogeography, 34, 1679-1690.

Sleeman, D. P. (1983). Parasites of deer in Ireland. Journal of Life Sciences Royal Dublin Society, 42, 203-210.

Stearns, S. C. (1992). The evolution of life histories. Oxford, UK: Oxford University Press.

Stearns, S. C., Hoekstra, R. F. (2005). Evolution: An Introduction. New York, NY: Oxford University Press.

Thomas, F., Guégan, J.-F., Renaud, F. (2009). Ecology and evolution of parasitism. Oxford UK: Oxford University Press.

Thulin, C-F. (2006). Microsatellite investigation of roe deer (*Capreolus capreolus*) in Scandinavia reveals genetic differentiation of a Baltic Sea Island population. European Journal of Wildlife Research, 52, 228-235.

Tiilikainen, R., Solberg, E. J., Nygrén, T., *et al.* (2012). Spatio-temporal relationship between calf body mass and population productivity in Fennoscandian moose *Alces alces*. Wildlife Biology, 18, 304-317.

Tobin, P. C., Berec, L., Liebhold, A. M. (2011). Exploiting Allee effects for managing biological invasions. Ecology Letters, 14, 615-624.

Tschirren, B., Bischoff, L. L., Saladin, V., *et al.* (2007). Host condition and host immunity affect parasite fitness in a bird–ectoparasite system. Functional Ecology, 21, 372-378.

Välimäki, P., Kaitala, A., Madslien, K., *et al.* (2011). Geographical variation in host use of a blood-feeding ectoparasitic fly: implications for population invasiveness. Oecologia, 166, 985-995.

Välimäki, P., Madslien, K., Malmsten, J., *et al.* (2010). Fennoscandian distribution of an important parasite of cervids, the deer ked (*Lipoptena cervi*), revisited. Parasitology Research, 107, 117-125.

Wharton, D. A. (1999). Parasites and low temperatures. Parasitology, 119, S7–S17.

Yeh, P. J., Price, T. D. (2004). Adaptive phenotypic plasticity and the successful colonization of a novel environment. American Naturalist, 164, 531-542.