



MINOR REVIEW

Biology and conservation of the European stag beetle: recent advances and lessons learned

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Abstract. 1. Reliable information for the conservation of many insects is lacking due to a poor knowledge of their ecology. Here, we review the biological knowledge about the European stag beetle (*Lucanus cervus*), in which recent advances are improving the basis for successful conservation.

2. A review of the biological and ecological literature about this species identified an exponential increase in both total and peer-reviewed articles after Natura 2000 regulations.

3. Recent progress in the last two decades has been made in solving taxonomic problems, as well as in habitat description through radiotelemetry and habitat models. Dependence on large old-growth forest has given place to a more complex picture of habitat use along the distribution range of this species. Monitoring protocols have been developed that will allow to assess conservation status and actual decline.

4. Stag beetle conservation would benefit from a better understanding of larval demography, quantification of microhabitat requirements, landscape genetics and quantification of historical and current threats.

5. Lessons learned include the need to solve taxonomic problems and to target methodological bottlenecks. The stag beetle is one of the few European saproxylic organisms that can engage the broad public through outreach activities and therefore its role as an umbrella species should be promoted.

Key words. Critical assessment, *Lucanus cervus*, methodological bottlenecks, monitoring, natural history.

Introduction

Conservation of a threatened species should be based on precise knowledge on distribution, reasons and magnitude of decline, identification of threats – e.g., risks derived from demographic and genetic stochasticity – and monitoring programs to assess the conservation status (Caughley, 1994; Frankham *et al.*, 2004; Lindenmayer & Burgman, 2005). However, such evidence is lacking for many insects of conservation concern (Nieto & Alexander, 2010) due to poor knowledge of their ecology (Cardoso *et al.*, 2011). Conservation of such species is often based on guessing, natural history, expert opinion or knowledge imported from species with hopefully similar ecology and threats. Here, we review the biological knowledge about the European stag beetle (*Lucanus cervus* L., 1758), in which recent advances have improved the basis for successful conservation. We highlight

historical background information vs. recent progress and lessons learned in the last two decades.

Insect conservation relies on a well-developed theoretical and methodological basis (Samways, 1994, 2005, 2019; New, 2009; Samways *et al.*, 2010). Tools implemented include ecological networks (Kietzka *et al.*, 2015), population viability analysis (Melosik *et al.*, 2018), population genetic assessment (Mongue *et al.*, 2016; Melosik *et al.*, 2018), captive breeding (Pearce-Kelly *et al.*, 1998), reintroduction and reinforcement of populations (Oates & Warren, 1990; Thomas *et al.*, 2009) and habitat recreation (Woodcock *et al.*, 2012). However, success stories are scarce (Thomas *et al.*, 2009). Conservation action often faces practical problems derived from a lack of ecological knowledge about the species (Cardoso *et al.*, 2011). Conservation of many threatened insects is hindered by these uncertainties (Bedick *et al.*, 1999; Shaw & Hochberg, 2001; Shaw, 2006; Huang, 2014; Ulyshen *et al.*, 2017; Silva *et al.*, 2019).

The European Stag beetle is a conspicuous, popular species, known since the ancient Greek times (Sprecher-Uebersax, 2008; Parker, 2019). Its large size and striking appearance has

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prompted a lot of attention among entomologists. As a result, faunistic and natural history reports have been published beyond count and it has become an icon for insect conservation in Europe since its inclusion in the Bern Convention. This could give the impression that its biology is well understood. However, progress has been slow. Until very recently, management had to rely on classical literature, that had four main drawbacks (Table 1): (i) “common wisdom” that could not be traced back to any published source, (ii) very general statements with no quantification, (iii) anecdotal, rather than systematic, observations or (iv) conflicting information among sources. In addition, the elusiveness of this beetle, that flies at dusk and whose larvae develop underground for several years (Bardiani *et al.*, 2017), has been a persistent obstacle for proper biological studies. This situation is being reverted thanks to recent studies that address these drawbacks and offer guidance for conservation actions. In the last decades, several peer-reviewed articles (Harvey *et al.*, 2011a; Bardiani *et al.*, 2017) and books have summarised its biology (Klausnitzer, 1995; Mader, 2009) and at least five PhD theses have been devoted to different aspects of its ecology and conservation (Sprecher-Uebersax, 2001; Rink, 2006; Harvey, 2007; Romiti, 2017; Tini, 2017). With over 40 papers included in the Science Citation Index (SCI) solely devoted to this species, the European stag beetle is among the best studied beetles of conservation interest.

Therefore, the aim of this article is to review what is known about the biology and conservation of the European stag beetle, stressing recent advances and lessons learned in the past two decades. Based on a literature survey on the ecology and biology of the stag beetle, we: (i) identify fundamental evidence for the conservation of this beetle and clearly separate background information and natural history from recent progress; (ii) highlight major gaps in current understanding of the ecology of this iconic species and suggest ways to fill these gaps; and

(iii) distil lessons learned that may inspire researchers to tackle similar information gaps to the ones identified for the European stag beetle.

Literature survey

We conducted a literature search of papers dealing with the biology, ecology and conservation of the stag beetle included in Web of Knowledge as to 1 April 2020. We used “Lucanus” or “Stag beetle” as search terms. From the 60 papers retrieved, we retained the 41 papers (SCI papers) in which the European stag beetle was the main topic. In addition, we used the literature gathered for more than 10 years by both authors and searched the entomological literature outside SCI, using repositories of scholarly literature (Google Scholar, Research Gate, JSTOR, Biodiversity Heritage Library) and contact with colleagues. In total, we compiled 269 scientific references. Although far from exhaustive, this overview encompasses much of the relevant literature. We sorted this literature into six main topics: (i) taxonomy, including faunistics, biogeography, and phylogeny; (ii) genetics, including population genetics, genetic markers and genomics; (iii) physiology, biochemistry, and biomechanics; (iv) ecology, excluding conservation; (v) conservation, including threats and monitoring; and (vi) others, including miscellaneous information. Allocation to a topic was based on the main result of each paper. Papers dealing with many topics were allocated to the category “others”.

Studies retrieved originated from 21 countries that span most of the distribution of the species, but mainly western Europe (Supporting Information Table S1). Almost two thirds (61%) of the literature has been published since 2000, after this species was included in the Natura 2000 network of the EU (Fig. 1). Since 2000, the number of topics addressed as well as the number of SCI papers has grown exponentially (Fig. 1). Thus, we used 2000 as a pragmatic time point to separate background information from recent advances. In the following, we summarise this literature, briefly summarising the background information and highlighting progress in the last two decades.

Table 1. Four causes of poor ecological knowledge of the European stag beetle that needed to be overcome to achieve sound conservation, illustrated with a few, non-exhaustive, examples.

1. Common wisdom not traceable back to published sources	The main threat is habitat loss (claimed in, e.g., JNCC, 1995, with no support). There are 4-year cycles in abundance (claimed in the study by Drake, 1994, with no support).
2. General statements with no quantification	Number of eggs laid (Tochtermann, 1992). Larval habitat (Palm, 1959).
3. Anecdotal, rather than systematic observations	Fights among males (Braatz, 1914; Baudrimont, 1931; Tippmann, 1954). Massive swarms of males (Tippmann, 1954; Wüest, 1993).
4. Conflicting information among sources	Habitat: forest (Palm, 1959; Pawłowski, 1961; Kuźmiński <i>et al.</i> , 2020) vs. open (Hachtel <i>et al.</i> , 2006; Thomaes <i>et al.</i> , 2008b; Fremlin, 2009). Larval development: 2–7 years (Pawłowski, 1961; Radnai, 1995; Bowdrey, 1997; Rink & Sinsch, 2008a; Hendriks & Méndez, 2018).

Taxonomical problems

Lucanus cervus has a wide distribution within Europe, ranging from Portugal to the Ural mountains in Russia and from central Spain, central Italy, Greece and Caucasus to southern Sweden (Harvey *et al.*, 2011a). In Southern Europe it overlaps with four other *Lucanus* species: *L. barbarossa* (Fabricius, 1801), *L. ibericus* Motschulsky 1870, *L. pontbrianti* (Mulsant, 1839) and *L. tetraodon* Thunberg, 1806 (Bartolozzi *et al.*, 2016a).

Considerable morphological variability in mandibles and antennal club (Colas, 1962; Lacroix, 1962, 1969; Mal, 1972; Clark, 1977; Bessonat, 1983) within its distribution range has led to the description of several forms and subspecies, such as *pentaphyllus*, *capreolus* and *pontbrianti* in Europe (Baraud, 1993) and subspecies *L. c. akbesianus*, *L. c. judaicus*, *L. c. laticornis* and *L. c. turcicus* in Turkey and minor Asia (Didier & Séguéy 1953; Baraud, 1993; Bartolozzi *et al.*, 2016a).

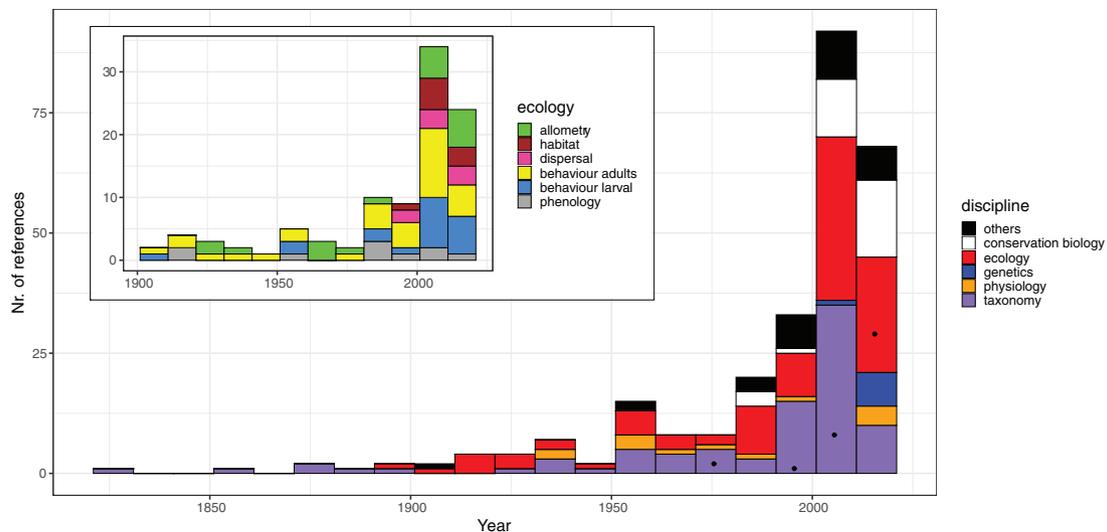


Fig. 1. Number of references studied ($n = 269$) set out along publication date separated by discipline in bins of 10 years. Number of papers in Science Citation Index ($n = 41$) are added as black dots. Subdisciplines of ecology are represented on the inset graph. [Color figure can be viewed at wileyonlinelibrary.com]

Their taxonomic status is controversial (Bartolozzi *et al.*, 2016a, b). In addition, frequent intraspecific variation in populations where stag beetles coexist with related species (*L. pontbrianti*: Mal, 1972; Bessonat, 1983; *L. tetraodon*: Solano *et al.*, 2016) suggests that hybridisation could explain part of this morphological variation.

Recently, phylogenetic tools are starting to clarify taxonomical problems and claims of hybridisation (Cox *et al.*, 2013; Solano *et al.*, 2016). First, *L. pontbrianti* (Mulsant, 1839) has been given specific status (Boucher, 2014), while the form *turcicus* is related to a different glacial refugium population (Cox *et al.*, 2019). Secondly, no cases of hybridisation have been confirmed. Intermediate forms of *L. cervus* and *L. tetraodon* from central Italy could be genetically allocated to one species and the origin of these intermediate traits remains uncertain (Solano *et al.*, 2016).

Molecular studies have contributed to clean up subspecific claims to some extent, but further work in the Middle East is needed (Cox *et al.*, 2013, 2019). The availability of the complete mitochondrial genome (Chen *et al.*, 2019) can help future phylogenetic studies. Solving taxonomic problems is an important lesson learned, because widespread endangered species can harbour substantial genetic and morphological variation that needs to be understood for conservation purposes (Coates *et al.*, 2018). In some cases, this variation can turn out to hide previously un- or ill-recognised species, as in another iconic saproxylic beetle from Natura 2000, *Osmoderma eremita* s.l. (Audisio *et al.*, 2009).

Habitat

Larvae feed on decaying wood, mainly in the subterranean part of stumps (de Ligondes, 1959; Pawłowski, 1961; Owen, 1992; Sprecher-Uebersax, 2001; Rink & Sinsch, 2008a;

Fremelin, 2013), but also under fallen logs (Palm, 1959; Sprecher-Uebersax, 2001; Whitehead, 2007; Fremelin, 2013). They can also occur in standing dead trunks but not in branches (Palm, 1959). Traditionally, the stag beetle has been linked to old growth oak (*Q. robur*) forests (Palm, 1959; Pawłowski, 1961). The presence of larvae only in moderately decayed wood (Pawłowski, 1961), in a middle to late position in the process of wood decomposition (Ingles, 1933; Mamaev, 1960, 1961; Pawłowski, 1961; Dajoz, 1966) and in wood above certain diameter (Palm, 1959) also seemed to support a dependence on old growth forest. However, larvae are also found in agricultural or suburban areas, where they rely on composted sawdust, wood chips (Tochtermann, 1987; Pfaff, 1989; Owen, 1992), fences, wooden poles (Klausnitzer, 1995; Sprecher-Uebersax 1995; Franciscolo, 1997) or railway sleepers (le Sénéchal, 1901; Harz, 1957).

Abiotic conditions suitable for this species are known broadly speaking. In Central and Northern Europe, a thermophilic preference (Whitehead, 1993; Hawes, 2000, 2005) is suggested based on (i) main presence in the edge, not inside the forest (Sprecher-Uebersax, 2001), or in south facing slopes and sandy soils that heat up faster (Thomaes *et al.*, 2008b); (ii) intolerance of larvae to frost (Rink & Sinsch, 2008a); (iii) a distribution limited by the 4°C isotherm in winter (Percy *et al.*, 2000). Temperature or humidity could also explain the presence of larvae in loam and lutolites, but not in clayey soils (Whitehead, 1993; Hawes, 2000, 2005).

Recent studies have added much detail to habitat, substrate and environmental requirements of the stag beetle. The stag beetle inhabits not only old growth forest but a broad range of lowland (Campanaro *et al.*, 2017) deciduous forests and only rarely mixed forests with conifers or coniferous forests (Jurc *et al.*, 2008; Manu *et al.*, 2017; Méndez *et al.*, 2017; Kuźmiński *et al.*, 2020). It also occurs in forest edges (Thomaes, 2009), and in mildly to heavily anthropic settings, from agricultural or

suburban (Hendriks & van der Ploeg, 2006; Breitenmoser, 2013) to urban areas (Hachtel *et al.*, 2006; Thomaes *et al.*, 2008b; Fremlin, 2009, 2013; Thomaes, 2009). Due to its widespread presence in humanised habitats, it is not considered as an indicator species of the ecological continuity of mature forests (Alexander, 2004).

Tree species and wood substrates used by larvae have been recently quantified (Hawes, 2009a; Fremlin, 2013; Tini *et al.*, 2017a). *Q. robur* was the most common host tree (Hawes, 2009a; Tini *et al.*, 2017a) but artificial substrates – fence posts, compost heaps and railway sleepers – were important in suburban areas (Hawes, 2009a; Fremlin, 2013). Stumps were the main substrate in a suburban area (Fremlin, 2013) while in a forest, lying wood was more often used (Tini *et al.*, 2017a). The range of trunk diameters (Sprecher-Uebersax, 2001; Rink & Sinsch, 2008a; Tini *et al.*, 2017a) and stages of decomposition used (Tini *et al.*, 2017a) have also been documented (Supporting Information Table S2).

Larvae or emergence holes have been found on many broad-leaved tree species, as well as in conifers and exotic trees (Percy *et al.*, 2000; Supporting Information Table S3). Generalism in wood source, also present in other Lucanidae (Araya, 1993; Fearn, 1996), can be due to their late successional appearance in the decomposition process but also to a stronger dependence on wood-decaying fungi compared to tree species (Wood *et al.*, 1996). Fungi associated with larvae include crab-of-the-woods (*Laetiporus sulphureus*) (Scherf, 1985), oak maze-gill (*Daedalea quercina*), red belt conk (*Fomitopsis pinicola*), robustus conk (*Phellinus robustus*), beefsteak fungus (*Fistulina hepatica*) (Tochtermann, 1992) and artist's bracket (*Ganoderma lipsiense*) (Rink, 2006; Rink & Sinch, 2008a).

Habitat modelling at regional (Della Rocca *et al.*, 2017), national (Thomaes *et al.*, 2008a; Chefaoui *et al.*, 2011; Katušić *et al.*, 2017) and European scales (Della Rocca & Milanese, 2020) offers a way forward in establishing abiotic conditions and general habitat description. These models have confirmed minimum thermal requirements (Thomaes *et al.*, 2008a) and rough estimates of forest area required (Thomaes *et al.*, 2008a; Della Rocca *et al.*, 2017). Additional habitat models would be welcome, ideally moving from human classifications (e.g. urban, forest, or other phytosociological terms) to features relevant to stag beetles (e.g. canopy openness, soil texture, amount of dead wood). Radio-tracking is also a promising tool to document local habitat use (Rink & Sinsch, 2006).

An important lesson learned is that early emphasis on the dependence of stag beetle from large old-growth *Quercus* forests has to be replaced by a more complex picture of habitat use. In many parts of its range, this species is rather generalistic and occurs in a gradient from forest to urban areas. These habitat differences across European ecoregions need to be quantified and understood, taking advantage of the growing international network of researchers on the stag beetle (Harvey & Gange, 2011). In addition, future studies should target quantification, dependence on and preference for various habitat features including tree species, density of dead wood, fungi identity, decay stage, hardness and wetness of the wood or sun exposure. Telemetry is providing novel information on habitat use and behaviour at a local scale (Sprecher-Uebersax & Durrer, 2001;

Rink & Sinch 2007; Schut *et al.*, 2014; Tini *et al.*, 2017a, b, 2018; Thomaes *et al.* 2018). These observational studies need to be complemented with experimental (cafeteria) studies.

Larval ecology and demography

Larval development is mainly known from captive rearing (de Ligondes, 1959; Saint-Etienne, 1970; Radnai, 1995). Eggs hatch within 1 month from laying (Pawłowski, 1961; Saint-Etienne, 1970; Radnai, 1995) and go through three larval instars (Radnai, 1995). The whole larval period can last from 1 to 7 years (Pawłowski, 1961; Saint-Etienne, 1970; Tochtermann, 1992; Radnai, 1995; Bowdrey, 1997). Pupation occurs during summer, in a cocoon located in the soil, close to the stump (de Ligondes, 1959; Pawłowski, 1961). Metamorphosis occurs in the autumn and adults hibernate within the cocoon until their emergence next year (Horion, 1958; de Ligondes, 1959; Pawłowski, 1961).

Aside of a general description of the larval development, literature previous to 2000 offered only fragmentary information about other aspects of larval life, such as unusually high larval densities (Chalmers-Hunt, 1987), coexistence of different ages (Paulian, 1959), mammal predators (Tochtermann, 1992) and parasitic invertebrates, including one nematode and two *Megascolia* wasps (Pawłowski, 1961; see also Vereecken & Carrière, 2003).

Recent research on larval life has confirmed the information provided by former studies (Sprecher-Uebersax, 2001; Harvey & Gange, 2003a; Rink, 2006; Whitehead 2007; Rink & Sinsch, 2008a; Hendriks, 2011; Fremlin & Hendriks, 2014; Hendriks & Méndez 2018) and added details about the duration of larval stages (Supporting Information Table S2), addressed the role of stridulation (Sprecher-Uebersax & Durrer, 1998b; Harvey *et al.*, 2011b) and reported sexual dimorphism in larvae (Fremlin & Hendriks, 2014; Hendriks & Méndez, 2018) and cocoons (Sprecher-Uebersax, 2001). An exciting advance involved the identification of symbiotic and species specific yeasts that allow cellulose digestion (Tanahashi *et al.*, 2010; Tanahashi & Fremlin, 2013) and their vertical transmission from female mycangium to larvae (Hawes, 2013; Fremlin & Tanahashi, 2015; Hawes & Tanahashi, 2016).

Two important aspects of larval ecology deserve further study: the factors that influence growth rates and the sources of larval mortality. Variation in the duration of each instar and in the whole larval development is likely due to differences in rearing conditions, such as temperature (Hendriks & Méndez, 2018). Substrate quality can also influence larval growth in Lucanidae (Tanahashi *et al.*, 2018), but the evidence for the stag beetle is inconclusive (Rink & Sinsch, 2008a; Hendriks & Méndez, 2018).

Information on larval mortality rates is required for demographic models and viability assessment of populations (Huang, 2014). Mortality rates of each instar have not been reported, but they seem to decrease from the first to the third instar in another *Lucanus* species (Huang, 2014). Extrinsic sources of mortality, such as predation due to high densities of wild boar are considered as problematic for the conservation of this beetle (Ebert & Müller-Pfannenstiel, 2008). In addition, a better understanding is needed about intraspecific competition. Larvae seem to be stratified by size, with small larvae close to

the stump and large larvae in the periphery of the root area (Sprecher-Uebersax, 2001). This suggests that competition or even cannibalism could be an issue. However, competition and cannibalism observed in other Lucanidae have been interpreted as an artefact of the small housing (Lai & Shin-ping, 2008; Tanahashi & Togashi, 2009) and have not been documented in the stag beetle (but see Saint-Etienne, 1970). Larvae can coexist with other saproxylic Lucanidae and Scarabaeoideae (Sprecher-Uebersax, 2001; Whitehead, 2007; Fremlin, 2013). There is evidence for segregation of spatial niche among Lucanidae (Pawłowski, 1961; Ulyshen *et al.*, 2017; Huang, 2018) but whether it also applies to coexistence with other saproxylics is unclear (Simandl, 1993; Whitehead, 2007).

Larval demography and ecology are relevant for conservation because stag beetles spend most of their lives as larvae, but intrinsic difficulties of their study make it one in which less recent advances have been performed. A future challenge is to develop a strong research line in larval demography and ecology, following the lead of pioneer studies by Huang (2014).

Adult ecology and demography

Adult phenology has been documented extensively both in classic and recent times. Adults are present from late May to late August, depending on the country (Palm, 1959; Pawłowski, 1961; Lacroix, 1969; Álvarez Laó & Álvarez Laó, 1995; Sprecher-Uebersax & Durrer, 1998a; Percy *et al.*, 2000; Hachtel *et al.*, 2006; Vrezec, 2008; Rink & Sinsch, 2008b, 2011; Fremlin 2009; Thomaes *et al.*, 2010; Harvey *et al.*, 2011b; Vrezec *et al.*, 2011; Breitenmoser, 2013; Scaccini & Anaclerio, 2016; Campanaro *et al.*, 2017; Méndez *et al.*, 2017; Soutinho *et al.*, 2017; GTLI, 2018). A wide scatter exists in the earliest and latest dates of observation (references above). Occasional observations of adults in winter have been interpreted as overwintering (Muzik, 1912; Roubal, 1912; Marie, 1959), but they could result from untimely emergences (Roubal, 1912; Marie, 1959). Shorter and earlier phenologies have been found at higher latitudes in regional studies (Moretti & Sprecher-Uebersax, 2004; Romiti *et al.*, 2017; see, however, Campanaro *et al.*, 2017) but not at an European scale (Campanaro *et al.*, 2016; Thomaes *et al.*, 2017). In the same way, the peak of adult activity varies widely among years (Verdcourt, 1988; Morris, 1991; Spooner, 1992; Álvarez Laó & Álvarez Laó, 1995; Sprecher-Uebersax & Durrer, 1998a; Moretti & Sprecher-Uebersax, 2004; Breitenmoser, 2013; Scaccini & Anaclerio, 2016; Méndez *et al.*, 2017; Thomaes *et al.*, 2017).

Males appear earlier than females (Clark, 1964; Tochtermann, 1992; Álvarez Laó & Álvarez Laó, 1995; Percy *et al.*, 2000; Rink & Sinsch, 2008b, 2011; Fremlin, 2009; Harvey *et al.*, 2011b; Breitenmoser, 2013; Scaccini & Anaclerio, 2016; GTLI, 2018) and population sex ratio shifts from male to female biased along the summer (Tochtermann, 1992; Fremlin, 2009). The proximate mechanism seems to be a shallower burying depth of male, compared to female, cocoons (Tochtermann, 1992).

Adult activity reaches a peak at dusk (Lacroix, 1969; Paulian & Baraud, 1982; Bessonat, 1983). During the day, adults remain hidden or buried (Harz, 1957), although some diurnal activity has been found (Mal, 1972; Álvarez Laó & Álvarez Laó, 1995; Hallengren, 1997; Tini *et al.*, 2017b), apparently more frequent in Mediterranean areas (Colas, 1962; Lacroix, 1962). Daily activity of adults does not seem to depend on moon phase or most weather conditions, other than temperature (Supporting Information Table S2).

Recent progress has been done in three topics of major concern for the conservation of the stag beetle: climatic correlates of phenology, dispersal ability and reliable sampling methods of adult populations. Climate has been found to potentially influence phenology at several temporal scales. At a scale of decades, a shift in phenology to earlier dates after 1980 could be ongoing (Vrezec, 2008; GTLI, 2018), but its link to global warming is uncertain. In addition, interannual variation in the peak of adult activity (references above) is positively related to winter rainfall (Méndez *et al.*, 2017), but many time series are too short to detect climatic influences on phenology (Rink & Sinsch, 2011). At a seasonal scale, the length of the period of adult occurrence (Supporting Information Table S2) is negatively related to summer temperature (Rink & Sinsch, 2011).

Recent studies of dispersal ability do not confirm old anecdotal reports of mass migrations in stag beetles (Companyo, 1863, cited in the study by Lacroix, 1962; Paulian & Baraud, 1982). Instead, capture-mark-recapture (CMR) studies recovered marked individuals near the capture place (Fremlin, 2008, 2009; Hawes, 2008; Fremlin & Hendriks, 2011). Both CMR and telemetry studies show dispersal distances lower than 2 km (Sprecher-Uebersax & Durrer, 2001; Rink & Sinsch, 2007, 2011; Hawes, 2009b; Schut *et al.*, 2014; Thomaes *et al.*, 2018; Tini *et al.*, 2018). Females sometimes do not fly (Sprecher-Uebersax & Durrer, 2001; Hawes, 2009b). Dispersal distances could be higher in unfavourable habitat (Tini *et al.*, 2018; Thomaes *et al.*, 2018). Dispersal activity decreases along the season (Tini *et al.*, 2018) maybe due to atrophy of muscle fibres with aging (Paulian, 1988).

Current understanding of dispersal ability faces two limitations. First, most telemetry studies have used less than 15 individuals (Hallengren, 1997; Sprecher-Uebersax & Durrer, 2001; Tini *et al.*, 2017a; Thomaes *et al.*, 2018). Second, rare events of long distance dispersal are difficult to detect by means of CMR studies or telemetry. However, these rare events can be ecologically relevant and could also contribute significantly to gene flow. Landscape genetics seems a more sensible way forward to assess dispersal ability (Cox *et al.*, 2020), taking advantage of recent development of microsatellites (McKeown *et al.*, 2018). CMR and telemetry should not be abandoned, only repurposed (see below for CMR and “Habitat” for telemetry).

A major recent finding has been a reliable monitoring method of adult populations, after a decade of search (Hawes, 2005, 2008; Vrezec & Kapla, 2007; Campanaro *et al.*, 2011, 2016; Harvey *et al.*, 2011b; Vrezec *et al.*, 2011; Chiari *et al.*, 2014; Bardiani *et al.*, 2017). CMR have been rarely used to assess population size (Chiari *et al.*, 2014) and can be now superseded (Della Rocca *et al.*, 2020). Transects at dusk (Campanaro *et al.*, 2016) provide now a standardised index of population size.

Population sizes obtained using different procedures have reported very variable results (Supporting Information Table S4). Total abundance differs between years (Supporting Information Table S4), probably related to winter rainfall (Méndez *et al.*, 2017). Four-year cycles in abundance related to a fixed 4-year development time (Drake, 1994) can be rejected (Cox *et al.*, 2020).

A major lesson learned is that a methodological bottleneck, namely, lack of a monitoring protocol, was hindering progress in habitat characterisation and decline assessment. Continuous monitoring and long time series will allow to relate abundance with climatic and land use variables (Thomaes *et al.*, 2017), thus providing a mechanistic understanding of adult phenology and abundance. Transects and dusk can be combined with other monitoring methods (Della Rocca *et al.*, 2020).

Reproductive behaviour

Reproductive behaviour in the stag beetle is related to the sexual dimorphism in body and mandible size, one of the few aspects of stag beetles' biology quantified extensively (le Sénéchal, 1901; Huxley, 1931; Paulian, 1959; Clark, 1964, 1977; Colas, 1962; Lacroix, 1962, 1969; Bessonat, 1983; Sprecher-Uebersax & Durrer, 1998a; Rink & Sinsch, 2008a; Harvey & Gange, 2003b, 2006; Snegin, 2011; Breitenmoser, 2013; Scaccini & Anaclerio, 2016). In males, mandibles are enlarged and their size is positively related to body size (Lacroix, 1962, 1969; Clark, 1977; Lagarde *et al.*, 2005; Hardersen *et al.*, 2011; Harvey *et al.*, 2011a; Romiti *et al.*, 2015, 2016). The existence of two distinct morphs, major and minor, with contrasting mandible development and mating strategies (Otte & Stayman, 1979; Kawano, 1989) has been debated for decades. Some studies found only unimodal continuous variation in male body size (Huxley, 1931; Paulian, 1959; Lacroix, 1962, 1969; Clark, 1977; Møller, 2002; Harvey *et al.*, 2011a), while others found separate morphs (Eberhard & Gutiérrez, 1991; Knell *et al.*, 2004; Lagarde *et al.*, 2005; Hardersen *et al.*, 2011; Romiti *et al.*, 2015, 2017; Thomaes & Camps, 2016).

Whether divided into two distinct morphs or not, size has important biological consequences for mating. Males gather around sap runs (Tippmann, 1954; Tochtermann, 1992) or in places of female emergence (Rink & Sinsch, 2008b). In the gathering places, males fight with their mandibles for access to the females, until one of them is tipped out of balance or chased away (Zimmermann, 1914; Baudrimont, 1931; Tippmann, 1954; Cruysbergh, 1986; Fremlin, 2009). Fights last less than 1 min (Sprecher-Uebersax, 2001; see, however, Cruysbergh, 1986) and are harmless to the loser (Zimmermann, 1914; Baudrimont, 1931). Serious injuries or death, as reported in other species (Siva-Jothy, 1987), seem to be anecdotal in the stag beetle, both in the wild (Tippmann, 1954; Hallengren, 1997) and in terrarium (Braatz, 1914; Tippmann, 1954; Sprecher-Uebersax, 2001). An advantage of big males in fights was suggested by Darwin (1871), and it has been found in other horned beetles (Palmer, 1978; Eberhard, 1979; Brown & Bartalon, 1986; Siva-Jothy, 1987).

Females mate once (Rink & Sinsch, 2008b), but males can mate several times with the same (Weber, 1902) or different females (Hallengren, 1997). Females bury themselves in the ground for

laying the eggs (Harz, 1957; Sprecher-Uebersax, 2001), lay up to 30 eggs (Tochtermann, 1992; Sprecher-Uebersax, 2001; Hawes, 2009a) and can retain eggs and lay them in different places (Tochtermann, 1992; Tini *et al.*, 2018).

Recent advances include the study of geographical variation in body size and allometry, the advantage of body male fitness and sexual behaviour. Geographic variation in size has been documented at national and continental scales (Harvey & Gange, 2006; Harvey *et al.*, 2011a) and follows Bergmann's rule (Romiti *et al.*, 2017). The slope of the allometric relationship between body and mandible size also increases with latitude (Romiti *et al.*, 2017). However, the significance of this geographical variation is difficult to interpret. Both environmental (food quality: Colas, 1962) and genetic (Paulian, 1988) factors have been suggested to explain this variation, but experimental tests are still to be performed.

The advantage of big males in fights has been confirmed in recent times (Lagarde *et al.*, 2005). In addition, male stag beetles that succeed in mating show less fluctuating asymmetry in mandibles than those that do not mate (Møller, 2002) and fluctuating asymmetry of horns is larger than in elytra (Møller, 2002) as predicted for traits under sexual selection. On the downside, disproportionate investment in mandibles, compared to wings, in large males can hinder their ability to search for females (Thomaes & Camps, 2016). Large males may also have trouble in mating with small females (Harvey & Gange, 2006). Small males seem to have higher survival but higher risk of predation by corvids (Chiari *et al.*, 2014; Romiti *et al.*, 2015). Whether males of different size show different phenology is controversial and has been found only when scoring dead specimens (Hardersen *et al.*, 2011), not alive ones (Romiti *et al.*, 2015).

New observations of mating behaviour have revealed details of the duration of mating (Supporting Information Table S2) and guarding of the females by males (Sprecher-Uebersax, 2001). In addition, radiotelemetry has allowed to follow females after mating and unveil their behaviour (Tini *et al.*, 2018). Attempts to identify sexual pheromones have failed (Sprecher-Uebersax, 2001). Longifolene could be an analog of such pheromone and attraction to it has been documented under lab (Harvey *et al.*, 2011b) but not under natural conditions (Chiari *et al.*, 2014).

Elusiveness and crepuscular habits of this species have hindered detailed observations of reproductive behaviour in the wild. Nevertheless, basic knowledge provided by classic studies can now be expanded and quantified using modern camera trapping, genetic and telemetric tools. A deeper understanding of sexual selection in the stag beetle would benefit from further work on the frequency of male fights, duration and actual damages, frequency of mating guard behaviour and its consequences for multiple paternity, the relationship between fecundity and female size or condition, and the role of nature vs. nurture in the development of mandibles. Recent studies of mandible biomechanics in relation to muscle mass and body size (Goyens *et al.*, 2016) should be connected to sexual selection.

Threats and conservation measures

The stag beetle was included in the Bern Convention in 1979 due to a perceived decrease in abundance and distribution in Central Europe. Subsequently, many European countries protected the

species and its habitat. In 1992, the species was included in annex II of the Habitat Directive engaging member states to bring this species to a favourable state of conservation by, among others, delineating special protection areas. This species was listed as endangered in many national and regional red lists (Supporting Information Table S5), but it was only assessed by IUCN in 2010 and rated as “Near threatened” (Nieto & Alexander 2010). This evaluation was justified based on its decline in the north and central part of its range and negative future trends of its habitat. Both the legal protections as the red list evaluations have mainly been based on expert judgement of the species decline.

At a national level, its red list status has been assessed in 20 countries and three regions (Fig. 2; Supporting Information Table S5). Red list status has not been assessed in other 14 countries. Furthermore, the species is no longer present in Luxembourg and Latvia, although it is not officially evaluated. This species seems to show a gradient of threat from the south, where it is predominantly Least Concern, to northern countries, where it is endangered or extinct (Fig. 2). The exceptions are Sweden and UK, where a long tradition of red lists may have resulted in assessments only reflecting the recent decline, and Slovenia, where the species is widespread and common (Al Vrezec, pers. comm.) despite its Endangered status.

Our review identified seven threats in the recent literature, but only four were backed up with evidence (Table 2). Habitat loss is the main perceived threat (Table 2), but studies on the effect of habitat fragmentation and connectivity are only starting

(Della Rocca *et al.*, 2017). Habitat models show that the stag beetle strongly depends on the continuity of its habitat and that dispersal to newly established areas is limited (Thomaes, 2009; Thomaes *et al.*, 2018). For example, Horák (2010) finds presence of stag beetle only in grids where the coverage of deciduous forest is greater than 5%. The presence of empty suitable habitats in highly fragmented landscapes (Drake, 1994; Percy *et al.*, 2000; Della Rocca *et al.*, 2017), suggests local extinctions and potential metapopulation dynamics, as well as limited recolonisation ability. Nevertheless, the stag beetle has been found in small forest fragments embedded in an agricultural or scrub matrix (Méndez *et al.*, 2017), suggesting resilience to habitat fragmentation and degradation. Further work on the effects of habitat fragmentation is urgently needed.

Climate change threatens other *Lucanus* species (Huang, 2014) and could pose a threat to the stag beetle, especially at its southernmost distribution edge. The reason is that, although this species is considered as thermophilic in Central Europe, high temperatures involve a loss of condition in adults (Rink & Sinsch, 2011). Nevertheless, a niche model at European scale predicts an increase in range size for the stag beetle, even after accounting for its limited dispersal ability (Della Rocca & Milanesi, 2020). Additional niche modelling, as well as experimental setups, at a European scale are needed under different scenarios of climate change. Preferably, such models should include physiological information about threshold temperatures for larvae (Thomaes *et al.*, submitted) and adults (Rink & Sinsch, 2011).

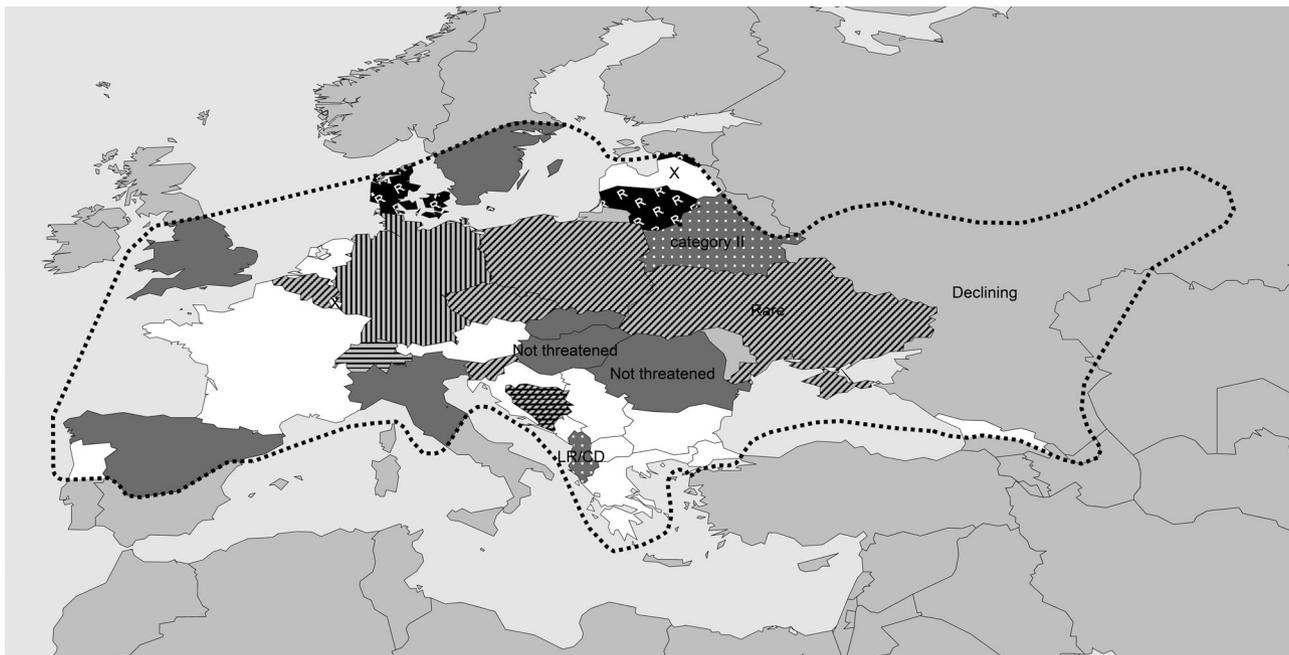


Fig. 2. National or regional (Belgium and Bosnia and Herzegovina) red list assessments for *Lucanus cervus*. Black with white ‘R’: Regionally Extinct; vertical stripes: Critically Endangered; diagonal stripes: Endangered; horizontal stripes: Vulnerable; dark grey with white dots: Near Threatened; dark grey: Least Concern; white: Not Evaluated. For countries using regional criteria, the assessment is written in the country (LR/CD: Lower Risk/Conservation Dependent) and the associated IUCN colour is given. X: no longer present but not officially evaluated in Luxembourg and Latvia. Occurrence of the species in Norway requires confirmation.

Table 2. Documented or inferred threats to the European stag beetle, based on the revision of 41 SCI papers.

Documented threats
1. Habitat destruction or fragmentation (Rink & Sinsch, 2007; Hawes, 2008, 2009b; Thomaes, 2009; Harvey et al., 2011a; Della Rocca et al., 2017; Cox et al., 2019; Della Rocca & Milanessi, 2020)
2. Land use (Thomaes et al., 2008a; Della Rocca & Milanessi, 2020)
3. Climate change (Rink & Sinsch, 2011; Della Rocca & Milanessi, 2020)
4. Predators out of natural balance (Campanaro et al., 2011)
Inferred (mentioned but not documented in the study)
1. Habitat destruction, including intensive forest management and lack of dead wood continuity (10 studies)
2. Genetic erosion due to habitat fragmentation (7 studies)
3. Predators out of natural balance (3 studies)
4. Climate change (3 studies)
5. Collection (1 study)
6. Road casualties (1 study)
7. Genetic introgression with exotic Lucanidae (1 study)

Threats are ranked according to the number of studies that mention such threat. A single study could document or infer more than one threat. Ten studies did not mention any threat.

Predators out of natural balance (Méndez et al., 2015) could negatively affect stag beetle populations. Wild boar preys on larvae and has interfered with translocation projects (Ebert & Müller-Pfannenstiel, 2008). Predation by corvids can be conspicuous based on the accumulation of corpses (Campanaro et al., 2011; Fremlin et al., 2012; Breitenmoser, 2013), but their impact on populations should be further investigated.

Conservation consequences of population genetic structure have barely been studied. Genetic diversity is high throughout Europe, particularly in Greece and decreases towards the North and West (Cox et al., 2019). Local studies in Ukraine also found high genetic diversity (Snegin, 2011, 2014) but showed indication of lower genetic diversity in an anthropogenically influenced population (Snegin et al., 2017). A population genetic study near Brussels indicates a loss of the metapopulation structure in the last decades (Cox et al., 2020).

A detrimental effect of collecting has been suggested for the European stag beetle (Lipińska & Gołąb, 2008), as well as for Asian Lucanidae species (New, 2005; Huang, 2014). Stag beetles seem to be among the more popular beetles sold on Internet, mostly with no indication of the origin of the specimens (Lipińska & Gołąb, 2008). Although this species is not included in CITES, its collection and sale has been banned in many countries (e.g. Belgium: Thomaes et al., 2015; The Netherlands: Smit, 2005; United Kingdom: Percy et al., 2000).

The main conservation measure has been legal protection. The inclusion of the stag beetle in the EU Habitats Directive has triggered renewed research on this beetle, including national programs about the distribution (Thomaes et al., 2010; Katušić et al., 2017; Manu et al., 2017; Kuźmiński et al., 2020) and monitoring (Katušić et al., 2017). Citizen science projects have been performed (Campanaro et al., 2017) or are in place

(e.g., Houard et al., 2012; Soutinho et al., 2017). Monitoring is providing useful information about distribution (Zapponi et al., 2017) and in a few cases several snapshots are available for comparison (Percy et al., 2000; Smith, 2003, 2011). Although abundance trends are scarce and time series are still too short to allow assessment of trends, tools are being developed to infer decline (Thomaes et al., 2017).

In the face of habitat destruction or degradation, ambitious programs of habitat conservation and management should be implemented (Augustynczyk et al., 2018). At the EU level, Natura 2000 has been the main tool to guarantee the conservation of the stag beetle and other saproxylic species. Endorsement of close-to-nature forest management (Gustafsson et al., 2012) has been variable across the EU countries, with the main examples in Scandinavia (Siitonen, 2001) and Slovenia (Veselič et al., 2008), but awareness is growing related to forest conservation and certification (Maesano et al., 2018). Special attention should be given to forest ecotones and their historical management as the stag beetle, among others, is a species of open forest and forest edges (Thomaes et al., 2017). At a local scale, habitat enhancement has been implemented sporadically. For example, artificial log pyramids (Tochtermann, 1987) have been built to increase the habitat of the stag beetle in several countries. Other conservation measures include translocation of stumps colonised with stag beetle larvae with a large tree transplanter (Ebert & Müller-Pfannenstiel, 2008; Ebert, 2011). Similar actions at smaller scale, have been executed at least in United Kingdom and Belgium, probably also elsewhere. A large-scale reintroduction has been performed in Denmark (Damm et al., 2013). Monitoring the success of these actions is essential (Margoulis & Salafsky, 1998) but has rarely been carried out (Ebert, 2011).

Legal protection has been guaranteed at international level and in most parts of its range despite national differences in regulations. The main lesson for conservation is that the stag beetle decline is explained by lack of habitat continuity. Its habitat requirements – sufficient underground dead wood and open to semiopen habitat – can be easily restored but recolonisation is limited. Conservation actions should move from local to broad strategies of nature-friendly forest management. To achieve this ambitious objective, current challenges include monitoring of habitat quality, assessing the restoration potential, quantitative assessments of the impact of other human activities, such as fire and collection. Assessment of historical and current threats should be priority and take advantage of advances in sampling protocols and genetic tools. The stag beetle is one of the few saproxylic organisms that can engage the broad public through outreach activities (Percy et al., 2000; Campanaro et al., 2017) and therefore act as an umbrella species.

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Conflict of interest

All authors declare that they have no conflict of interest.

Data Availability Statement

This is a literature review and no original data are available.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1: Supplementary Information

Table S1 Total (all) or Science Citation Index studies about *Lucanus cervus* published up to 1 April 2020, listed by country in which each study was conducted.

Table S2 Quantitative data on basic aspects of the biology of the European stag beetle.

Table S3 A non-exhaustive list of tree species reported as food sources for stag beetle larvae.

Table S4 Population size in different countings of stag beetles.

Table S5 National (or regional, Flanders: Belgium) red list assessments for *Lucanus cervus*.

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