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Demographic data on a stag beetle (*Lucanus cervus*) population self-established in an artificial suburban habitat

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Front cover: Male stag beetle at Jagersveld, Watermael-Boitsfort, 22 June 2010. © R. Cammaerts

Demographic data on a stag beetle (*Lucanus cervus*) population self-established in an artificial suburban habitat

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Abstract

A population of *Lucanus cervus* (L., 1758) stag beetles, self-established in an oak stockade bordering the entrance of a schoolyard in a suburban locality of Brussels, was monitored from 2001 to 2023. Two capture-mark-recapture (CMR) exercises, carried out in 2001 and 2007, provided phenological and demographic information. The systematic collection of beetle remains abandoned by their predators allowed to follow annual morphometric and quantitative changes as well as to try to assess the sex ratio of this population.

Stag beetles appeared later and for a shorter period of time during the hot, dry season of 2001 than during the more temperate, rainy season of 2007. After the very first males appeared, the number of new individuals increased geometrically for about a week, and then more steadily, reaching a plateau 3 or 4 weeks after the start. Females can still be seen more than a month after the males disappeared.

The number of males whose duration of life is known from marking to the end event taken as their permanent disappearance from the study site, whether through death or loss of follow-up, decreased exponentially according to this apparent longevity, until they were about a week old. Thereafter, only 25% of the males remained, whose numbers decreased more slowly. In a Kaplan-Meier survival analysis, based on only death as the end event, the male median survival probability corresponds to a survival time of 11 to 17 days. Apparent longevity and survival probability are matched by a Weibull distribution.

Approximately 30% of the 148 (in 2001) or 172 (in 2007) tagged males were recaptured. Episodes of 2 consecutive evenings of presence totaled only 18% of the total confirmed lifetime of the males, even much less for episodes of 3 or 4 consecutive evenings, the maximum in a row. Only 8% (in 2001) to 20% (in 2007) of the ca. hundred tagged females were recaptured, none of them for more than 3 consecutive days. The average number of evenings of absence from the study site was higher than the number of evenings of presence. The longest period of absence was 26 days for a male and 22 days for a female.

The number of unique males observed was 173 (in 2001) and 196 (in 2007), which is about half the average number (299 and 378) estimated to have been present using the Jolly-Seber method. The number of unique females observed was 105 and 115, but the estimation of their population size is too imprecise, due to a very high coefficient of variation. In none of the evenings spent at the CMR site were observed more than 15% of the different males and no more than 10% of the different females that were encountered during the entire season. A simulation shows that replacing some of the evenings in the daily sampling of a CMR exercise by dummy evenings without observations reduces the estimated total number of individuals and widens its confidence interval.

The size of the beetles of the 2007 CMR exercise was not related to the date of their first capture. In contrast, there was a significant annual difference in head width on stag beetle remains left behind by predators over the years 2002-2023. Moreover, male beetles from the CMR site were

found smaller than males from two historical populations that were collected a few hundred meters away, one in 1924 in oak railway sleepers and the other in 1986 in the natural habitat from which the current population has evolved.

The number of victims of corvid predation was high until 2015, with lower numbers in 2001 and 2007, maybe due to the deterrent effect of human presence during the CMR exercises. The decrease in the number of victims after 2015 may correspond to the degradation of the nursery habitat.

The sex ratio based on remains left behind by predators had such a high annual variability (from ca. 1.0 to 5.4) that an annual measurement cannot be considered reliable. Established over 20 years on 1734 beetles, the overall sex-ratio was 2.23, and when the 61 natural deaths were added, 2.05.

Keywords: Capture-mark-recapture, dynamics of appearance, apparent life duration, survival rate, population size, morphometry, predation, sex-ratio, Weibull distribution

Introduction

Quantifying demographic parameters of a population is an essential objective to manage its preservation. The stag beetle, *Lucanus cervus* (Linnaeus., 1758), an insect protected under the European Habitats Directive (Council Directive 92/43/ECC), does not escape this rule. The present author lives in a suburban environment of the city of Brussels, amidst a population of stag beetles that he has been able to follow since 1964 and has found himself concerned, over time, by changes in its abundance. This prompted him to quantify certain features of its biology.

The Natura2000 qualification of the stag beetle means that its conservation status must be monitored. It is rated, on the whole, as ‘near threatened’ in the European Red List of Saproxyllic Beetles (CÁLIX *et al.*, 2018). However, its conservation status is based mainly on expert opinion and may differ according to the country. Among the 41 national assessments listed in the census of MÉNDEZ & THOMAS (2021), it has the status of ‘extinct’ in 4 countries, ‘critically endangered’, ‘endangered’, ‘vulnerable’, ‘threatened’, ‘declining’, ‘conservation dependent’ or ‘rare’ in 13 countries, ‘not threatened’ in 2 countries, ‘least concern’ in 5 countries and was not evaluated in 17 countries. As far as Belgium is concerned, establishing a trend in the conservation status of the stag beetle is hampered by the difficulty of comparing its geographical distribution between before and after 1950, since before this date its presence is known incompletely (THOMAS *et al.*, 2010). However, among 33 adjacent communes in the Mid-Brabant region in which the present study is located, the beetle disappeared before the year 2000 in 18 of them (THOMAS *et al.*, 2010). In a more distant past, since at least 1855, the species was very common in the suburban south-east of the city of Brussels, where from the locality of Watermael it was reported as very abundant (35 captures in half an hour) by MÉLISE (1880). This abundance was confirmed for the adjacent locality of Boitsfort from the years 1960 until the years 1980, by personal observations and surveys. Since then, the species has seen its numbers declining in Boitsfort, the only locality in the Brussels region where it still breeds in sustainable numbers. The present study aims to quantify demographic patterns of a part of this population.

Assessing demographic data can theoretically be done by focusing on the biology of the beetle’s larvae or adults. Stag beetle larvae live in damp dead wood, from which they feed through the intermediary action of symbiotic yeasts present in the female’s mycangium and inoculated onto the food substrate when the eggs are laid (FREMLIN & TANAHASHI, 2015). The larvae develop through 3 stages (FREMLIN & HENDRIKS, 2014). Depending on soil temperature, this

development takes place, in the north-western part of Europe, over 2 or 3 years (THOMAES *et al.*, 2022) before that the larva migrates in late spring or summer into the surrounding soil, where it builds an earthen cocoon lined with gut contents and in which it reaches the pre-pupal stage before transforming into a pupa. This cocoon phase lasts around 2 months. The pupa metamorphoses after about another month, already in summer, with the adult resting in its cocoon until it emerges from soil next year (HENDRIKS, 2011). The complete cycle takes so 3 or 4 years. After emerging from the ground in late spring or early summer, adult stag beetles are most active in the evening during a relatively short period of the year which, in the Brussels region, extends mainly from mid-June to mid-July, with females lasting up to a month longer.

While attempts have been made to detect the presence of larvae by the sounds they make when stridulating (HARVEY *et al.*, 2011a) or by their odor (e.g., longifolene; *ibidem*), their lifestyle does not allow a practical assessment of the quantitative importance and monitoring of a population.

Collecting the remains of adult beetles left behind by their predators is one method of assessing the presence, abundance and monitoring of the species. However, when collected during a transect, the spatial distribution of these remains may be heterogeneous if the distribution of the beetle is uneven (CAMPANARO *et al.*, 2011), or if the predator does not consume its prey on site, but takes it home with it as documented in the case of the eagle-owl (*Bubo bubo*, a bird however not present in the study area; OVERMANN & TÖPFER, 2021).

Quantitative monitoring can also be done by counting sighted live beetles during an evening walk along a transect under a protocol providing a standardized index of the population size (CAMPANARO *et al.*, 2016). Another, recently applied method, counting beetles on selected tree trunks exuding sap during diurnal surveys was proved to be more effective than walk transects in providing an accurate population density estimate (DELLA ROCCA *et al.*, 2020). However, this method is not appropriate where exuding trees are rare as for the present study, which was carried out in the Brussels region.

Another, but more time-consuming quantitative method is based on capturing, marking and releasing (CMR) beetles on a series of evenings, what allows not only to get a minimum number of distinct individuals present in the prospected sector, but also to assess the expected number of beetles present in the sampling area, as well as to gather information about e.g., their apparent life duration and fidelity to the sampling area. Population size estimates that have been made through CMR protocols are highly valuable tools for stag beetle monitoring, but most of these already published investigations have not been analyzed in order to compute a population estimate, with the exceptions of the transect-based CMR's conducted in Italy by CHIARI *et al.*, 2014 (using not only visual inspection, but also pit traps and suspended traps) and GIANNETTI *et al.* (2023). However, the low number of recaptures obtained during these transects made the statistical accuracy of population size assessment problematic (GIANNETTI *et al.*, 2023). It was primarily a CMR method based on sampling at a fixed site that was chosen in the present study to assess data of demographic interest on a stag beetle subpopulation in the locality of Boitsfort.

In the 1960s, the most abundant stag beetle Brussels suburban population was located in the locality of Boitsfort (municipality of Watermael-Boitsfort). It had naturally established by itself in the wooded slope bordering the Trois-Tilleuls street (Fig. 1, 50°48'05.93"N 4°24'53.67"E) and this, well before 1949, the first year of its known presence according to the investigation carried out by the author among local residents. In 1964 it was so abundant that the residents were obliged to barricade their windows with mosquito nets and that the few collectors of the time quickly got tired of trying to capture these beetles. In 1986 it was still easy to collect 47

males indiscriminately and within an hour for a biometric study, but in 1999 a similar attempt yielded only 23 males in 3 hours spread over 3 days. Having visited this population every year since 1964, it has indeed appeared to me that it has declined since the late 1990s. Although in regression, this population of the embankment of the Trois-Tilleuls street is still present and

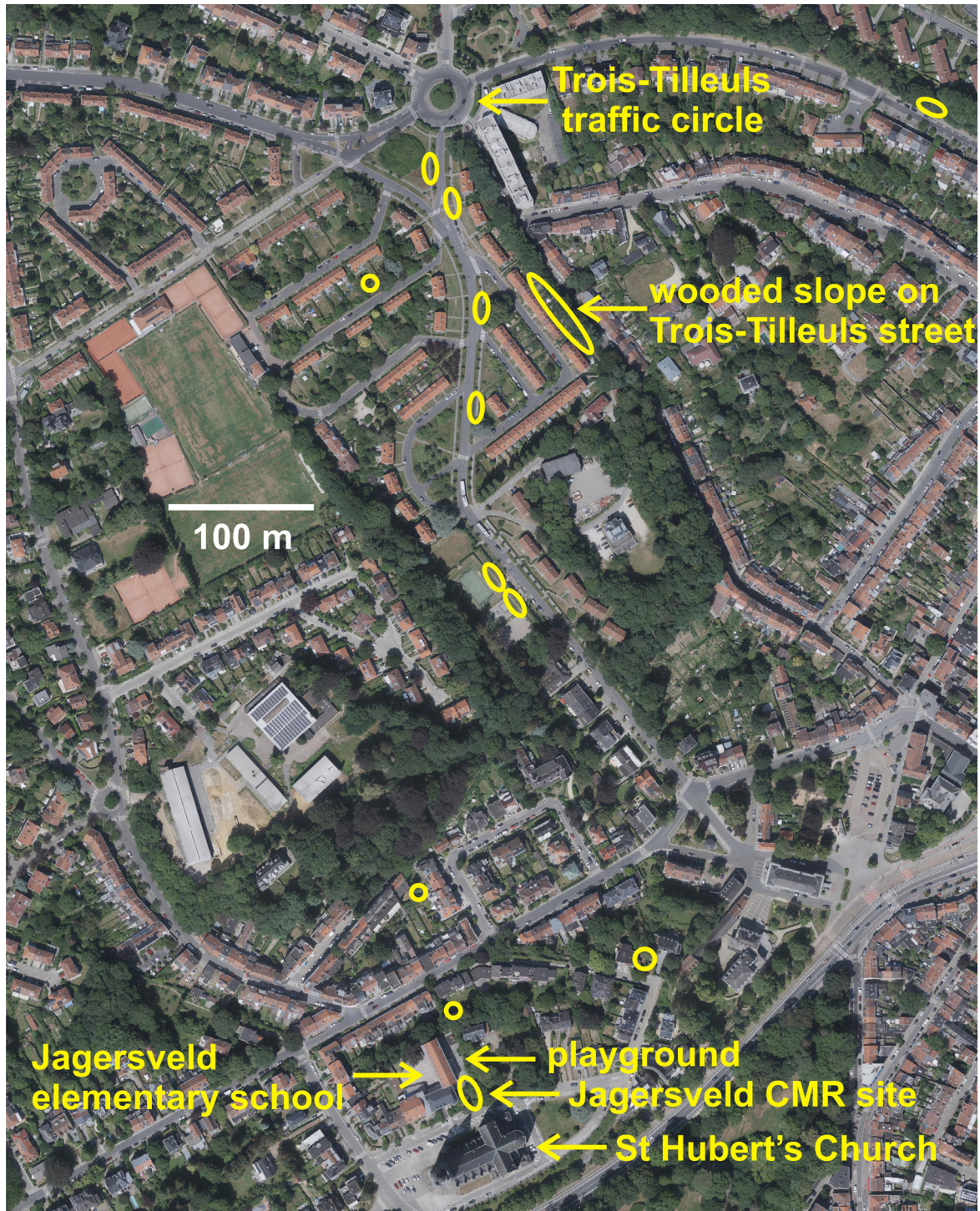


Fig. 1. Aerial view of part of the locality of Boitsfort, a suburb in the south-east of the city of Brussels, with, encircled in yellow, the stag beetle brood sites as they were known for at least the years 2000–2010. Larval sites were (and are) mainly located outside densely wooded plots, and even in the alignments of ornamental cherry trees along certain avenues. Note also the dispersion of these sites, whose circle size do not prejudice the size of their beetle population. Orthophoto plan from UrbIS datastore.brussels.

in the meantime has colonized new sites, sometimes temporary, at a distance of a few tens or hundreds of meters in the surroundings, so that in the years 2000, one could speak about a metapopulation dispersed on the territory of the sub-locality of Boitsfort (Fig. 1). From the beginning of that decade, it was obvious that the correct assessment of the size of this stag beetle metapopulation was an impossible task for a single operator because the area to be surveyed was too large, circumscribed in an ellipse of 400 m by 700 m, and that the daily period during which it is possible to capture stag beetles in sufficient numbers is short (nightfall). For practical reasons of quietness and adequate working space for a reliable census of a sufficiently dense population of stag beetles, it was thus chosen, in 2001 and 2007, to limit the study side to a sub-population sufficiently isolated from the others and which was estimated at that time to be the most abundant on the territory of Boitsfort. This sub-population had colonized an artificial wood boarding on the Jagersveld plateau (Fig. 1, 50°47'48.25"N 4°24'49.96"E), at ca. 550 m from the population located in the natural embankment of the Trois-Tilleuls street and from which it originates. This, either by direct dispersal or indirectly through some small stepping populations (Fig. 1) that may have existed in the environment of the garden city of Boitsfort, on the edge of which the Trois-Tilleuls site and, further away, the Jagersveld plateau are located. Recent sightings, year after year, of new stag beetle spots show that this process of dispersal and fragmentation of breeding sites is still ongoing.

Genetically, the Jagersveld population (and *a fortiori* that of the Trois-Tilleuls slope) differs from the nearest large population, located in the locality of Overijse (50°46'25.68" and 4°32'5.28"), from which it is separated by the large wooded massif of Sonian Forest. These two populations are distinguished by their microsatellite assemblage, despite some overlap and genetic evidence of immigration by a few individuals (Cox *et al.*, 2020).

The Jagersveld stag beetle population established itself in a palisade of oak beams shoring up a concrete ramp allowing emergency vehicles to access the Jagersveld 'Assomption-St Joseph' elementary school playground located to the side of the transept of the imposing St Hubert's Church (Fig. 1). This ramp with a 5-meter elevation change (Fig. 2A) was dug in 1986 through the sandy slope bordering Jagersveld street. To prevent the sand from slumping, both sides of the ramp were shored with new oak beams partially driven into the ground, lining the sides of the concrete ramp and the cut-out in the slope, between which they form open-air planters (Fig. 2B). On the upper right side of the ramp, along its concrete floor, they also line a horizontal platform of bare soil (Fig. 2C). The colonization of this new artificial habitat may have been rapid because a study in England (in Cochester: FREMLIN, 2008) showed that 3 to 6 years after the felling of a tree, lucanid beetle larvae were already present in its stump, whereas the larval cycle duration varies from 2 to 3 years depending on soil temperature (THOMAES *et al.*, 2022). Fifteen years were therefore sufficient for a large population of stag beetles to develop in the fungus-affected parts of the wooden beams. As shown by some fallen beams, not all were colonized by the beetles, as some situations appeared not very favorable to them.

In addition to the dispersal of brood sites, several demographic characteristics indicate that the Jagersveld population is open. Apart from the emergence holes that appeared in the ground over a fairly period of time (at least along two weeks: see Results, 'Dynamics of appearance of new beetles'), stag beetles, especially males, are known to make crepuscular flights, as demonstrated by the discovery of some of them that were found dead elsewhere in the same locality, far away from any larval site. The study of a population opens to the birth of new individuals (emergence), immigration, emigration and mortality requires the capture of a sample of individuals, their individual marking and their return to the population. In subsequent captured

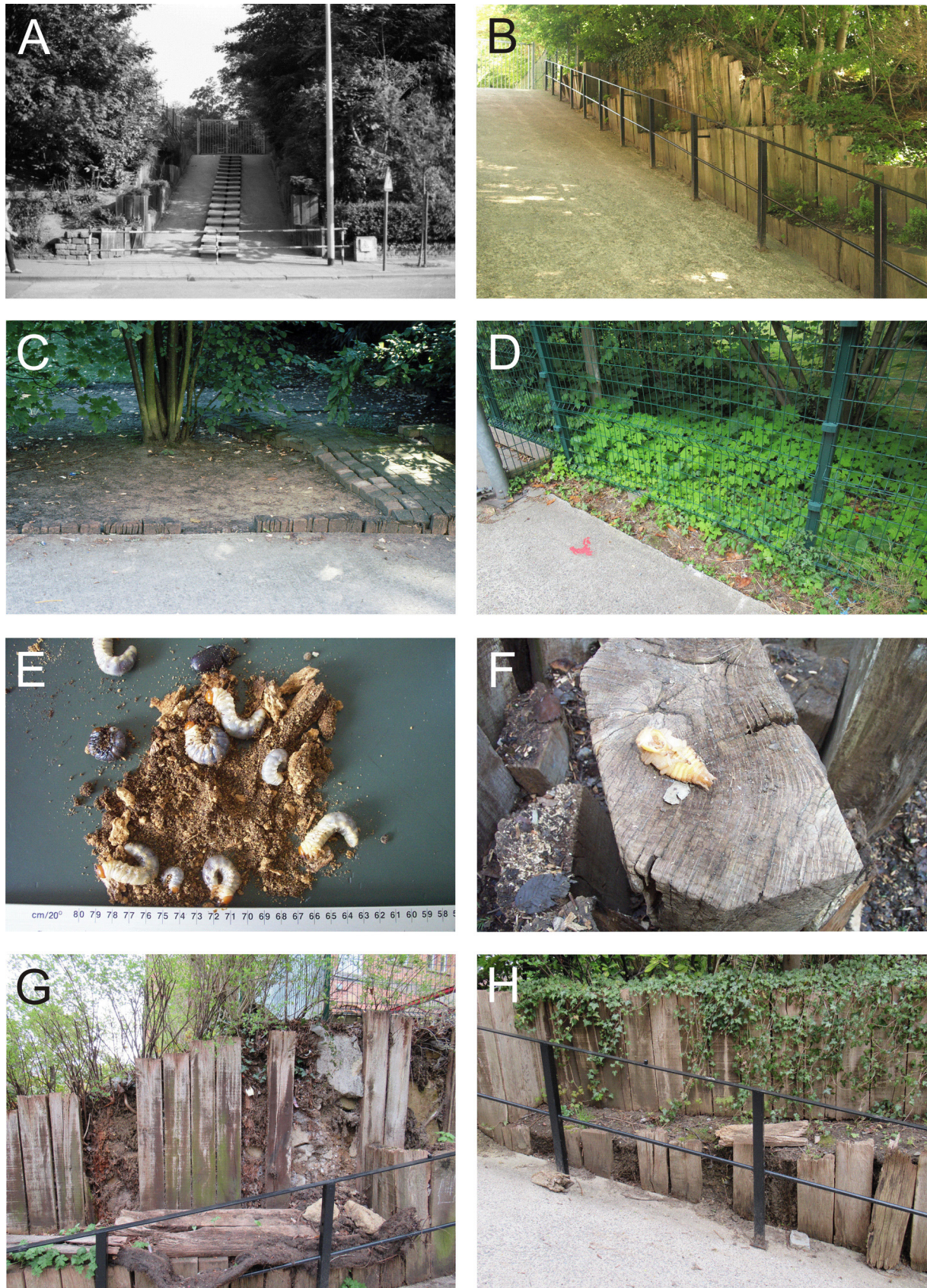


Fig. 2. **A**, The ramp to the playground of the Jagersveld school, with its central staircase in 2001. **B**, The palisade of beams of the east side of the ramp in its 2007 state, however photographed in 2013, the staircase having been removed in the meantime. **C**, The earthen platform at the top of the ramp in 2002, with the alignment of short beams separating it from the concrete of the ramp. **D**, The same platform fenced and overgrown with maple saplings, as viewed in 2022. **E - F**, Stag beetle larvae and a pupa found in 2005 when some of the beams were replaced. **G - H**, damage to the paling, west side and east side, in 2021. © E and F, courtesy Olivier Beck.

samples, the individuals previously marked and those not yet marked will be distinguished, the latter being in turn marked. These capture-mark-recapture (CMR) sessions were carried out in 2001 and 2007, every evening throughout the stag beetle season on the access ramp to the school playground and its most immediate surroundings. The analysis of abundance was done using an appropriate stochastic method, for which gains (emergence and immigration) and losses in numbers (mortality and emigration) can vary from one sampling to another. Individual tagging of imagoes not only allowed to estimate the abundance of individuals present, even if not captured, at the tagging site, but also to collect information e.g., about the dynamics of their appearance on the site, their known longevity, duration of absences from the site and survival. From this information, collected during the 2001 and 2007 CMR sessions, we can draw lessons that are still valid today because their scope is more general than purely of local interest.

A portion of the Jagersveld CMR site was fenced off in the fall of 2007 and, rendered inaccessible, could not be cleared of dead leaves in subsequent years to make the ground surface more visible, as it had been every year before. These dead leaves gradually accumulated into a thick mat covering the floor of the lateral platform and this portion of the site was later covered with a dense carpet of natural seedlings of Norway maple (*Acer platanoides*, Fig. 2 D), making the floor invisible. This has seemingly reduced the opportunity for stag beetle oviposition and emergence at this location and for the researcher to see and capture any beetles present. Moreover, the lack of maintenance of the soil along the beams boarding the ramp also had the effect of increasing their vegetation, which is probably not ideal for the stag beetles, which prefer open environments. This has discouraged further CMR operations aiming to monitor the quantitative evolution of this population. Already before this partial fencing, some of the oak beams in which larvae were living were already so degraded after having been placed 20 years earlier that in 2005, out of a total of more than 200 beams, 36 were replaced by the Brussels Institute for Environmental Management (IBGE; Fig. 2 E-F). But the most damage to the site has occurred in the last few years, caused by numerous deliberate degradations to the wood boarding (Fig. 2 G-H), which is likely to have had an impact on the abundance of the beetles.

A systematic daily search for stag beetle remains left by their predators at the Jagersveld CMR site itself, was started in 2001 and continued until 2017 and repeated in 2021 until 2023. This attempt to assess the abundance of the stag beetle population, which is less time consuming than CMR sessions, was carried out mainly by counting the number of beetle heads left by their predators on site. Heads, along with the elytra, are almost the sole remains of stag beetles left behind by Corvids, which only eat the abdomen. Measuring the head allowed to establish if there is an annual variation in the size of the individuals.

Literature data on stag beetle population abundance trends are, on the whole, scarce and time series are still too short to allow assessment of trends (MENDÉZ & THOMAS, 2021). Ideally, to properly assess the status of a population, a good monitoring protocol should thus be conducted over years. The present study allows this to a certain extent for a small population living in an artificial suburban site and followed over more than twenty years. Moreover, environment in (sub)urban spaces being highly variable, studying the reaction of their saproxylic insect populations to changes in their habitat conditions provide opportunities to assess the effect of anthropogenic disturbance (HORÁK, 2018).

The insights gained from this study should lead to sustainable management of the Jagersveld and other stag beetle populations, as it is clear that conservation of the species must focus on its biology and local features (HARVEY *et al.*, 2011b).

Material and methods

THE SAMPLING SITE

The stag beetle breeding area of the Jagersveld school site stretches along a maximum of 61 meters of oak beams of various lengths and with a cross section of 10-11 by some 21 cm. These beams retain the sides of the trench leading to the playground and also line the concrete ramp, between which they form 6 garden beds of 2.1 to 3.5 m long by 40 cm internal width. Beams cut close to the ground along the passageway also line a horizontal platform of 2.5 m x 2.7 m bare ground located along the highest right side of the ramp. These areas were very attractive to beetles and their emergence holes were the easiest to see on the platform. In addition to these breeding locations, the actual sampling area included the ground space where beetles were easily visible from the top of the ramp, i.e., the first 10 meters of the playground (an additional 113 m² was visible this way) and a small yard of 114 m² to its left. The sidewalk at the entrance to the ramp and the immediate surroundings of the street (4 x 4 m = 16 m²) were also included. In total, some 326 m² were easy to monitor.

The ramp and the nearby playground were lined by shrubs and small trees, goat willow (*Salix caprea*), hazelnut (*Corylus avellana*), hawthorn (*Crataegus sp.*), sweet cherry (*Prunus cerasus var. avium*), sycamore maple (*Acer pseudoplatanus*) and Norway maple (*Acer platanoides*), along which stag beetles, especially males, liked to fly.

At the time of the CMR samplings, a white light placed at 12 m high on the school wall, lit a small part of the playground since 22:30 h onwards, with an intensity of 20 lux at 1.5 m above ground. There was also a street lamp which did not lit the Jagersveld ramp itself, but produced a yellowish light of 11 lux at 1.5 m above the street pavement close to the entrance slope and of 26 lux in the middle of the street.

CMR SAMPLING AND MARKING

On every evening of the stag beetle season, regardless of the weather, the author was permanently present on the Jagersveld school ramp and its immediate surroundings in 2001 and 2007, from 21:00 to 23:15 (summer time) from mid-May till end July. In August, according to the shortening length of the day, it was from 20:30 to 22:45, and during the first half of September, it was from 20:00. All beetles that were seen during these time periods were captured, in flight with a butterfly net, or on the ground or in the vegetation by hand. The sampling effort was systematic, intensive (i.e., as complete as possible, not random), always over the same limited area. All captured beetles were recorded, those newly encountered being tagged by individual number marks. Moreover, a visit to the sampling site was made every day around 7 a.m. and 18:30 p.m. in order to collect any dead beetle.

In 2001, an early attempt of marking with white Typex® dots on the underside of the insect was not conclusive to univocally differentiate a large number of individuals, and was quickly replaced by an individual numbering with white lacquer on the top of the head and prothorax and black lacquer on the elytra (Edding 780® marker pens). This dorsal marking being the least rubbed, except the head in females, appeared to be the easiest to identify the beetles. The mentum was also marked with a white dot in order to be sure, in extreme cases, to recognize if a damaged head left on the spot by predators (Corvids) came from a marked individual or not. This dorsal marking is likely to increase the visibility of the beetle for its predators, but for the observer, at a few meters away it was disruptive and did not allow to distinguish a marked

beetle from an unmarked one. Even partially erased, what remains of the marking was found usable for at least three weeks. Where necessary, markings were re-drawn. The combination of individual marking and of recorded morphological characteristics and, in 2007, of the total length of the individuals (TL, measured to the nearest mm, the beetle being held flat on the ground), allowed the unambiguous recognition of the identity of individuals.

The exploitation of the data is based on a *calendar of captures* (Fig. 3) allowing to follow the recaptures in the form of ‘presence-absence’ and to indicate the daily number of captures and released individuals.

Marked and recaptured individuals:	Encounter histories of recaptured males in 2001																													
	June														July															
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Released	1	6	25	10	20	6	17	12	6	0	1	3	2	2	0	4	11	11	13	13	16	12	14	3	5	0	0	1	0	
MNA	1	6	28	14	25	13	28	21	11	5	4	4	3	3	0	4	13	15	18	17	24	25	20	7	7	3	3	2	1	

Encounter histories of recaptured males in 2007																																					
June																July																					
3	5	7	9	11	13	15	17	19	21	23	25	27	29	1	3	5	7	9	11	13	15	17	19	21	23	2	4	6	8	10	12	14	16	18	20	22	24
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5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
6	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
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9	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
10	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
11	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
12	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
13	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
14	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
15	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
16	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
17	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
18	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
19	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
20	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
21	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
22</																																					

Fig. 3. Calendar of male capture and recapture histories at the Jagersveld site. The marked individuals are sorted by date of first capture and by known duration of longevity. 1: captured. 0: not encountered in the interval where the individual was known to be alive. +: found dead by predation on the sampling site. *: natural death. MNA: minimum number known alive.

DYNAMICS OF APPEARANCE OF NEW BEETLES

The climate data for the years 2001 and 2007 were taken from the websites of the Royal Belgian Institute of Meteorology

(<https://www.meteo.be/fr/climat/climat-de-la-belgique/evenements-remarquables-depuis-1901/evenements-remarquables/decennies/2001-2010>, <https://www.meteobelgique.be/article/donnees-statistiques/uccle-depuis-1833> and <https://www.meteo.be/fr/climat-en-belgique/normales-climatiques-a-uccle/temperature-de-lair/temperature-moyenne>). The nearby meteorological station 6647 of Uccle provided also information on daily rainfall and, for 2001, on storm events.

KNOWN LIFETIME BEFORE PERMANENT DISAPPEARANCE FROM THE CMR SITE

Two kinds of analysis were performed. In the present one, the known lifetime of a stag beetle is measured from the day it was marked to the day it was last found, whether alive or dead (Fig. 3). The end event in a beetle's life is here its permanent disappearance from the CMR study plot, indiscriminately through loss of follow-up or death. In the latter case, the beetle is considered as having been alive on his last day, just before the time of sampling (for a detailed justification see the 'Predation' section in 'Results').

The lifetime of the beetles before their tagging is unknown (only one male was tagged on emergence, in 2007), as is the time they may have lived after being lost to follow-up.

The distribution of the known and apparent longevity of male beetles is detailed in a cohort life table of the recaptured individuals (Table 1) which shows, from left to right columns, the number (x) of days elapsed since marking, the number (N_x) of individuals known to be alive up to then as well as the $[N_x - N_{(x+1)}]$ number of them disappearing in the interval between days $(x+1)$ and x . The following columns show the proportion of N_1 individuals surviving at day x (N_x / N_1), the proportion of N_1 individuals disappearing between days x and $x+1$, i.e. $[(N_x / N_1) - ((N_{x+1}) / N_1)]$, the average life expectancy in days, $\sum_{x=i}^{x=j} [(N_x + N_{(x+1)}) / 2] / N_1$ and the age-specific life expectancy, $\sum_{x=i}^{x=j} [(N_x + N_{(x+1)}) / 2] / N_x$.

Exponential growth curves corresponding to the observed data were calculated using Statistica® v.10 software. Weibull distribution parameters and goodness-of-fit testing were assessed using package 'weibullness' (see hereunder, next section).

MALE SURVIVAL ANALYSIS

Another analysis focus on the male survival rate. The time to event is here the time from marking to death. Times to death and to loss to follow-up of recaptured individuals are extracted from Fig. 3. The decrease, as a function of the number of days elapsed since tagging, of the conditional probability of survival of a male cohort was calculated using the Kaplan-Meier (K-M) product-limit estimator, based on the ratio between the number of deaths occurring in the interval between two days and the number of individuals still at risk at the start of this interval. The number at risk is the number of individuals alive at the start of the previous interval, minus the number of individuals who died or were lost to follow-up during this previous interval. Individuals whose follow-up is definitively incomplete constitute the censored data (KAPLAN & MEIER, 1958; KLEIN & MOESCHBERGER, 2003; KLEINBAUM & KLEIN, 2005).

Core Team's R software v 4.1.2 was used to calculate Kaplan-Meier estimators and to draw survival curves (package 'survival' of THERNEAU & LUMLEY (2018), function `survfit`) as well as to statistically compare two K-M survival curves by using the log-rank test (idem, function `survdif`). Defining the maximum likelihood estimates of Weibull distribution parameters and

testing the goodness-of-fit of Weibull curves with the observed data was done using package ‘weibullness’ (functions `weibull.mle`, `rweibull` and `wp.test`) of PARK (2022), based on formal statistical considerations developed in Park (2017). Drawing Weibull survival curves was done using package ‘eha’ of BROSTRÖM & JIN (2023), function `weibreg`. Non-parametric K-M survival distributions and parametric Weibull survival distributions were graphically compared by superimposing them, as in MACHIN *et al.* (2006).

POPULATION SIZE BASED ON CMR SAMPLINGS

The POPAN formulation of the Jolly-Seber (J-S) method implemented in the software program MARK (SCHWARZ & ARNASON, 2020) was used to parametrize the underlying population processes for males and females. The calculation of parameter estimates was rendered possible by the suppression of the evenings without any capture, the number of time intervals (days) between samplings being then adjusted accordingly.

Among the assumptions for a correct use of the Jolly-Seber method, the sampling area has to remain constant and the marks cannot be lost and must remain readable, what was the case. Moreover, sampling has to be enough ‘instantaneous’ between the sampling occasions to enable the released beetles to mix and disperse with unmarked beetles in the sampling area. This assumption is difficult to ascertain because the beetles are mostly inactive in the day and that sampling occasions had to take place every evening because daily captures of more than 10 individuals were concentrated in no more than two weeks. The problem of fulfilling this assumption of free dispersal between sampling occasions is approached and discussed in the ‘Results’, sections ‘Jolly-Seber assumptions’ and ‘Daily sampling versus every 2-3 days’. Assumptions of equal catchability and survival probabilities for marked and unmarked beetles were tested using the goodness-of-fit (GOF) Tests 2 and 3 of program RELEASE implemented in MARK (COOCH & WHITE, 2022). Moreover, Leslie’s test (LESLIE, CHITTY & CHITTY, 1953, well exemplified in KREBS, 1999 p. 54) was used to test equal catchability between the marked individuals in the marked-recaptured segment of the population, a necessary condition for a correct estimation of the survival probability (ϕ).

Choosing a model according to the kind of time-dependence of the survival and recapture probabilities

J-S models differ according to the kind of survival probability taken into account from one sample to the next (ϕ) and according to the kind of encounter (capture) probability in each sample (p). These probabilities may be constant (.) or vary along time (t , corresponding to evenings). Four “classical” models, $\phi(.) p(.)$, $\phi(t) p(.)$, $\phi(.) p(t)$ and $\phi(t) p(t)$ were thus tried. The ‘best’ model, i.e., the one that is deemed to fit the best to reality, was chosen as being the most parsimonious, based on the number of estimated parameters, on the magnitude of difference between the models according to the Akaike Information Criterion corrected for small sample sizes (AICc) and on the model likelihood criterion (which is the strength of evidence of the model relative to the model with the lowest AICc).

A model with ϕ constant during some time, then gradually varying along time (as noted in the section ‘Known duration of life’) could not be implemented as these age-dependent survival probabilities cannot be sorted in distinct classes because the some 10 (in 2001) or 15 (in 2007) concerned males appeared separately over the sampling season. The Manly-Parr formulation (MANLY & PARR, 1968) allows age-dependent survival rates, thus unequal survival probability between individuals, but could also not be reliably used, due to the too few capture numbers (BLOWER *et al.*, 1981), a drawback leading to variation coefficients well above 0.50 (as explained in SEBER, 1982).

According to the concept of SCHWARZ & ARNASON (1996), the population studied is considered as a super-population which size is estimated as the total number (N) of unique stag beetles that were available in the study area, i.e., being native to the sampling site as well as immigrating. N is calculated as the addition of the number estimated present at the time of the first sampling occasion and of the estimated net number of new entrant beetles (the probability of entry, $\text{pent}(t)$, of course varies according to the time of each sampling) in each of the following sampling occasions, and which did not die before being found at a subsequent occasion.

The estimated daily numbers (N_i -hat) of beetles express for each sampling occasion the number of already marked beetles estimated to be present plus the estimated number of entrants that returned to the sampling site after having temporarily emigrated. The total of the daily numbers ($\sum N_i$ -hat) of course exceeds that of the estimated total number (N).

The simple enumeration method of the daily minimum number alive (MNA), adding the individuals caught at the day of the sampling and not caught but present before and after the time of sampling provides the daily minimum number of beetles attending the sampling site. It is the observed lower limit of the daily population size, and its estimates will converge with the Jolly-Seber estimates only when all animals are caught each sampling time (KREBS, 1999). The method suffers thus from a negative bias, especially when catchability is low (JOLLY & DICKSON, 1983).

MORPHOMETRY

The total body length (TL) of live beetles held flat on the ground was measured during the 2007 CMR exercise to the nearest mm using a millimetric ruler. The head width, measured to the nearest 0.1 mm, on beetle remains or on entire dead individuals collected in 2001-2022 on the Jagersveld site, is defined as the maximum distance between the head ridges (designed KB in Fig. 1 of KUYTEN, 1964), the same calipers having been used on the whole series of measurements. These measurements could be compared with a sample of 47 males collected alive and indistinctly in 1986 during a single evening on the natural site of the Trois-Tilleuls embankment located at ca. 550 m from the CMR site (Fig. 1), as well as with 22 males collected in 1924 on the artificial site of the old railway station of Boitsfort. In the no longer extant latter site, located 475 m away, a population of stag beetles had developed in railway oak sleepers recovered at the end of their use in order to fence the access path to the station (personal communications from the late Professors Max Poll and Emile Janssens of the Free University of Brussels (ULB), who as young students experienced the heyday of this population) (collection A. Janssens deposited in the Royal Belgian Institute of Natural Sciences (RBINS) for the 1924 sample and author's collection for the 1986 sample).

The distributions of measurements were tested for normality and equality of variance and, depending on the result, compared statistically by means of a parametric ANOVA or the non-parametric Kruskal-Wallis (K-W) test as well as, for multiple comparisons, by the use of the dedicated Newman-Keuls, Tukey or Kruskal-Wallis tests (Statistica® v10 software). However, the corresponding graphs, shown in Figures 8 and 9, have been chosen because they are the most expressive, depending on whether they are based on the mean or the median. This did not preclude the use of the kind of statistical analysis best suited to the distribution of measurements.

PREDATION AND SEX-RATIO BASED ON BEETLE REMAINS

Stag beetle remains left on the site by their predators were collected each year, daily throughout the season, around 7 or 8 o'clock as well as between 20 and 22 o'clock. Only single heads or heads attached to body parts or whole bodies were taken into account to establish the sex-ratio.

Results

DYNAMICS OF APPEARANCE OF NEW BEETLES

The curves (Fig. 4) accumulating the number of new individuals caught during the sampling season show that in 2001 the males appeared about 10 days later than in 2007 and that the bulk of the population appeared in early summer rather than late spring. For females, the time lag between the first individuals in these two years was about 5 days (Fig. 4). These two years were characterized by notable climatological differences that could explain this discrepancy. Indeed, the climatological data recorded at the weather station of Uccle, located at 3,9 km from the Jagersveld site and at a comparable altitude (ca 100 m compared to ca 85 m) indicate that in 2001 the month of April was cold and rainy (134 mm of rain, a record, the normal being 51 mm) while the months of May and June were warm and moderately rainy (75 mm distributed over 18 days). Then it was totally dry from June 19 to July 6 and, although June had an average temperature of 15.7°C (the normal being 16.2°C), the end of this month was torrid (up to 31.4°C). The average July temperature (18.7°C) corresponded to the normal (18.4°C), but rain

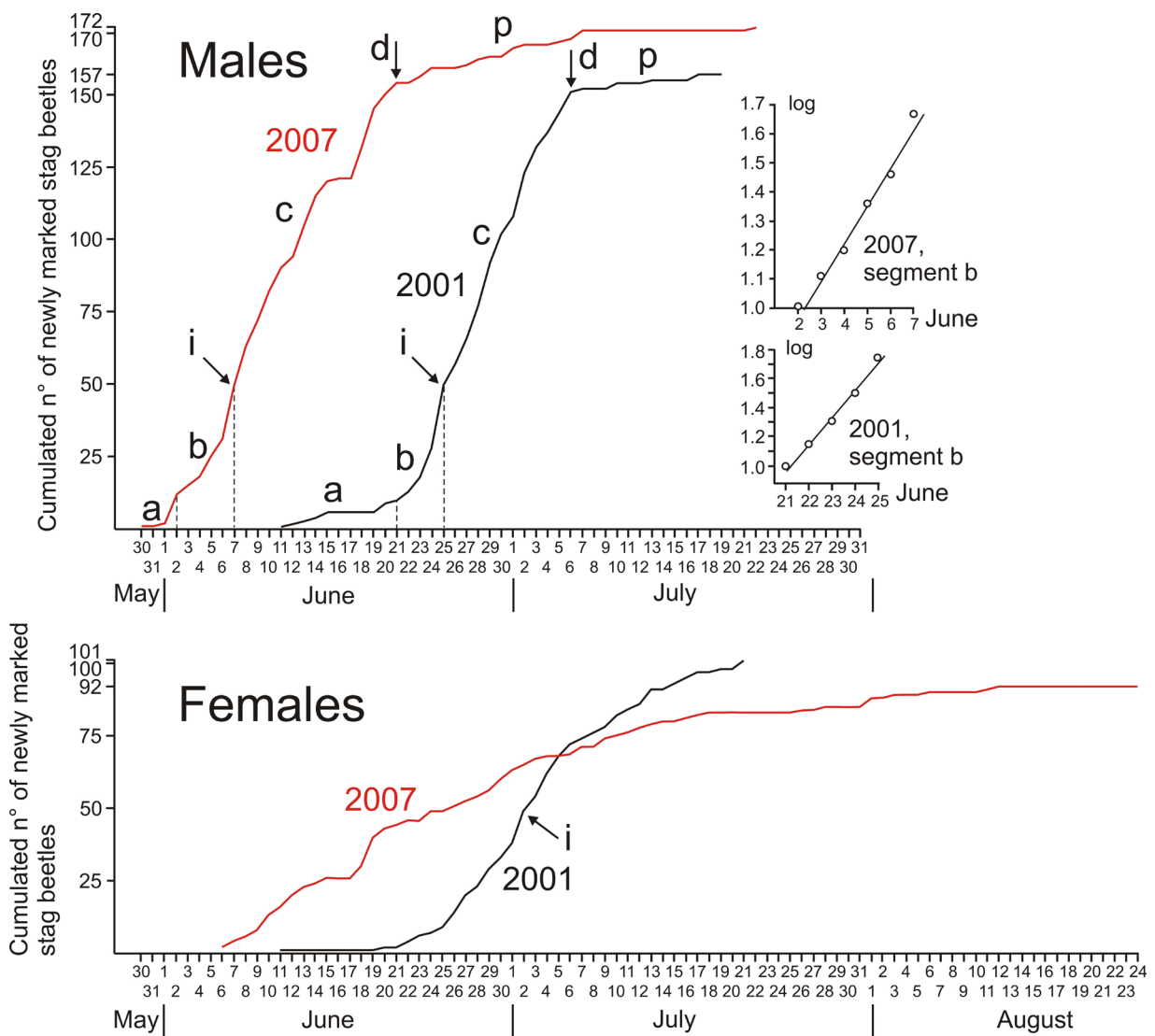


Fig. 4. Cumulative number of new individuals at the Jagersveld site during the CMR sessions of 2001 and 2007. (a): appearance of the first males. (b): geometric increase of new individuals during a short period. The graphs in the right insets show this increase in semi-logarithmic coordinates. (i): inflection point. (c): more regular increase of new individuals until reaching (d) a plateau (p). The increase of new females was more progressive.

only started again on July 7, when the stag beetle season ended that year. An overview of the drought in the summer of 2001 is shown in Fig. 7, which also shows that storm events had no influence on the presence of beetles that year. In 2007 the months of April, May and June were abnormally warm (respective averages of 14.3, 14.6 and 17.5°C, the normals being 9.8, 13.6 and 16.2°C), the 5th of May having already accumulated more than 20°C for 14 consecutive days. It was totally dry from April to May 6 (a record of 36 days), after which the remaining days in May and June accumulated 203 mm of rain over 41 days. July and August were temperate (average 17°C) and regularly rainy (with 97 and 57 mm of rain). The sampling seasons were indeed perceived by the observer as hot and dry in 2001 and temperate and rainy in 2007.

New emergence holes appeared on the bare ground of the horizontal platform from 8 to 26 June (i.e., over 18 days, $n=9$, but data incomplete) in 2001 and from 30 May to 16 June (i.e., over 18 days, $n=18$) in 2007.

Fig. 4 shows that after the sparse appearance of the first few males (a), the daily increase of new male individuals was geometric (b), but over a short period not exceeding one week. The cumulative numbers of section b fit very well with a growth that increased at a geometric rate of 1.53 (in 2001) or 1.37 (in 2007) (χ^2 goodness-of-fit test: $0.80 < P < 0.90$ in 2001 and $0.95 < P < 0.98$ in 2007). As an illustration, the section b transposed into semi-logarithmic coordinates (inset graphs) becomes a straight line with coefficients R^2 of 0.9853 in 2001 and 0.9890 in 2007. Then, after an inflection point (i) the number of new males grow more slowly but regularly (c) during about ten (in 2001) or fifteen (in 2007) days and ended (d) with a plateau (p). The last new males were marked on 17 July 2001 (2 males) and 22 July 2007.

The first females appeared about a week after the males, the number of new ones increasing gradually and more slowly. This dynamic is thus not very marked, except for the presence of an inflection point in the 2001 curve (Fig. 4). The last new females to appear have been marked on 21 July 2001 (3 individuals) and 24 August 2007 (this very last female was eaten by a bird two days later). Females were thus seen for a longer period of time in 2007, which may reflect a longer lifespan due to a wetter climate as by July and August, the emergences were long over.

KNOWN LIFETIME BEFORE PERMANENT DISAPPEARANCE FROM THE CMR SITE

As a reminder, the known lifetime of a stag beetle is that measured from the day of its first capture (marking) to that of its last known presence on the study site. This apparent longevity is assumed to be, to some extent, proportional to the actual life duration.

Males

Table 1 shows the distribution of the number of males that were recaptured at least once, in relation to the number of known days of life since their tagging and provides information on some important parameters. At the apparent age of one day, these individuals formed a fictitious cohort of 46 in 2001 and 48 in 2007, out of a total of 148 and 172 tagged males respectively (Table 2). The cohort declined rapidly: around 75% of individuals did not exceed the known age of 6 days in 2001 and 8 days in 2007.

In 2001, the known lifespan of males averaged 4.04 ($\sigma = 4.21$) days, with a median value of 2 (1 - 5.75) days; in 2007, it was 6.56 ± 7.24 days, with a median of 4.5 (2 - 9) days. The high standard deviations reflect the non-normal distribution of longevity and the wide disparity, given the small numbers involved. A non-parametric test of the median reveals no difference between the known longevity of males tagged in the first or second half of the tagging season. The longest known lifespans of males were 19 days in 2001 and 36 days in 2007 (Fig. 3). The beetles therefore lived longer in 2007.

The (apparent) life expectancy on the second known day of existence (= the day following tagging) was 3.79 days in 2001 and 6.08 days in 2007 (Table 1).

Table 1. Cohort life table of known lifetime of male stag beetles marked and recaptured in 2001 and 2007. The table starts on the day following the day of marking and the known lifetime ended when the beetle permanently disappeared from the CMR site, whatever by death or loss of follow-up. Beetles that were found freshly dead at most a few hours prior to the time of an evening sampling were recorded as having lived that day. Formulae for mean life expectancy and age-specific life expectancy are given in Materials and Methods.

Number of days (x) elapsed since marking	Number of individuals (Nx) known to be alive up to day x	Number of individuals disappearing between days x and (x+1)	Proportion of N1 alive at day x (= Nx / N1)	Proportion of N1 disappearing between days x and (x+1)	Average life expectancy in days	Age-specific life expectancy
2001 :						
1	46	18	1.00	0.39	3.79	3.79
2	28	8	0.61	0.17	2.74	4.50
3	20	2	0.44	0.05	2.22	5.10
4	18	2	0.39	0.04	1.80	4.61
5	16	4	0.35	0.09	1.43	4.13
6	12	1	0.26	0.02	1.13	4.33
7	11	4	0.24	0.09	0.88	3.68
8	7	1	0.15	0.02	0.68	4.50
9	6	1	0.13	0.02	0.54	4.17
10	5	2	0.11	0.04	0.42	3.90
11	3	1	0.07	0.03	0.37	5.17
12	2	0	0.04	0.00	0.28	6.50
13	2	0	0.04	0.00	0.24	5.50
14	2	0	0.04	0.00	0.20	4.50
15	2	0	0.04	0.00	0.15	3.50
16	2	0	0.04	0.00	0.11	2.50
17	2	1	0.04	0.02	0.07	1.50
18	1	0	0.02	0.00	0.03	1.50
19	1	1	0.02	0.02	0.01	0.50
20	0		0.00			
2007 :						
1	48	11	1.00	0.23	6.08	6.08
2	37	4	0.77	0.08	5.20	6.74
3	33	8	0.69	0.17	4.47	6.50
4	25	1	0.52	0.02	3.86	7.42
5	24	5	0.50	0.10	3.35	6.71
6	19	4	0.40	0.09	2.91	7.34
7	15	2	0.31	0.04	2.55	8.17
8	13	1	0.27	0.02	2.26	8.35
9	12	1	0.25	0.02	2.00	8.00
10	11	1	0.23	0.00	1.76	7.68
11	10	2	0.23	0.03	1.53	6.68
12	8	3	0.17	0.03	1.33	8.00
13	5	0	0.10	0.00	1.20	11.50
14	5	0	0.10	0.00	1.09	10.50
15	5	0	0.10	0.00	0.99	9.50
16	5	0	0.10	0.00	0.89	8.50
17	5	2	0.10	0.04	0.78	7.50
18	3	0	0.06	0.06	0.70	11.17
19	3	0	0.06	0.00	0.64	10.17
20	3	1	0.06	0.02	0.57	9.17
21	2	0	0.04	0.00	0.52	12.50
22	2	0	0.04	0.00	0.48	11.50
23	2	0	0.04	0.00	0.44	10.50
24 - 28	2	0	0.04	0.00	0.40 - 0.23	9.00 - 5.50
29	2	1	0.04	0.02	0.19	4.00
30	1	0	0.02	0.00	0.15	7.00
31 - 35	1	0	0.02	0.00	0.11 - 0.03	5.50 - 1.50
36	1	1	0.02	0.02	0.01	0.50
37	0		0.00			

Males over the (apparent) age of 6 days in 2001 were no more numerous at the beginning than at the end of the season: 7 appeared during the period from June 21 to 30 ($N = 24$) versus 5 during the period from July 1 to 6 ($N = 22$) (χ^2 test: $P \sim 0.90$). Similarly for males over the apparent age of 8 days in 2007: 8 appeared during the period from June 2 to 17 ($N = 25$) and 5 during the period from June 18 to July 7 ($N = 23$) (χ^2 test: $0.50 < P < 0.70$).

Females

The 8 females recaptured in 2001 had an apparent longevity of 6.00 ± 5.93 days [quantiles: 3.5 (2-6.5) days]. In 2007, the known longevity of the 19 recaptured females averaged 9.79 ± 7.74 days [7 (3 - 15) days]. The longest known longevity was 15 days in 2001 and 26 days in 2007. As with males, females therefore lived longer in 2007 than in 2001.

Distribution of the number of males according to their known duration of life

As stag beetles can appear and disappear randomly from the observer's field of vision through uncontrolled migration (population open to emergence, immigration and emigration) or mortality (indistinct victims of predators), a constant rate of decline in the number of individuals at risk of disappearing through death or loss of follow-up was hypothesized. It's worth mentioning that the individuals tagged and found dead (17% of the total recaptured in 2001 and 29% in 2007) were not found dead at a particular point in the beetles' known lifespan, but throughout it (these deaths were spread evenly over the 1 to 11 days of known lifespan in 2001, and over 1 to 17 and even 36 days in 2007; these data are not in a Figure).

We can see (Fig. 5A) that an exponential growth curve with equation $y = a + e^{(b + c \cdot x)}$ fits with the observed decline in the male cohorts, although it is not an exponential curve in the strict sense (in this case it would have been $y = a \cdot e^{c \cdot x}$). The agreement between observed values and those predicted by the regression equation is excellent (for 2001: $R^2 = 0.98$, $\chi^2 = 3.75$; $df = 11$; $0.98 < P < 0.99$, and for 2007: $R^2 = 0.99$, $\chi^2 = 3.56$; $df = 21$; $P > 0.99$). This allows us to use the regular plotting of this theoretical curve to interpret the biological significance of the observed distribution.

Let's take as an example the expected regression curve for the year 2001, whose equation, reduced to two decimal places, is: $y = 1.30 + \exp(4.01 - 0.30x)$. Transposing the theoretical number of survivors into logarithmic values (Fig. 5B) produces a regression curve that can be broken down into two sections. From zero to 6 days of age, the regression is quasi-linear, indicating that the decline is exponential, uniform, with the number of survivors on day x being proportional to that on day $x - 1$. Up to 6 days of age, therefore, the rate of loss is constant, indicating that, during this period of the beetle's life, the probability of disappearing on day x ($x = 1$ to 6 days after marking) does not depend on its age (i.e., does not depend on its physiological state or age-related behavior). The equation of this segment of straight line is $y' = 4.01 - 0.28x$ with a R^2 of 0.9998 and its slope -0.28 y/x . Returning to the initial variables, we determine the equation of the associated exponential curve:

$$y = \text{antilog}_e(4.01 - 0.28x)$$

$$y = \exp 4.01 * (\exp -0.28)^x$$

$$y = 55.38 * 0.76^x$$

The value 0.76 is the daily remanence of the number of males, and the corresponding daily decrease is $1 - 0.76 = 0.24$. So, when the known age does not exceed 6 days, the theoretical model predicts that about a quarter of the number of males will disappear each day. During this period, we can also calculate the cohort's half-life: $T = \ln 2 / 0.28$, i.e. ≈ 2.5 days.

From the seventh day of apparent age, the function obviously deviates from a straight line (Fig. 5B), and the 24% of males who exceeded the apparent age of 6 days (Table 1, columns 3 and 4) had theoretically a higher probability of survival than before.

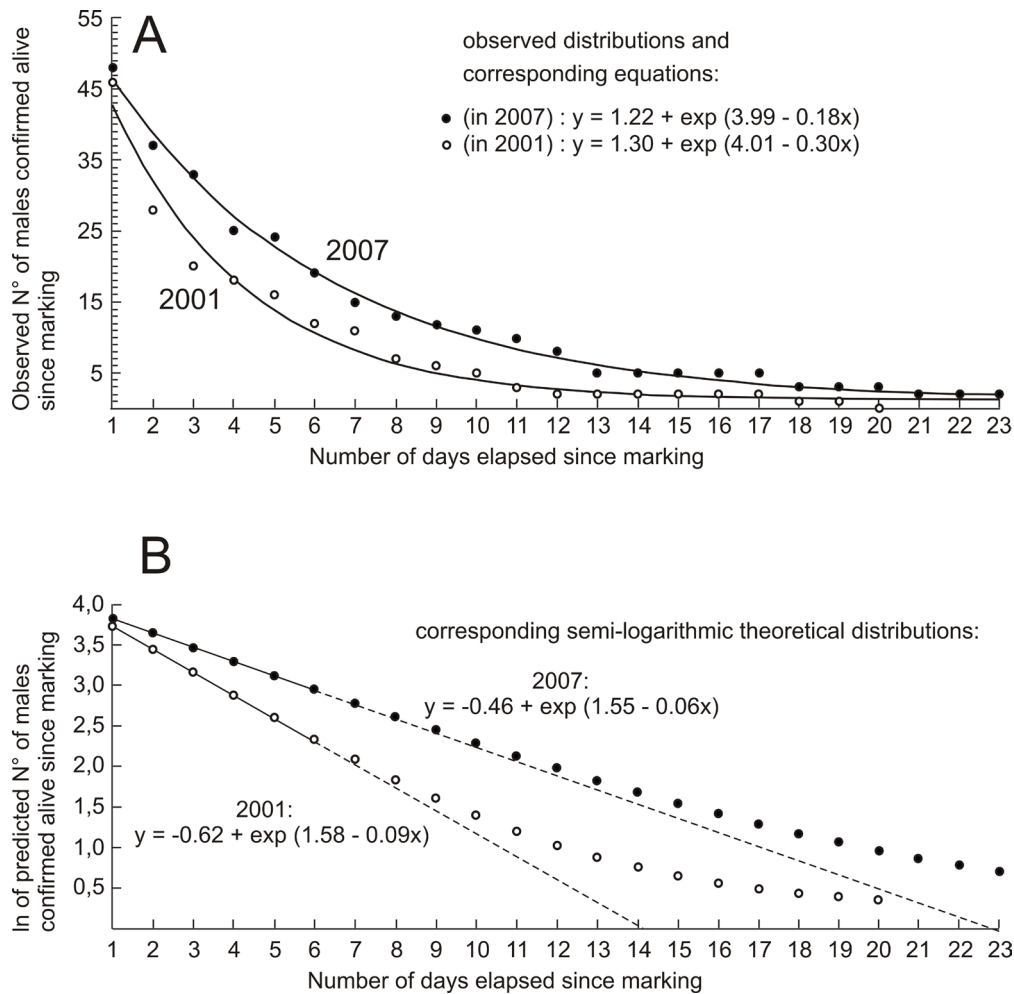


Fig. 5. Distribution of the number of males confirmed to be still alive, as a function of the number of days elapsed since they were marked during the 2001 and 2007 CMR exercises. The construction of the curves is based on the first two columns of Table 1 and is limited to 23 days for the year 2007.

The theoretical regression curve for the year 2007, obtained after transposing the number of survivors into logarithms, has the same appearance as the one of 2001 (Fig. 5B): the decrease is quasi-linear up to the known age of 8 days. The equation of this segment of straight line ($R^2 = 0.9999$) is $y' = 4.00 - 0.17x$, which translates into an associated exponential curve of equation $y = 54.55 * 0.84^x$. The daily remanence of the number of males is 0.84 and therefore, their daily decrease 0.16, i.e., around 16% of the previous daily number. So, in 2007, when the known age did not exceed 8 days, about one-sixth of the number of males disappeared every day. During these first 8 days, the cohort's half-life was theoretically $T = \ln 2 / 0.17$, i.e. around 4 days. As in 2001, and here from the ninth day of life since marking, the 25% of males who exceeded the apparent age of 8 days (Table 1, columns 3 and 4) had theoretically a higher probability of survival than before (Fig. 5B).

This is also reflected in age-specific life expectancy which, although fluctuating, tends to increase when apparent life durations exceed ten days, with some older individuals having a better chance of survival than younger ones (Table 1 last column and Fig. 3).

With a rate of loss of individuals that is partially non-constant over time, and a decrease function that contains an exponential component, the observed longevity frequency distributions appear to correspond to a Weibull curve. The weibullness test (wp.test) confirms this match: $P = 0.55$ in 2001 and 0.48 in 2007. Weibull curve parameters for curve shape (k) and distribution scale (λ) are 0.8397 and 8.5330 for 2001 and 0.8854 and 9.8744 for 2007.

MALE SURVIVAL ANALYSIS

The Kaplan-Meier step curves in Fig. 6A-B represent the daily decrease in the cohort's survival conditional probability. The confidence intervals are wide, due to the high proportion of censored events: of the 46 lifetimes followed in 2001, 83% ended in loss to follow-up, and of the 48 lifetimes in 2007, 73%. Taking into account these numerous cases of censoring, the median survival time since marking was 11 days in 2001 and 17 days in 2007. So, from one day upwards, the probability of achieving a longer duration of life fell below 50%.

Fig. 6C, limited to the apparent age of 20 days, shows that the decay rates of the 2001 and 2007 curves are statistically indistinguishable, as confirmed by statistical tests performed on the full data set: $P = 0.70$ for the log-rank test and $P = 0.80$ for the Gehan-Wilcoxon test, which puts more weight on early differences.

In Fig. 6A-B, the Kaplan-Meier step curves have been superimposed with continuous Weibull survival curves, calculated taking into account the dates of death and censorship. There is a very

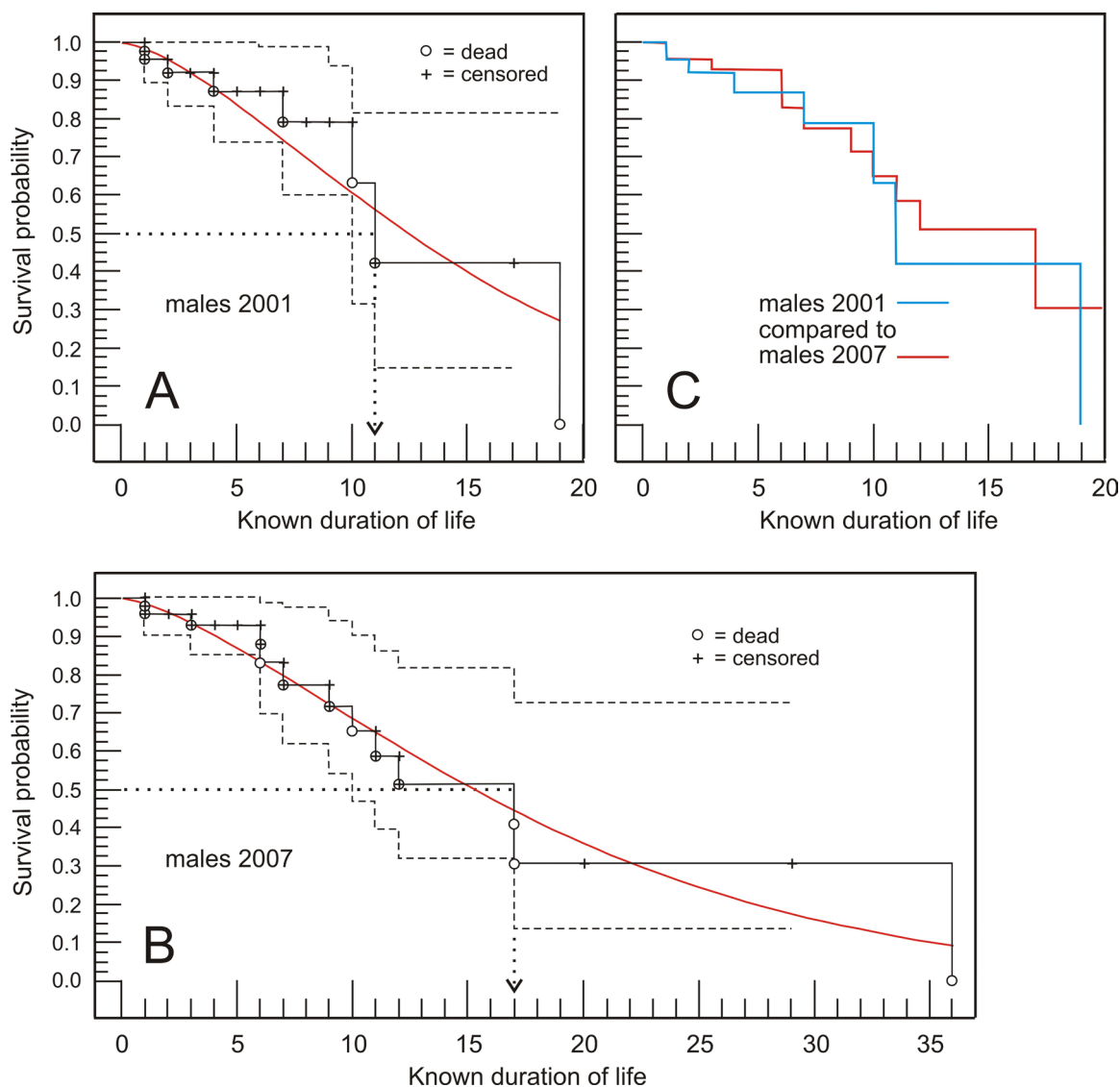


Fig. 6A-B. Survivorship curves of marked male stag beetles during (A) the 2001 and (B) 2007 CMR exercises, in function of death as end event. Kaplan-Meier step-curves with 95% upper and lower confidence bounds. The arrows indicate the medians of the known life span. A Weibull curve is drawn over the K-M curve. C: illustrating the lack of statistical difference between the 2001 and 2007 K-M curves.

good correspondence between the Kaplan-Meyer and Weibull survival probability distributions. These Weibull curves with equation $y = \exp(-(x/\lambda)^k)$ are in perfect agreement with the observed data (wp.test: $P = 0.83$ and $P = 0.75$) and have, for shape (k) and scale (λ) parameters, values of 1,490 and 15,877 in 2001 and 1,433 and 19,651 in 2007 respectively. These Weibull curves show an inflection point at around 9 days of age, indicating that from this known longevity onwards, the probability of survival decreased less rapidly.

FIDELITY TO THE SAMPLING SITE

Only 31 and 28% of males tagged in 2001 and 2007 were recaptured at least once at the tagging site. For females, these proportions were less: only 8% in 2001 and 20% in 2007 (Table 2).

Periods of presence

The 94 males recaptured during the two CMR exercises were only observed on 44% (265) of the evenings out of their total of 600 confirmed life days (life span from the day of tagging to the last known presence of the individual at the site), more precisely on 53% of the evenings (127/238 days) in 2001 and on 38% of the evenings (138/362 days) in 2007. Females were observed on 35% of their total 48 days of confirmed life in 2001 and 23% of their total 177 days of confirmed life in 2007.

Stag beetles do not stay in one place for long. Of the 94 males recaptured, 50 had 54 periods of 2 consecutive evenings of presence, which totaled only 18% of 600 days of confirmed life, 7 males were present for 3 consecutive evenings (3.5% of total days of confirmed life) and 2 males for 4 consecutive days (1.3% of total). No male was observed for more than 4 days in a row. Of the 27 females recaptured, 8 were captured on 2 consecutive days and one on 3 consecutive days.

Periods of absence

A significant part of the life span of the beetles sampled at the Jagersveld site is therefore made up of absences, which can be counted when the known life span is at least 2 days after the day of marking and which duration is very generally higher than the duration of the presences.

In males with a known life span of at least 3 days, absences constitute 56% of the total days in 2001 (111/197 days) and 66% (224/340 days) in 2007. From the first to the last appearance the average is 3.96 days of absence for 3.07 days of presence in 2001 (Wilcoxon test on 28 individuals including 22 active: $P = 0.32$) and 6.05 days of absence for 3.14 days of presence in 2007 ($N = 37$ including 31 active: $P = 0.0008$).

One of the males, marked on 20 June 2007 and present the next day and on 24 June at the CMR site, was found on 25 June some 140 m away, in a garden. On 1 July, it was again found at the site of marking, but freshly killed by a Corvid. The longest consecutive absences of males were 7, 8 and 13 days in 2001 and 15, 15 and 26 days in 2007. Upon returning from the latter absence, 27 days after being marked on 13 June, this male attempted to mate with a female that was marked that day, 10 July.

Females with a known lifetime of at least 3 days were absent from the CMR site for 74% of their known lifetime in 2001 (31/42 days) and for 81% of their known lifetime in 2007 (141/175 days), averaging 6.2 days of absence for 2.2 days of presence in 2001 (Wilcoxon test: $N = 5$ individuals including 4 active: $P = 0.47$) and 9.4 days of absence for 2.3 days of presence in 2007 ($N = 15$; $P = 0.0038$). The longest consecutive absences were 13 and 14 days in 2001 and 17, 19 and 22 days in 2007.

POPULATION SIZE

Observed number of males

In 2001, the observed population was 173 different males in the period from 8 June to 19 July, including 25 beetles that were not used in the CMR analysis, i.e., 16 unmarked males that were found dead, victims of predators and 9 live individuals from an unsuccessful preliminary tagging attempt carried out between June 7 and 20. Of the 148 beetles included in the CMR analysis, 46 (31%) of them were recaptured at least once. During this period, the maximum number of males observed during a single evening was 25 on June 25 (Fig. 3). Thus, during a single evening spent on a small area such as the CMR site, no more than 15% (25/173) of the different males (alive or dead) that were encountered during the entire season were observed!

In 2007, 196 different males were observed in the period from June 2 to July 24, among which 172 were live and marked and 24 dead, unmarked. Of those marked, 48 (28%) were recaptured at least once. The maximum number of males observed in one evening was 22 (20 alive (Fig. 3) and 2 unmarked, found dead on June 19). On this evening of highest stag beetle abundance, only 11% (22/196) of the different males (alive or dead) encountered during the entire season were observed at the site.

Observed number of females

In 2001, the total number of females observed from 11 June to the end of July (and August) was 105 different females, 101 of which were alive and marked, of which only 8 (8%) were recaptured at least once, as well as 4 unmarked females found dead. The highest number of females observed in one evening was 11 individuals on July 2, which represents only 11% (11/105) of the different females (alive or dead) encountered during the season.

In 2007, the number of different females observed from June 6 to end August was 115 individuals, including 94 live and tagged of which 19 (20%) were recaptured at least once as well as 21 untagged females found dead. The maximum number of females observed in one evening was 11 individuals on June 19. During this evening only 10% (11/115) of the different females (alive or dead) encountered during the season were observed.

Daily minimum number of beetles known alive (MNA)

Figs 2 and 7 show that the daily number of males known to be alive never exceeded 28 in 2001 (on 25 June and 3 July) and 26 in 2007 (on 19 June). The number of females never exceeded 11 on July 2, 2001 and 13 on June 19, 2007.

Jolly-Seber assumptions

The assumption of dispersal between evening sampling occasions appears to be fulfilled if we take account of the observed large absence periods between captures and recaptures of the marked individuals (see Fig. 3 and the sections ‘Fidelity to the sampling site’). The use of the goodness-of-fit (GOF) Tests 2 and 3 shows that the assumptions of equal catchability and survival probabilities for marked and unmarked beetles were met, at least when there were sufficient data to be tested (not in a Table). Moreover, by using Leslie’s test it was verified that there was equal catchability between the marked individuals in the marked-recaptured segment of the population.

Choice of a Jolly-Seber model

Males, year 2001: the model $\phi(.) p(.)$ is the most parsimonious, having 17 estimated parameters instead of 32 for the nearest ‘best’ model, $\phi(t) p(.)$, from which it differs by an AICc value of 4.35, what is a good empirical support for a real difference between them (BURNHAM & ANDERSON, 2004). Moreover, the likelihood of the model with constant ϕ and p is 8.82 times greater than that of this nearest model, whose standard errors are, for the most, countless. The models $\phi(.) p(t)$ and $\phi(t) p(t)$ are even more distant, with delta AICc values of 20.84 and 28.35.

Males, year 2007: the model $\phi(.) p(.)$ is, by far, the most parsimonious (20 parameters instead of at least 77 for the other models). Its nearest model, $\phi(.) p(t)$ is considerably distant by a $\Delta AICc = 81.70$ and, moreover, has countless standard errors.

Females, year 2001: the model $\phi(.) p(.)$ is, by far, the most parsimonious (20 parameters). Its nearest model, $\phi(t) p(.)$, has 59 parameters, a $\Delta AICc$ value of 199.45 and moreover has most of its standard errors countless.

Females, year 2007: the model $\phi(.) p(.)$ is the most parsimonious (24 parameters). The nearest model, $\phi(t) p(t)$, has 109 parameters, differs by a $\Delta AICc$ of 56.28 and moreover has countless standard errors. Other models, though with calculable SE's were far more distant.

The here above models with constant survival and capture probability were thus considered as fitting the best to the reality. They need nearly only half, or even less of the number of estimated parameters than models with variable survival or recapture probabilities. Moreover, a model with constant ϕ and p avoids parameter confusion at the start and at the end of the sampling period and produces therefore more robust estimates than those of a full model, $\phi(t) p(t)$.

Results of the $\phi(.) p(.) pent(t)$ model

Table 2 shows that according to a $\phi(.) p(.) pent(t)$ model, the survival probability between samplings (ϕ) is fairly high. The capture probability (p) is satisfactory in males, but it is very low in females and this influences the precision of the estimation of their population size (POLLOCK & ALPIZAR-JARA, 2005, p. 44), especially for the year 2001.

Table 2: CMR results from the $\phi(.) p(.) pent(t)$ models. *: including unmarked beetles found dead on the site. CI: confidence interval. CV: coefficient of variation. ϕ : survival probability between samplings. p : capture probability.

Gender, year	Observed N*	Marked N	Recaptured N (%)	Estimated N	95% CI	CV (%).	ϕ	p	Estimated N / Observed N*
Males, 2001	173*	148	46 (31%)	299	252 - 369	9.9	0.72	0.22	1.73
Males, 2007	196*	172	48 (28%)	378	319 - 460	9.4	0.80	0.15	1.93
Females, 2001	105*	101	8 (8%)	933	507 - 1806	33.8	0.74	0.03	8.89
Females, 2007	115*	94	19 (20%)	368	256 - 556	20.3	0.85	0.06	3.20

As an alternative to observation-based counting (see above, 'Observed number...'), the proportion of male individuals that could be present (even if not observed) on the CMR spot on a daily basis in relation to the estimated total number in the population can be given by the probability of capture, which is constant in the model used. Table 2 shows that this probability was 22% in 2001 and 15% in 2007. The daily proportion of females corresponding to their capture probability was only 3% in 2001 and 6% in 2007 (Table 2).

Table 2 shows also that the estimated total number (Estimated N) of unique males in the super-population present in the area of the sampling site during the whole beetle season was about 300 (250 – 370) individuals in 2001 and ca. 380 (320 – 460) in 2007, with acceptable coefficients of variation (CV). In contrast, the estimates of female population size, i.e., ca. 930 (500 – 1800) in 2001 and 370 (260 – 560) in 2007, are burdened by high coefficients of variation, especially in 2001, which strongly suggests that these estimates are unreliable. This may be explained by the low proportion of recaptured females.

The estimated total number of male beetles equals about twice the number that was really observed (Table 2: Estimated/Observed ratio of N: 73% more individuals estimated than observed in 2001 and 93% more in 2007) and reciprocally, that the observed number equals about half the estimated one. As expected from their high CV, the Estimated/Observed ratio of number of female beetles looks by far, exaggerated.

Fig. 7 shows that the highest daily male estimated abundances in 2001 were reached on June 25 (97 [67-139]), followed by two other peaks, on June 29 (94 [61-143]) and on July 2 (88 [57-136]), but with coefficients of variation (CV) of respectively 19, 22 and 22%. After that, the daily population size gradually tapered off. In 2007, the estimated highest daily male number was reached on June 7 (145 [106-198]), followed on June 8 (115 [83-160]), June 10 (102 [75-140]) and June 13 (104 [77-141]) with CV's of respectively 16, 17, 16 and 15%. These somewhat high variation coefficients account for the level of uncertainty in the daily estimation of \hat{N} .

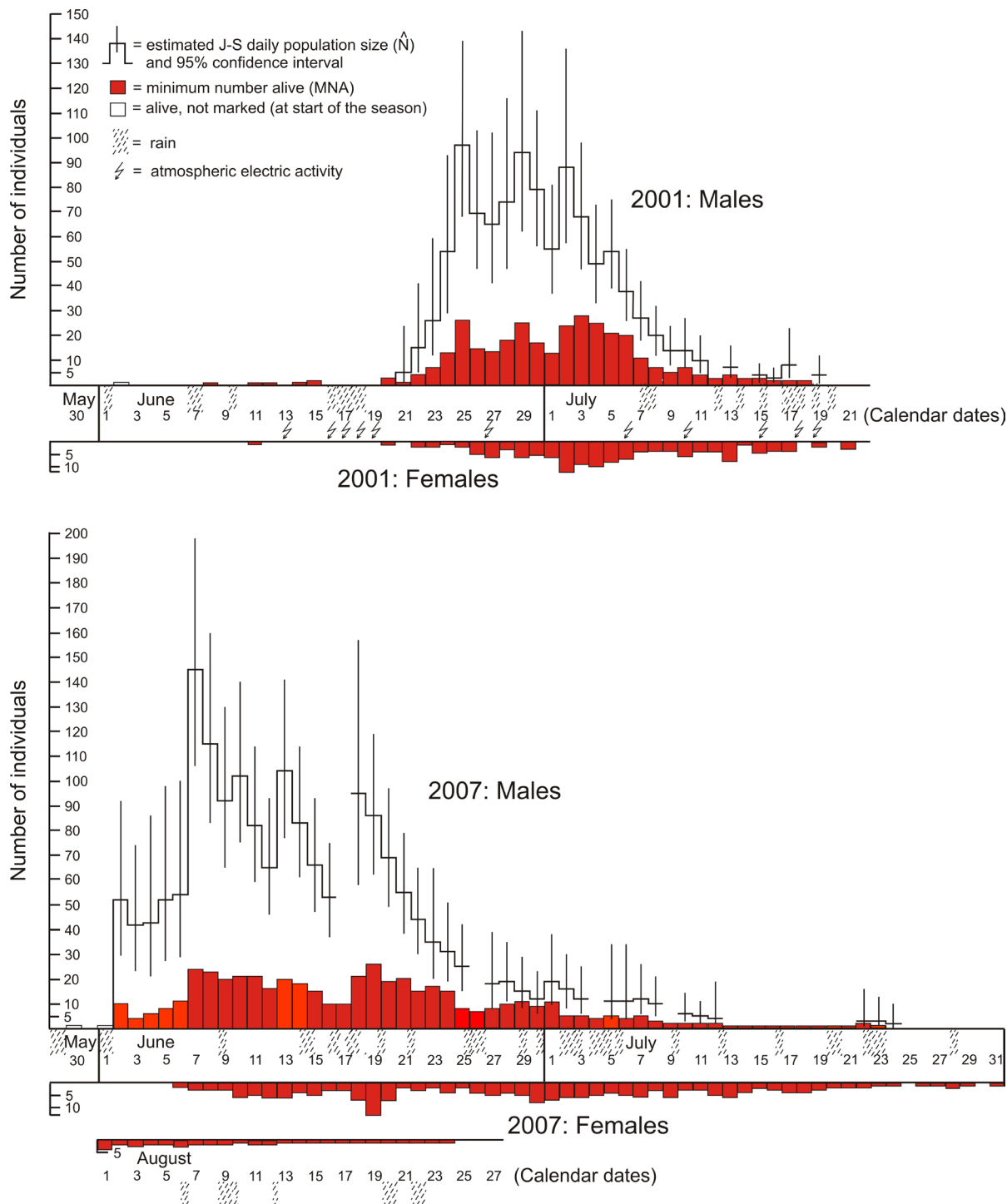


Fig. 7. Daily estimates of the number of beetles at the Jagersveld site in 2001 and 2007 according to the POPAN formulation of the Jolly-Seber method, under the acceptance of constant survival and capture probabilities over time. Minimum daily number of known survivors (MNA). Rainy periods and, for 2001, stormy evening episodes, are figured at the bottom of the graphs.

Table 3: Effect of intercalating one or two days without observation between regular samplings. Besides the result of the daily sampling, the table shows the result that would have been obtained if the surveys had been done every 48 or 72 hours. The models used are phi (.) p (.) pent (t). Legend as in Table 2.

Gender and year	Time lapse between samplings	Number of sampling occasions	Marked N	Recaptured N (%)	Estimated N (95% CI)	CV	phi	p	Estimated N / marked N
Males									
2001	24 h	26	148	46 (31.1%)	299 (252-369)	9.9%	0.72	0.22	2.02
2001	48 h	15	96	11 (11.5%)	281 (195-444)	21.7%	0.70	0.21	2.93
2001	72 h	8	64	6 (9.4%)	230 (118-575)	45.0%	0.71	0.20	3.59
Males									
2007	24 h	42	172	48 (27.9%)	378 (319-460)	9.4%	0.80	0.15	2.20
2007	48 h	22	101	17 (16.8%)	285 (209-416)	18.0%	0.80	0.17	2.82
2007	72 h	14	75	10 (13.3%)	174 (105-399)	37.8%	0.70	0.35	2.32
Females									
2007	24 h	52	94	19 (20.2%)	368 (256-556)	20.3%	0.85	0.06	3.91
2007	48 h	29	52	5 (9.6%)	254 (141-507)	34.5%	0.87	0.07	4.88

Fig. 7 also shows that the male daily estimated numbers of the super-population of stag beetles in the vicinity of the Jagersveld site are much higher than the observed minimum numbers of beetles known alive (MNA) in the samples captured on the site, the lower limit of the 95% confidence intervals not even reaching this minimum.

As an ancillary information, Fig. 7 shows that the electric atmospheric activity (lightning), monitored only during the season 2001, had obviously no influence on the presence of stag beetles.

Daily sampling versus every 2-3 days

A prerequisite of capture-recapture methods is that individuals released during one sampling must mix with other individuals in the population before the next sampling. If sampling takes place every evening (as is usually the case when monitoring a stag beetle population) the individuals should be able to mix with the rest of the population before the next evening i.e., during the day, which is a time of day when they are not very mobile, except before sunrise (Cammaerts, unpublished observations). However, the long absences that can be seen between some of the CMR sampling sessions suggest that stag beetle mobility is not negligible. Nevertheless, allowing a day or two to pass without sampling could theoretically allow for greater mixing in the population.

To test the effect of a time-lapse greater than 24 hours between sampling events, field data were fictitiously reduced to the observations that occurred every 2-3 days (Table 3). The phi (.), p (.) model is the one chosen for comparison because this model is most often the one with zero $\Delta AICc$ and has values of N and CV that appear acceptable.

As is shown in Table 3, intercalating 1 or 2 days without observation between successive and regular samplings has the expected effect of marking and totaling fewer individuals than daily samplings would allow. For an interval between samplings, of 24 h, 48 h or 72 h, 148, 96 and 64 males were or would have been marked in 2001 and 172, 101 and 75 in 2007 respectively. Similarly, there were or would have been proportionally fewer individuals recaptured compared with the number of marked individuals (the percentage of males recaptured was or would have been 31%, 12% and 9% in 2001, and 28%, 17% and 13% in 2007 respectively).

In terms of number of marked individuals there is an obvious disadvantage to spacing the sampling sessions (Table 3). Moreover, intercalating blank days decreased the population size estimate (although in some cases not very much, e.g., for a time lapse of 48 h in 2001) while widening the confidence interval, thus decreasing the relative precision of the estimate (the coefficients of variation increased from about 10% to 22% and 45% for males in 2001 and from about 9% to 18% and 38% in 2007). The ratio estimated N/marked N also varied markedly. In contrast, the overall values of the phi and p probabilities did not differ greatly.

As for the females, the very small number of recaptures does not allow to calculate the estimated number of individuals present with sufficient confidence. In 2001, for an interval of 48 or 72 h between two samplings there were only 2 and 1 recaptured beetles, i.e. 3.6% and 2.6% of the tagged individuals and in 2007, 5 and 1 recaptures, i.e. 9.6% and 2.9% of the tagged individuals). Only the data concerning the females sampled every two days in 2007 allow the calculation of a population size, which is estimated at 254 (141-507) individuals, but with a CV of 34.5% (Table 3).

MORPHOMETRY

Beetle size homogeneity along the season

The total length of males or females measured during the 2007 CMR exercise was normally distributed (Henry's line), with equal variances between weeks or 10-day periods (Bartlett's test, males: $\chi^2 = 3,41$, $df = 3$, $P = 0.33$; females: $\chi^2 = 7,94$, $df = 4$, $P = 0.094$). These lengths were thus compared using parametric ANOVA.

Fig. 8 shows that the size of the beetles did not significantly vary according to the period (week or decade) of their first apparition (ANOVA, males: $F = 0.096$, $df = 3$, overall $P = 0.90$; females: $F = 0.564$, $df = 4$, overall $P = 0.69$); pooling period 4 with periods 5 to 7 for the females did not change this result: $P = 0.59$. No significant difference existed of course between any of the weeks for the males or 10-day periods for the females: Newman-Keuls test: all $P \geq 0.64$).

Variation of beetle size between years

Measured on entire individuals collected over years in the locality of Boitsfort, the head width (KB) was found to be linearly correlated ($P < 0.001$) with total length (TL): $R^2 = 0.954$ on 264 males and 0.900 on 145 females. The head width could thus be used as an indication of the body length (unpublished results).

In contrast to the total length of beetles measured alive during the 2007 season, the yearly head widths of males, measured on the remains abandoned by predators at the same Jagersveld

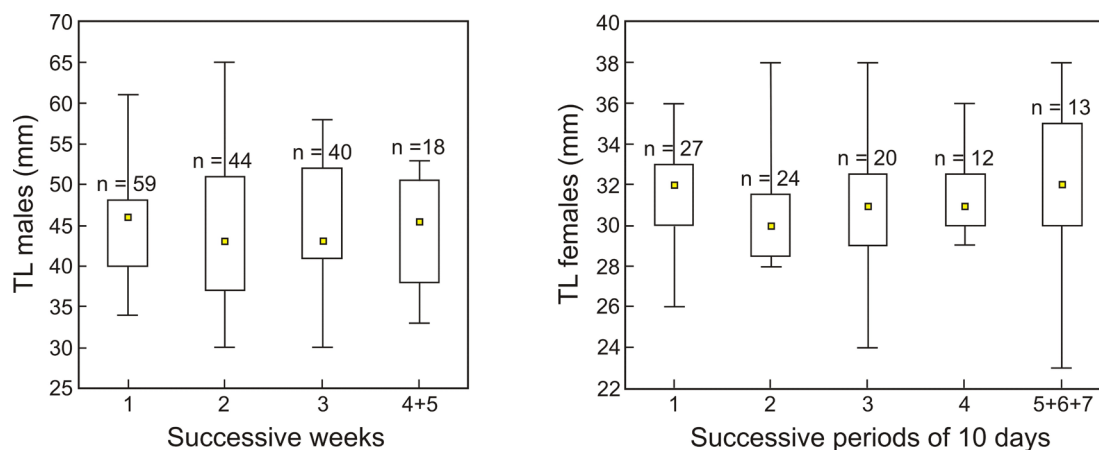


Fig. 8. Box plots of total length (TL) of stag beetles measured in the order of their first appearance at the Jagersveld site during the capture-mark-recapture exercise of 2007. Median, quartiles and extremes of male sizes over successive weeks and of female sizes over successive ten-day periods.

spot, were non-normally distributed (Henry's line), with highly unequal variances (Bartlett's test: $\chi^2 = 69,42$, $df = 19$, $P < 10^{-6}$). The Kruskal-Wallis non-parametric test was thus used, which showed that the head dimension of the males varied significantly between almost all successive years (Fig. 9; K-W overall test: $P < 10^{-4}$).

The dimensions of male stag beetle heads collected at the Jagersveld CMR site from 2002 to 2023 were compared between years as well as with those of whole males collected at two other sites in the same locality of Boitsfort that had dense and long-established populations at the time of their sampling. These populations are those of the artificial site of the old railway station of Boitsfort, sampled in 1924, and of the natural site of the slope of the Trois-Tilleuls street sampled in 1986. The latter (Fig. 1) is at the origin of the population established in the Jagersveld site. The individuals in the 1924 sample were collected alive, but it is not known whether they were selected in the field based on their size, although their size is not significantly different from the individuals in the 1986 sample. The 1924 sample is therefore included in the analysis only as a guide. In contrast, the individuals from the 1986 population were all collected alive and randomly (i.e., indiscriminately) in a single evening and are therefore as comparable as possible to the individuals whose remains were found at Jagersveld. As is inferred from their head width, the size of male individuals from the 1924 (mean: 12.96 mm) and 1986 (mean: 13.11 mm) samples is significantly larger than that of male individuals whose remains were collected from 2002 (mean: 11.65 mm) to 2023 (11.14 mm) at the Jagersveld site (the year 2021, with only 7 heads, was not taken into account) (K-W test for multiple comparisons: already $P = 0.029$ between 1986 and 2002 and $P = 0.00006$ between 1986 and 2003). The sample of the year 2006

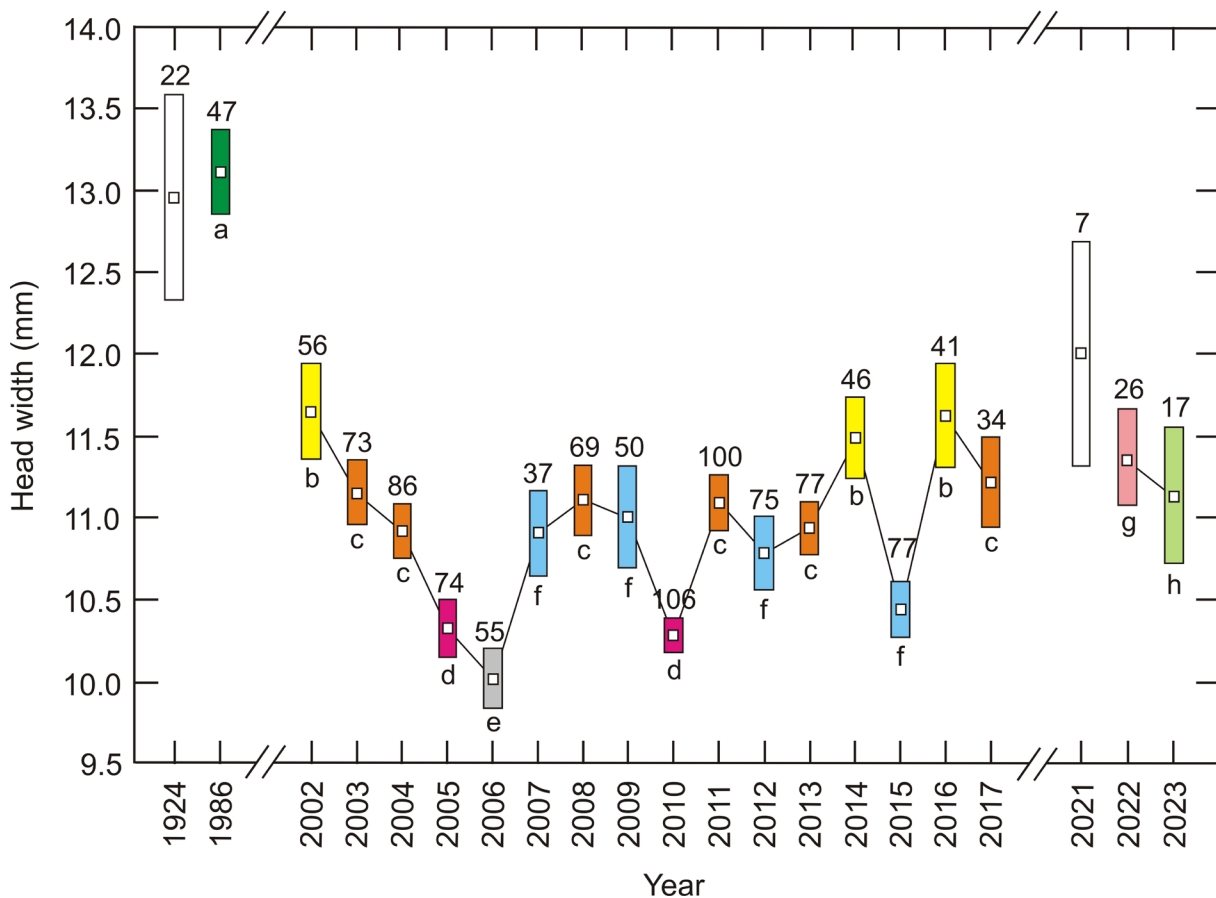


Fig. 9. Variation, as a function of year, of the mean and standard error of head width (KB) of males found dead at the Jagersveld CMR site. Numbers indicate the size of the samples, and letters and colors indicate samples not significantly differing in size from each other at the $P = 0.05$ threshold, by using the non-parametric Kruskal-Wallis test for multiple comparisons. Samples of years 1924 and 2021 were excluded from the K-W analysis.

is the one with the smallest heads: meanly 10.02 mm. Fig. 9 shows these annual variations, the years that do not differ significantly from one another being represented by the same color and letter. There was no significant increase from 2007 to 2023 (Spearman's $R = 0.0844$).

Not surprisingly, the difference in head width (KB) between the males of the year 1986 ($N = 47$) and the remains of predation victims of the year 2007 CMR ($N = 37$) ($P = 0.00014$, from of a K-W test for multiple comparisons) was also reflected in the difference in total length (TL) between the 1986 males ($N = 47$) and those measured alive during the 2007 CMR ($N = 161$) ($P = 0.00007$, Mann-Whitney test).

The yearly head widths of females were fairly normally distributed (Henry's line) with equal variances (Bartlett's test: $\chi^2 = 19.76$, $df = 18$, $P = 0.35$). These lengths were thus compared using parametric ANOVA. Significant differences between the years were only found between 2003 (mean width: 8.27 mm; $N = 36$) and 2006 (mean width: 7.49 mm; $N = 38$; Tukey's test for multiple comparisons: $P = 0.0004$) as well as 2010 (mean width: 7.66; $N = 65$; $P = 0.0057$). These results for females are not shown in a figure.

PREDATION AND YEARLY VARIATION IN POPULATION SIZE

On a total of 1795 beetles that were found dead, 1734 were victims of predators (1197 males and 537 females), while only 61 were found having died from a natural cause (9 males and 52 females, i.e., 3.34%, of the total). These natural deaths, whose annual totals are shown in Fig. 10, were more numerous in females (8,8% of 589 individuals) than in males (0,75 % of 1206 individuals).

The most important predators of the stag beetles were Corvids (carrion crows, *Corvus corone*, and magpies, *Pica pica*). These birds hunt the beetles on the ground during daylight hours, dismembering them with their beak on hard surfaces like the Jagersveld concrete ramp, and eat only the abdomen. The head is usually left on the spot, which facilitates a daily count of the victims. However, in 5.9% and 6.8% of predation cases involving 1,133 males and 499 females (years 2001 to 2017), only the abdomen was removed by Corvids, the beetle's body keeping the two elytra attached to the rest of the body, even though it had been mauled. There are nevertheless exceptions in their way of doing things because one can sometimes find a head of stag beetle in the ledges of houses. In the few cases where the head was not available for counting and there were no other remains left, legs still attached to a prothorax could provide information on the gender of the beetle. Rarely (4 times in 20 years on the CMR spot) have carrion crows left on the ground a regurgitation ball containing stag beetle remains.

Stag beetles found dead during the 2001 and 2007 CMR exercises were recorded as having been alive on the day of their discovery, some time before the evening sampling, although the precise moment of death is unknown. This is because Corvids, their main predators, were only active between dawn (e.g., at 5 a.m. on the solstice) and the early morning arrival of the observer who has come to look for any dead beetles from 7 a.m. onwards, and after that, the parents came to drop off their children in the playground. Due to playtime periods, to children returning home and a to second visit from the observer, predation of the beetles by Corvids mostly had to take place between 6:30 p.m. and the sampling time. As an example, during the 2007 CMR, the number of Corvid victims was 9 males in the morning and 28 in the evening, as well as one female in the morning and 24 in the evening. The recent death of the victims was evidenced by the remaining vitality of their forebody left in place and the absence of necrosis on the exposed tissues.

Corvid predation on the beetles begins as soon as the first cases of emergence, suggesting that these birds memorize this favorable moment from year to year or that they discover the first beetles at random during an active and permanent search for food. However, the majority of females found dead in August were intact, having naturally reached the end of their lives. Of

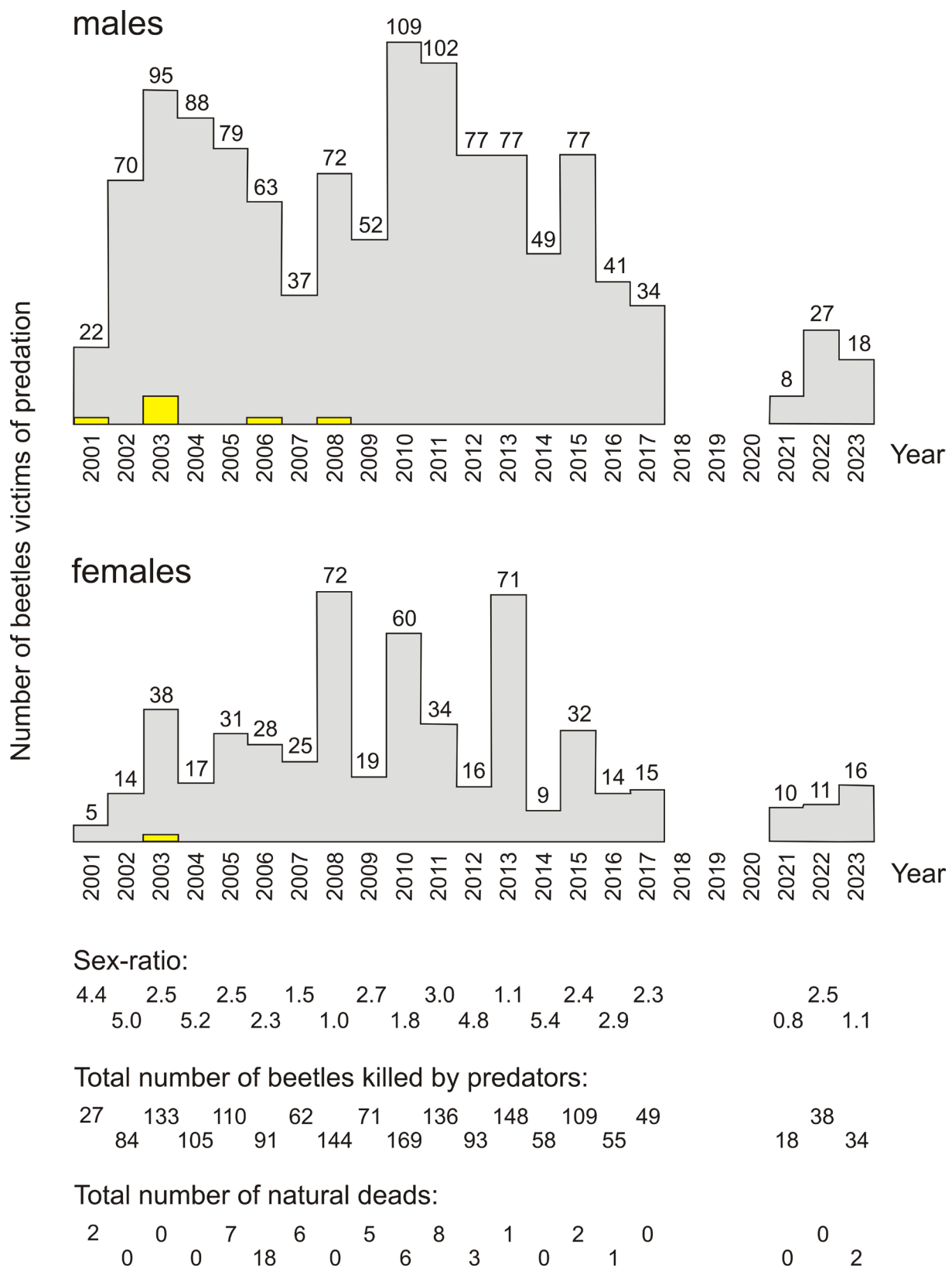


Fig. 10. Yearly number of stag beetles found dead by predation at the Jagersveld CMR site during the period 2001-2023. Areas in grey refer to predation by Corvids, areas in yellow to predation by hedgehogs. The annual sex-ratio measured on these beetle remains is indicated, as is the yearly total number of beetles killed by predators and the total number of natural deaths.

the 61 females found dead during that month, only 10 were victims of Corvids, while 51 died of natural causes. By comparison, prior to August, the proportion was 527 female victims of Corvids (and one of a hedgehog) for a single natural death. At the end of the stag beetle's season, it is clear that Corvids are no longer actively seeking out these insects to feed on, as they become too rare to be encountered and therefore, too costly to hunt.

There were also a few rare cases of hedgehog (*Erinaceus europaeus*) victims, the predator sometimes having betrayed itself by the imprint of its paw on the dusty ground. This insectivore disappeared after 2008. The remains of its victims were characterized by a crushed body punctuated by the small teeth of the mammal. Foxes and cats were not found to have had any impact on the stag beetle population of the Jagersveld CMR site.

Fig. 10 shows that the number of yearly predated individuals is largely variable. As inferred from the male record, it was at highest from 2002 to 2015, what presumably corresponds to the maximum abundance of the beetle population. In this period of highest abundance, the 2001 and 2007 CMR exercise years were characterized by a low number of recorded victims. After 2015, the number of stag beetles affected by predation decreased markedly and is currently at its lowest.

SEX-RATIO (SR)

Assuming that Corvids do not seek out males more than female beetles and that the latter are not cryptic (which they are!), the ratio of male to female prey should allow determination of the sex ratio. However, Fig. 10 shows a high annual variability of this index (from 0.8 to 5.4), which makes it unreliable. The sex ratio was found to be 1 or close to 1 in two of the cases where the number of beetles victims of predators was high (1.0 on 144 individuals in 2008 and 1.1 on 148 in 2013), which seems to accredit the validity of a unitary value. However, a high number of victims does not guarantee a unitary sex ratio: it was 2.5 for 133 individuals in 2003, 1.8 for 169 individuals in 2010 and 3.0 for 136 individuals in 2011. And in 2013, with only 34 individuals it was 1.1. More often than not, the number of females doesn't exceed that of males: on a total of 1734 predated beetles found at the Jagersveld site over 20 years, the SR was 2.23. When 61 natural deaths were added, the SR was 2.05 on a total of 1795 dead beetles.

The sex ratio established on only the beetles tagged during the CMR exercises in 2001 and 2007 was 1.47 (148/101) and 1.83 (172/94). In the latter case, the sex ratio established on the beetle remains found on site was 1.48. Based on all individuals observed (marked, and unmarked victims of predators) these years, the sex ratio was 1.65 in 2001 and 1.70 in 2007.

Discussion

DYNAMICS OF APPEARANCE OF NEW BEETLES

The appearance of newly sighted males was not regular, but began with a short geometric increase (labelled b in Fig. 4), followed by a steadier increase in the number of new individuals. New female individuals appeared at a slower rate and during a longer time (in 2007).

The time lag of about two weeks between the first appearance of males in 2001 and 2007 could be explained by the annual differences in air temperature, and consequently in soil temperature, before the emergence of the beetles, as well as by the difference in rainfall between these two years. Interannual differences in the appearance of the first beetles are the norm; they were also observed during studies conducted in other parts of the same locality of Boitsfort in the years 2000 to 2017 (Cammaerts, unpublished results).

Females appeared one week later than males at the Jagersveld site. In the comparable suburban habitat of Colchester, a lag of about 12 days was observed in 2007 (FREMLIN, 2009; FREMLIN & FREMLIN, 2010). These observations agree with those made more directly on the emergences themselves, in the years 2003-2005 in Rhineland-Palatinate, where females emerged from the ground one week later than males (RINK & SINSCH, 2008).

KNOWN LIFETIME

The known longevity of lucanid beetles was greater in 2007 than in 2001, a year in which the imago population clearly suffered from prolonged drought (on average, in 2007, the males lived ca. 2.5 more days and the females, 3.8 more days). RINK & SINSCH (2011) demonstrated the role of climatic parameters in the live duration of stag beetles in a population of the Moselle valley. The duration of their activity period was reduced in years with higher air temperatures. Their loss of body mass was 3 to 4 times higher in the hot summer of 2003 than in the more temperate summers of 2004 and 2005. At Jagersveld, the active lifespan of the beetles in 2001 only began at the start of the hot, totally dry summer, and was shorter than in 2007, when it began at the end of a warm spring that extended into a temperate, regularly rainy summer. Not only temperate temperatures, but also rain-moistened soils that allow the stag beetles to drink, are factors that prolong the life expectancy of these insects.

In the Italian Piedmont, the apparent average longevity of stag beetles captured and recaptured (only once) using aerial and ground traps was 5.4 days (maximum 14 days) for males and 6 days (maximum 8 days) for females (CHIARI *et al.*, 2014), more or less in line with what was observed in Jagersveld.

Leaving aside the influence of temperature and available water, the survival potential of a stag beetle is considerably greater than the 4 or 7 days known as the average longevity for males during the CMR exercises of 2001 and 2007. For the same Brussels region, MÉLISE (1880) indicates that individuals, both male and female, caught as they emerge from the ground and suitably fed in captivity by means of a brush soaked in a sweet liquid, can live for two or three months if care is taken to prevent mating. JANSSENS (1960) indicates that longevity in captivity can reach nearly 200 days for males and more for females. In the Boitsfort area, we only once saw a female stag beetle feeding on sap oozing from a crevice in the bark of an oak tree. It's clear that the probability of survival is much lower in the wild than in captivity. This is due to the limited opportunities these beetles have to feed in the wild, as well as to the impact of predation.

The known lifetime of the beetles being measured here from marking to permanent disappearance from the CMR study site, the decrease in a cohort of males corresponds to a curve with heterogeneous properties. Up to around 6 (in 2001) or 8 (in 2007) days of known existence, the curve of the surviving males is identified with a decreasing exponential, indicating that their probability of disappearing is not, within these limits, linked to their age, but proportional to a constant daily remanence. After these 6 or 8 days, the remaining 25% of males have a non-constant probability of disappearing over time and slightly higher than before. The decrease of this known and apparent longevity corresponds to a continuous Weibull distribution.

MALE SURVIVAL PROBABILITY

Based on death time as end event, a Kaplan-Meier survival analysis indicates a male median survival probability corresponding to a lifetime of 11 (in 2001) and 17 (in 2007) days after marking. The Kaplan-Meier step curves agree with continuous Weibull distributions.

The first part of these Weibull survival curves corresponds to the constant rate of definitive disappearance from the observer's field of vision shown in the above previous analysis of apparent longevity (i.e., it corresponds to a Pearl type II mortality survivorship curve, shown e.g., in KREBS, 1985). It may be hypothesized that, as stag beetles live on their energy reserves and do not feed, their vitality is not yet reduced at the start of their imago life in the open air, so that in their first few days they are all equally detectable by their predators.

The Weibull male survival curves have an inflection point around 9 days of age, indicating that a slowdown in the decrease in survival probability has occurred after this age. This second part of the survival curve corresponds to the slowdown in the rate of definitive disappearance of the beetles, as is shown in the analysis of apparent longevity, where from around one week

of known age, the number of males no longer decreased exponentially, and their average age-specific life expectancy became greater than before (this corresponds to the tail of a Pearl type III mortality survivorship curve). Pursuing our vitality hypothesis, we can imagine that as these individuals became older and did not feed, they weakened and, being less mobile, became less detectable by their predators. However, their vitality did not necessarily disappear as in the case of this male who attempted to mate on its 27th day of known life (see section ‘Fidelity to the sampling site’, subsection ‘Periods of absence’). Moreover, males known to have been alive for more than 6 or 8 days were no more numerous at the beginning of the season than at the end. Another hypothesis, not involving vitality, is that male beetles that pass the one-week mark in their (apparent) life time may be those that behave in a way that makes them less detectable by their predators.

FIDELITY TO THE SAMPLING SITE

The stag beetles were not very loyal to the location of their observation. The percentage of recaptured different individuals at the Jagersveld site was 28-31% for males and 8-20% for females, which can be compared to the 29% of males and 26% of females recaptured at Colchester in 2007 (FREMLIN, 2008), in an environment quite comparable to that of the garden city of Boitsfort, of which the Jagersveld site is an extension. These percentages are lower than the 36% of males and 42% of females recaptured during a CMR exercise made in Bentley (UK, Suffolk) in 2006, whose higher percentages are explained by the use of traps and by an active search by turning over pieces of wood (HAWES, 2008).

Approximately 30% of the males marked at Jagersveld site were recaptured at least once, and these recaptures occurred on approximately 40-50% of the total of days that the males were confirmed to be still alive. The number of evenings of continuous presence is tenuous, 18% of continuous presence does not exceed 2 days in a row.

Most of the known life span of male stag beetles corresponds to 55 - 65% of time absent from the sampling site, and more (75 - 80%) for females, which for an individual translates into more days of absence than the number of days present at the site. In the study done by CHIARI *et al.* (2014) in the Italian Piedmont, the average duration of absence periods and the maximum duration of an absence are of the order of magnitude of those in the Jagersveld population in 2001.

Where did the stag beetles go during their (apparent) absence from the sample site? Since flight is part of their dispersal strategy, some males may have migrated temporarily to the vicinity of the sample site and then returned, as was the case for one male found 140 m from the marking site to which he later returned. A more extreme case was that of a male that returned after 26 days of uninterrupted absence, which is an argument in favor of the idea that the Jagersveld population is one component of a meta-population in the locality of Boitsfort. One of the females ‘disappeared’ for 22 days before returning to the site. As females have a more cryptic lifestyle than males, it can be assumed that some of them remained hidden in or near the sample site without being seen by the observer. Long periods of absence are not exceptional: in a feeding experiment of (marked) stag beetles in Colchester with maple syrup in 2010, one male was found again after 36 days and one female after 19 days (FREMLIN & HENDRIKS, 2011).

A high number of individuals marked but not recaptured afterwards (69% of the males in 2001 and 72% in 2007, 92% of the females in 2001 and 80% in 2007) left the marking site permanently. This emigration corresponds to the dispersal behavior of the species, mainly for reproduction for the males and the colonization of new spawning sites for the females. For example, in a maple syrup feeding experiment conducted in 2009, a male was found 9 days later at 59 m distance and a female was found 37 days later at 95 m distance (FREMLIN & HENDRIKS, 2011). In a 2007 CMR experiment at the same garden city of Colchester, the maximum distance traveled by a male was 80 m in 2 days and a female 149 m in 3 days, in a straight line (FREMLIN, 2008).

Radio telemetry on a Rhineland-Palatinate population has shown that males can disperse much more, up to a total distance of some 2000 m, with a maximum observed of 1700 m in a single flight. Females, on the other hand, disperse less, at most over some 700 m (RINK & SINSCH, 2007). Another radio telemetry study, of 12 females in a mixed forest habitat with open areas located about 13 km from the Jagersveld site, showed that these beetles disperse up to a distance of about 500 m, with distances covered in one day ranging from less than one meter to 240 m. The most interesting result of this study was the finding of a negative correlation between distance traveled and the nearby presence of dead wood that could be nourishing and a positive correlation between distance traveled and canopy closure, the latter characteristic inducing female flight (THOMAS *et al.*, 2018).

POPULATION SIZE

One of the interesting findings from the daily CMR sessions was that in a single evening of observation at a single location, no more than 15% of the different males and no more than 10% of the different females that were seen alive or dead over the entire season were encountered. Another way of estimating the daily fraction of the population that might be seen in the course of an evening is by means of the capture probability (p) calculated by the probabilistic Jolly-Seber model. The capture or detection probability for males was 22% in 2001 and 15% in 2007. That of females was only 3% in 2001 and 6% in 2007.

On the Jagersveld sampling area that contained a breeding site situated amidst some 61 meters of wood boarding, the number (N) of unique stag beetles of the super-population that were available for capture between the first and last sampling occasions of a season was, on average, estimated to amount to about 300 males in 2001 and 400 males in 2007, with relatively low coefficients of variation. This is roughly twice (respectively by 1,73 and 1,93 times) the number of unique individuals found by the observer, whether marked or found dead.

The maximum number of males estimated to have been present in the superpopulation during a single evening was 90 (67-139) individuals in 2001 and 145 (106-198) in 2007. Needless to say, from the observer's point of view, such high numbers are unlikely to have been present during an evening spent at the precise location of the sampling site.

The lower limit of the estimated daily numbers should correspond to the daily observed minimum numbers of individuals known to be alive (MNA) if all beetles were caught each sampling time (JOLLY & DICKSON, 1983). This was by no means the case and indicates a low catchability, due to the fact that not every individual that returns to the study plot is encountered by the observer and that not every individual that survives to the next sampling occasion returns to the study plot. Even based on a confidence limit of 99.7%, the lowest values of the Jolly-Seber estimators on the days from June 23 to July 9, 2001 and June 2 to 25, 2007 did not reach the MNA value.

Females were less caught than males and their estimated abundance appears exaggerated and not reliable as their variation coefficients is twice to three times that of the males. This may be due to a small number of recaptured individuals (8% and 20%), owed to their cryptic way of life. The excessively large number of unique females estimated to have been present on the Jagersveld site recall the case of an Italian CMR experiment (CHIARI *et al.*, 2014) conducted along a 7 km path in a natural chestnut woodland, where 111 males and 85 females were marked over a season inside 140 aerial and pitfall traps, completed by a visual survey. Only 13% of the males and 8% of the females were recaptured in this experiment and this can explain the high number of males (2207) and of females (747) estimated by the Jolly-Seber method, with corresponding high CV's of respectively 21% and 37%.

Intercalating 1 or 2 days without observation between samplings had the expected effect of marking and thus counting fewer unique individuals during the season than with daily sampling, but also to reduce the proportion of individuals recaptured. The total number of individuals estimated by the Jolly-Seber method was reduced, while the confidence interval was widened, greatly reducing the precision of the estimate. Spacing out the sampling occasions had thus important disadvantages in the case of a demographic evaluation of stag beetles, although the overall survival and capture probabilities did not vary markedly. A daily sampling has of course the highest monitoring cost, but gets a more reliable coefficient of variation.

MORPHOMETRY

While there was no difference in the size of the stag beetles according to their date of appearance in a same season (2007) at the Jagersveld site, the size of the males, as measured by the width of their heads abandoned by predators, varied significantly between years. Male stag beetles at the Jagersveld artificial site are on average smaller than males from another artificial site (made of used oak railroad sleepers) in the same locality sampled in 1924, and also from the natural site of the Trois-Tilleuls street sampled in 1986, the latter from which the Jagersveld population originated.

HARVEY & GANGE (2006, p. 224) showed that males as well as females measurements pooled from 10 localities of South-west England differed in size between the years 2000 and 2004, the body length of both sexes being significantly higher in the year 2004. They hypothesized that size variation is caused by variation in larval food resources. As for the Jagersveld site, it benefits from a fairly homogenous distribution of wood resources, but it is possible that some dryer years have made this food resource less available.

Based on a set of 17 microsatellites, no significant genetic differentiation between years was found between the individuals of 3 stag beetle populations around Brussels, including that of samples of the years 2002, 2005 and 2008 from the Jagersveld population (Cox *et al.*, 2020). A lack of genetic differentiation between successive 5 years was also demonstrated using RADP and ISSR markers in a population of stag beetles from a forest located in Belgorod, Russia (SNEGIN, 2014). This suggests an overlap of annual generations due to uneven development of larval populations (SNEGIN, 2014; COX *et al.*, 2020), the cause of which may lie in differences in larval habitat temperature (THOMAS *et al.*, 2022). Therefore, the annual differences in size of the Jagersveld stag beetles and elsewhere would perhaps be sought in yearly variations of the larval development related to feeding or in temperature and other habitat conditions.

PREDATION AND VARIATION OF YEARLY POPULATION SIZE

The most obvious lesson that can be drawn from the annual record of stag beetle remains left behind by their predators at the Jagersveld site is that the beetle's abundance was maximum in the period before 2016. Inside this period, the lower number of stag beetle remains found in 2001 and 2007 may be explained by the greater human presence during the evenings devoted to CMR exercises, which must have had a deterrent effect on the Corvids. There is however no obvious explanation for the other inter-annual jumps in the number of stag beetle remains.

A decreasing trend of the number of beetle's remains is observed after 2015. The cause could be a decrease in the local stag beetle demography or/and a change in the nature or abundance of their predators. In the Brussels region, carrion crows show an average annual increase in numbers of 2.1% over the period 1992-2020, and are particularly well represented from the Jagersveld to the Trois-Tilleuls site. However, magpies, which are more active foragers than crows, saw their annual numbers fall by an average of 0.7% over the same period (Paquet, 2021), but in the future they may perhaps supplant crows as stag beetle predators since the requirement, made in 2023, to protect fragile bags of household garbage with hard, closed garbage cans.

The majority of the few beetles found dead from natural causes rather than predation were females during the month August, when these beetles became scarce and males had already disappeared. This suggests that Corvids, which are the main predators, stopped searching for stag beetles to feed on when the cost of doing so became too high in relation to the expected benefit.

SEX RATIO (SR)

The reliability of a stag beetle sex ratio established on predation remains must be questioned because this index varies strongly from one year to another on the same site and is dependent on the cryptic behavior of females. It is of course even less reliable if it is established on a small number of individuals.

Even when based on a large number of beetles' remains, the sex ratio does not always tend towards unity. For the total of 1734 victims found at the Jagersveld site in 20 years, it was equal to 2.23, while on the debris of 1255 individuals collected in 5 years in England, it was found to be 0.82 (HARVEY & GANGE, 2006). It was even as high as 18.13 on 306 remains found during a transect carried out on 23 km of tracks in 2008 in the Bosco Fontana forest in Italy (CAMPANARO *et al.*, 2011).

As for establishing a SR on the living community of tagged, thus uniquely identifiable beetles, it is almost systematically above unity: 1.47 out of 249 individuals in 2001 and 1.83 out of 266 individuals in 2007 at the Jagersveld site, as well as 2.63 out of 138 individuals in England, at Bentley in 2006 (HAWES, 2008). At Colchester, it was 2.74 out of 161 individuals in 2007 (FREMLIN, 2008; FREMLIN, 2009), 1.55 out of 84 individuals in 2009, but 1.09 out of 111 individuals in 2010 (FREMLIN & HENDRIKS, 2011). In northern Italy it was found to be 4.44 on 136 individuals (CHIARI *et al.*, 2014).

We should take in mind that the SR could be biased in case that the propensity for emigration differs between males and females, what is likely according to the finding of a higher genetic relatedness between males than between females (COX *et al.*, 2020). HARVEY *et al.* (2011a) proposed another way to measure SR, by trapping with attractive odors such as ginger, alpha copaene, avocado, or mango. Their essay is based on a rather low number of captures (30 males and 20 females, by aerial traps and on the ground by trapdoors, SR = 1.5) and should be confirmed by further trials. An ideal way to measure the stag beetle SR would be to sex the eggs of a clutch (SR at conception) or, in a controlled breeding operation, to sex the stage L3 larvae (cf. FREMLIN & HENDRIKS, 2014; SR at the end of larval growth) or to count males and females as they emerge from the ground (SR at emergence).

AND FINALLY, WHAT DOES THE FUTURE HOLD FOR THE JAGERSVELD POPULATION?

Based on the annual change in the number of predation debris found at the site, the current population of stag beetles is at its lowest level compared to previous samplings. The decrease in the number of live beetles, also evident to the observer, seems to go hand in hand with the slow physical degradation of the site. The degradation of the wood boarding that is the food source for the larvae remains thus the major concern. The Jagersveld population will disappear if the wood siding and adjacent soil that form the habitat for larvae and pupae continue to evolve as they do. There are only two solutions. Either replace the failing beams with new ones, as was partly done in 2005, and maintain the thinning of the adjacent ground surface that is otherwise overgrown or clogged with a dense mat of dead leaves and other debris (see Introduction), experience having taught me that an open ground around the feeding wood is a desired situation for the stag beetles. Or move the habitat by relocating what remains of the wood boarding and their larvae to nearby locations, for example in the form of constructed wood pyramids. In the meantime, a goat willow on the side of the site's ramp was felled in early 2023, leaving a 60 cm-diameter stump that could be colonized by future generations of stag beetles.

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