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Wing loading and habitat selection in forest beetles: Are red-listed species poorer dispersers or more habitat-specific than common congenerics?

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ABSTRACT

Traits such as poor dispersal ability and high habitat specificity are thought to predispose some species to a greater risk of extinction than others. Habitat preferences and morphological features associated with dispersal ability were compared between red-listed species and common congenerics co-occurring in boreal forests in northern Sweden. Measurements of body size, wing loading and wing aspect ratio were used to compare dispersal abilities, while catches from experimental treatments of dead wood were used to compare habitat preferences. We also compared how restricted red-listed species were to particular sites or habitats relative to common species. The red-listed *Epuraea longipennis* was longer and wider, while *Epuraea. deubeli* weighed less than common *Epuraea* species. In contrast to expectations, these red-listed species had a larger wing area (relative to their body mass) and thus a lower wing-loading than congeneric species, suggesting superior dispersal abilities. The red-listed *Tachinus elegans* possessed intermediate morphological characteristics, compared with common congenerics. However, the relationships between the risk of extinction in fragmented habitats and size and dispersal ability are likely to be scale-dependent, so intermediate or superior dispersal abilities may increase extinction risk at some scales. Red-listed species were not found in fewer sites or habitat types than congenerics so were not more likely to be habitat specialists. However, some red-listed species preferred deeply shaded and *Fomitopsis pinicola*-inoculated logs, relative to congenerics, suggesting that specificity to these particular microhabitats may be connected with extinction risk.

1. Introduction

Traits such as a low or fluctuating population size, rarity, poor dispersal ability and habitat specialisation may predispose some species to extinction (Henle et al., 2004) and species with combinations of extinction-promoting traits may be particularly vulnerable (Davies et al., 2004). Red-lists include species that are considered to be threatened because their populations are small or shrinking (Gärdenfors, 2001) and the primary threat to populations of many red-listed species in Scandinavia is the habitat loss and reduction in habitat quality caused by forestry (Stokland, 1991; Berg et al., 1994; Thor, 1998).

Intensive forestry has changed the composition and connectivity of forest habitats in Sweden considerably and less than 1% of the productive forest land is currently protected (Linder and Östlund, 1992; Löfgren, 1997; Anon., 2001). While the landscape was historically dominated by older forests, it

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also contained a patchwork of successional stages recovering after fire and other natural disturbances (Östlund et al., 1997). In the modern landscape, even-aged stands in earlier successional stages cover the majority of the landscape (Linder and Östlund, 1998; Axelsson and Östlund, 2001), creating a matrix of habitat that may not be habitable for those species that are dependent on older stand types. In order to survive in the modern landscape in the long-term, species dependent on older stand types must disperse through the matrix and successfully colonise new patches (Harrison and Bruna, 1999), or survive by spreading between connected patches before they are harvested.

Successful colonisers are characterised by superior dispersal abilities and/or high reproductive rates, although there may be some trade-offs between these traits (Rankin et al., 1994; Langellotto et al., 2000). Species relying on more persistent habitats, such as hollow trees (Nilsson and Baranowski, 1997; Ranius and Hedin, 2001) or stable bogs (Wikars, 1997) are expected to possess inferior dispersal abilities to those relying on less persistent habitats, such as recently fallen coarse woody debris (CWD) (Nilssen, 1984; Solbreck, 1980) and burned areas (Wikars, 1997), because short patch persistence times select for better dispersal abilities (Southwood, 1977; Nilsson and Baranowski, 1997). However, long-lived habitats are those most likely to disappear from the managed forests of northern Sweden, where the rotation cycles are approximately 120 years (Ranius and Kindvall, 2004). Species that are poor dispersers and dependent on long-lived habitats are thus most likely to become extinct in the managed landscape.

For insects, particularly those that are rare, dispersal can be difficult to measure directly or in laboratory situations (although see Jonsson, 2003). Fortunately, flight morphology and flight performance are associated, so morphology provides a useful indicator of dispersal ability (Berwaerts et al., 2002). In particular, a low wing loading (body mass divided by wing area), is thought to represent a superior flying ability because flight becomes more energetically efficient with decreasing wing loading (Angelo and Slansky, 1984). Long, narrow wings, which have a high aspect ratio (wing length divided by wing width), adapt a species to fast flapping flight (Norberg, 1990), while broad wings adapt a species to gliding flight (Wootton, 1992) and mayflies with short wings have been shown to occupy fewer sites than those with large wings (Malmqvist, 2000). Large body size improves dispersal ability because it reduces the mass-specific cost of flight (Roff, 1991; Berwaerts et al., 2002). Additionally, large insects maintain a higher thoracic temperature than small insects and may thus have greater flight musculature efficiency (Chapman, 1998).

Of the approximately 1000 saproxylic beetles in Sweden, 474 are red-listed (Gärdenfors, 2000). Apart from information on distributions, obtained through surveys, very little information is available on the ecology of red-listed saproxylic beetles in Sweden. Both landscape-scale habitat loss and the loss of coarse woody debris habitats within remaining forests are considered to be major threats to these species (Økland et al., 1996; Jonsell et al., 1998; Rukke, 2000). Red-listed species have either been observed to decline in abundance or have suffered destruction of their habitats and are thus considered to be at risk of becoming extinct from a region (Gärdenfors, 1996). Red-listed species are thus useful for testing a priori hypotheses concerning those characteristics that are typical of rare and threatened species. In this study, we use morphological characteristics and experimental substrate manipulations to determine which traits, if any, are characteristic of red-listed species. In particular, we hypothesize that red-listed species in boreal forests are poorer dispersers and have more specialised habitat preferences than common congenerics. A comparison of a red-listed species with several of its congenerics should allow us to better understand the subtle differences that result in one species being threatened by forestry, while a set of related species remain unthreatened.

Extensive collection of saproxylic species from experimental logs over a period of 3 years has provided us with an unusually large sample size for a number of red-listed species in a controlled experiment. We thus have a unique opportunity to specifically test hypotheses concerning dispersal morphology and habitat use. We address the following questions:

1. Do red-listed beetles have morphological characteristics (body size, wing loading and aspect ratio) that make them less efficient dispersers than their more common relatives?
2. Do red-listed species occupy fewer sites and habitat types than common congenerics?
3. Do red-listed species differ from common congenerics in terms of their substrate and stand type preferences?

We tested questions one and three for three red-listed species and common congenerics and question two for six red-listed species.

2. Methods

2.1. Study area

Beetles were collected from sites within the central-boreal vegetation zone of Sweden (Ahti et al., 1968), between 63.620° N and 64.285° N and 16.889° E and 20.132° E and ranging from 100 to 550 m above sea level. In total, 27 sites were sampled: nine in unmanaged Norway spruce (*Picea abies*) dominated forest stands in nature reserves and national parks, nine in nearby mature managed forest and nine in nearby clear-cut stands. The mature managed forests had probably been selectively logged for trees of large diameter, but never clear-cut. All "clear-cut" sites had been cut between 1999 and early 2001 (see Gibb et al., 2005 for further details). Old-growth forests (mean 72.5 m^3 ha^{-1}) contained considerably more CWD than both mature managed forests (mean 24.3 m^3 ha^{-1}) and clear-cuts (mean 13.6 m^3 ha^{-1}), particularly with respect to older and larger diameter logs and snags (Gibb et al., 2005).

2.2. Trapping methods

Insects were collected from logs of Norway spruce and birch, *Betula pubescens* and *B. pendula*, which had been placed out between September 2001 and March 2002. Logs were 4 m in