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Stag beetle (*Lucanus cervus*, (L., 1758), Lucanidae) urban behaviour

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ABSTRACT

This paper describes a capture-mark-release study of stag beetles (*Lucanus cervus*, (L., 1758), Lucanidae) in a small region in an urban habitat, Colchester, UK, in 2007, monitoring behaviour and mortality through the season. Females appeared after the males and were very scarce at first, eliciting strong interest in the males; the first females were found at a new ovipositing site and in an alleyway which acts as a natural trap. Female sightings gradually increased as the season progressed, with a corresponding decrease in interest from the males. Many beetles were recaptured, suggesting that some of them do not go very far. Among established gardens with some trees the stag beetles have been successful over many years.

Keywords: Behaviour, capture-mark-release, mortality, saproxylic, sex ratio, sexual dimorphism

INTRODUCTION

Stag beetles (*Lucanus cervus*, (L., 1758), Lucanidae) are classified as "Nationally Scarce Category B" and in the UK have received protection from sale under Schedule 5, Section 9(5) of the Wildlife and Countryside Act 1981 (Percy et al. 2000). Their range is mostly confined to southern England, especially the Thames valley, north Essex, south Suffolk, south Hampshire and West Sussex. They are also found in the Severn valley and coastal areas of the southwest. Elsewhere in Britain they are extremely rare or even extinct (PTES 2008).

I carried out this study in Colchester (Essex), a town situated to the north-east of their range. Colchester is 90 km north-east of London, and in its borough, and adjoining areas, there is a known stag beetle population even though there is a gap without records between London and Colchester (Bowdrey 1997; Percy et al. 2000; Smith 2003). Clark, a science teacher in at the Colchester Royal Grammar School (CRGS), was the first person to study the south-west area of town, where stag beetles are particularly abundant (Clark 1964, 1965), and later this was followed by Bowdrey who confirmed the hotspot in that part of town (Bowdrey 1997). I happen to live in the area studied by Clark since 1983, where this study is based, and its aim is to describe the behaviour of a population with indications of the reason for its success.

Over the years I have observed that *L. cervus* behaviour during its short emergence season follows a repetitive and predictable pattern, and this is well illustrated in the above mentioned surveys and in others (Sprecher 2001; Hawes 2004a,b; Rink 2006; etc.) and is the following: males emerge first, season peaks mid June, males die before the females. Moreover, in all surveys more males are observed than females; this is probably linked to their strong sexual dimorphism. Male stag beetles are famous for their fights (Mamonov 1991), but, as Arrow has pointed out, "the complete indifference of female beetles to the rivalry of their suitors, of which the evidence is plentiful, should be noted with attention" (Arrow 1951). Here I shall analyse from that point of view their behaviour throughout the 2007 season.

METHODS

The observations in this paper were made between May 18 and August 10 2007 in a small suburban area in south-west Colchester. Most came from monitoring a consistent path daily at dusk, from 21.00 hrs BST (20.00 hrs GMT) from May 12 to July 6, see Figure 1.

The monitored path was chosen in order to cover areas where, over the last 24 years, most stag beetles had been observed. It is mostly paved or covered with tarmac; therefore stag beetles are very easy to spot when monitored on a bicycle.

The behaviour of the beetles was recorded and whenever possible photographed; their flight was intercepted by hand. During 2007 stag beetles were systematically measured, marked and released. Each beetle, when first captured, was measured from the head to the tip of the abdomen, excluding the mandibles; given a coded number which was punctured on its elytra first using a battery operated cautery, AMI AM-21 UltraFyn, Aaron, and then a needle on a dowel because it was easier and more reliable to operate. The coding system used was the same as Mendéz (2008). Recaptured beetles were measured again, their marks checked and released.

RESULTS

Stag beetles are very easy to monitor in an urban area, they stand out on pavements, fences, and house walls. In 2007 there was a total of 384 sightings and the majority, 204 (53%), was in an alleyway, Cambridge Walk (CW) which runs along the back of well established gardens, and acts as a natural trap; that is the beetles in large sections have either to climb up the fences or to fly in order to get out. The most important sightings were in the vicinity of a cluster of five nests, three of which border CW (Figure 1).

Figure 1. Aerial photograph of the monitored area.
Its dimensions are 0.5km x 0.7km, © getmapping.com. The path followed is marked in dots, starting anti-clockwise from **x**. The playground of the school where Clark taught, CRGS, is partially visible at the top. There is a main road, running approximately NE; the others are minor roads. The land in the lower left corner is an allotment site. Cambridge Walk, running NNE, is an alleyway along the back of established gardens. Stag beetle nests are marked with letters: ***a***, ***b***, are in front gardens, ***c*** is in the author's back garden. Both nests ***d*** and ***e*** belong to Christ Church (building with large roofs and a car park), and have open access to the public; the former is right by an unfenced section of the alleyway.

Nests

There are stag beetle nests scattered all over the area, Figure 1, and presently I know of about 16, as the result of random feedback from the residents; however here I shall describe only the ones lying directly on the monitored path; for their photos visit my website (Fremlin 2008a).

Nest *a* is in a front garden in the roots of a holly (*Ilex aquifolium*) tree, felled Nov. 2005, the stump was shredded so that it could be lawned over; nest *b,* also in a front garden, is in birch (*Betula sp.*) tree roots, felled over 10 years ago. Nest *c* is in my back garden against the fence to CW, in two cherry (*Prunus sp.*) tree stumps which were felled in 2002 and 2005. *Dorcus parallelipepidus* and *Cetonia aurata* also nest in this area, the latter is locally abundant in this part of Colchester, the only records north-east of London (EFC 2008). Earlier this year three *L. cervus* larvae were disturbed when the fence next door was being renovated, only one of them escaped. Nest *d* is in the roots of a sycamore (*Acer pseudoplatanus*) tree felled in 2002 which is right by some railings in CW. I have found stag beetle larvae in all nests except nest *b*, however there is plenty of wood with the characteristic larval galleries, and several stag beetle fights have occurred in its vicinity since 2003. After the conference I found emergence holes around another holly stump; nest *e* is between nests *c* and *d*, and the holly tree was cut sometime after 2003.

Capture-mark-recapture study

Many of the sighted beetles were captured and recaptured, some several times, and the results are summarised in Table 1. There capture rate was high, and of the beetles captured and marked, over a quarter were recaptured at least once. The female-to-male ratio was roughly the same throughout.

Table 1. Total sightings, captures and recaptures of stag beetles during 2007. Sightings include all observations. "Captures" are the numbers of beetles which were marked. "Recaptures" are the numbers of marked beetles which were recaptured at least once.

	Males	**Females**	**Female-to-male ratio**
Sightings	270	98	1 : 2.8
Captures	118	43	1 : 2.7
Recaptures (excluding repeats)	34 (29%)	11 (26%)	1 : 3.1

Behavioural observations

The stag beetles' behaviour varied through the season. Figure 2 shows the recorded sightings during the season, with its characteristic peak distribution - compare with Graph 2, PTES 1998 survey (Percy et al. 2000).

I shall divide it into 3 main behavioural phases and analyse the behavioural changes in detail (Table 2). For the beetles' movements visit my website (Fremlin 2008a).

Phase I - Characterized by male sightings only. There were 37 sightings, of which 15 males were captured in 2 places in CW, where 6 stayed around by a fence for a few days, no nest the other side. Maximum distance travelled was 5 meters in 2 days, by a beetle recaptured twice (Table 2). One male hid in a gap of a brick wall, about 130 cm height, for a couple of days. There were 13 sightings of flying males.

Phase II - Marked by the first female sighting which coincides with a period of intense male activity. The males will fight in order to mate because the females are apparently very scarce or uncooperative. As, however, I have observed these spontaneous fights, over the years, only during a short period - late May to early June (n=12, May 27 – June 12) - I am dividing this phase into two parts, Phase IIa, during which fights occur, and Phase IIb, the remaining period during which the males are still seeking their mates very actively.

Phase IIa - Females fly and/or walk towards ovipositing sites; males fly to seek them out, and fights ensue. This was the most active period: 142 sightings. Peak flying activity: 41 sightings of flying males and 4 of stag beetles that I could not identify with certainty, possibly females. Fighting nights were on June 1, 2, 4, 7, 9 & 10, all in the vicinity of the five nests (Figure 1). The first fighting episodes were near nests *d* and *e*, around a female in a crevice in CW. First, she attracted 4 fighting males on June 1; and the next day 9 males even though she was not showing up at that time. The following day she was gone. On June 4, 6 males were fighting in the vicinity of nest *b*, around a

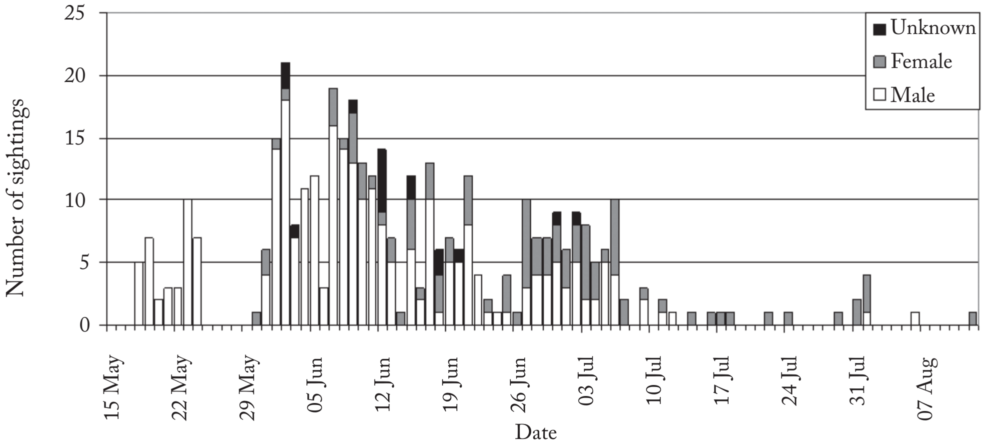

Figure 2. Stag beetle sightings during 2007.
Total sightings 384: 270 males, 98 females and 16 unknown. First male sightings were on May 18. No sightings during the cooler period of May 25 to 29. First female sighting was on May 30. Late June and July were unusually wet; I did no monitoring on the following rainy nights: May 27, June 14, 19 and 24. Phase I - May 18 to 29. Phase II - May 30 to June 21. Phase III - June 22 to August 10.

gap in the base of our house wall. Most certainly a female was there. Two of these males were found later across the road in nest *a*, the one under the lawn and easy to monitor. This area had 4 females which attracted 16 males during 3 nights only, 7 to 9 June; there I observed one mating in the first night, and fighting in all except on July 8. On June 9 there was a male attempting to mate with a freshly trodden on dead female near nest *d*. Later, June 10, in CW on the other side of the fence from nest *c*, I came across a bundle of 8 males fighting for a female that was walking away from them.

Two males in this bundle had first been captured 52 m away in nest *a*, three days before, the longest distance travelled between recaptures during this period (Table 2). Total sightings around the five nests were 68, 56% of the total number of sightings dur-

Table 2. Detailed stag beetle sightings, captures, and recaptures during 2007.
The observation period is divided into five sections. "Sightings in each column are separated into males, females and unknowns. Detailed stag beetle sightings, captures, and recaptures during 2007. Female-to-male ratios are indicated for each phase. "Captures" are the numbers of beetles captured for the first time in each phase. "Recaptures" in this table are the number of occasions on which a previously marked beetle was found again. The maximum distance travelled and the maximum time elapsed between recaptures are in the last two rows. All distances were measured in a straight line between recaptures.
† - the same beetle achieving maximum distance and time between recaptures, ‡ - two beetles recaptured exactly the same way, § - recaptured dead, | - trapped in a crevice.

	Individuals	**Phase I**	**Phase IIa**	**Phase IIb**	**Phase IIIa**	**Phase IIIb**	**Total**
	Date	**May 18-29**	**May 30-June10**	**June 11 - 21**	**June 22-July 6**	**July 7– August 10**	
Sightings	Males	37	122	61	44	6	270
	Females	0	16	22	43	17	98
	Unknown	0	4	10	2	0	16
Female-to-male ratio			1 : 7.7	1 : 2.8	1 : 1.0	1 : 0.4	1 : 2.8
Captures	Males	15	66	26	10	1	118
	Females		7	7	21	8	43
Recaptures (including repeats)	Males	8	16	6	19	4	53
	Females		2	1	7	4	14
Max. distance between recaptures, meters	Males	5†	52‡	80	7.5§	25†§	
	Females		0	149†	28†§	27	
Max. time elapsed between recaptures, days	Males	2†	20	6	13|§	57†§	
	Females		1	3†	4†§	46§	

ing this period. Maximum time elapsed between male recaptures was 20 days, about 10 meters away from the first sighting (Table 2). For some stag beetle photos taken during this phase visit my website (Fremlin 2008a).

Phase IIb - Females fly and walk towards ovipositing sites, possibly. No more fights, but males are still flying quite a lot. There was a total of 93 sightings, the female-to-male ratio is now much higher than in Phase IIa, 1 : 2.8 (Table 2). Flying sightings were 14 males, 4 females, and 5 unknown. One of the 4 flying females, #9, was sighted at 16.44 hrs in our garden, flying very low. Remarkably the only recaptured female, #5, was found in CW, on June 12, 149 m away from nest *a*, after 3 days (Table 2). She was in a section of CW which has brick walls on both sides; most possibly she covered that distance by flying, and was knocked down on her (last) flight, and found herself on the wrong side of a nest. The longest distance travelled by a male was 80 meters along CW to the vicinity of nest *c* (Table 2).

Phase III - Past the peak flying activity, female sightings now on the increase; they are often found walking along, and do not seem to elicit any interest from the males, which are the first to die. Females involved with their nidification.

Here I shall also subdivide this phase according to the way I monitored it. First part intensive monitoring every evening, second part casual monitoring.

Phase IIIa – Some males may stay in the same place; females walk about a lot, even during the day. Flying sightings were nil. On July 6 one male was attempting to mate with a dead female. There was an increasing number of recaptures. In particular in CW, under an overhanging privet bush, some males stayed around for several days, one up to 10 days; another unfortunate male was trapped in the same crevice as the uncooperative female in Phase II, and took 13 days to die (Table 2). The longest distance travelled by a male between recaptures was 7.5 meters, it was found dead under a car one day later. One female was found dead in our road 28 meters away after 4 days (Table 2).

Phase IIIb – Females still walking about probably some have already laid their eggs and will soon die. Flying sightings were nil. Female-to-male ratio now at its highest, 1 : 0.4 (Table 2). It is important to mention that 2 females were recaptured in nest *c*, the one in our garden. Only one of these females, #10, was found alive, first captured in our garden 33 days earlier, Phase IIa, 17 meters away; remarkably then she had already lost her front tarsi. The other female, #9, recaptured dead, was first captured when flying in the afternoon in our garden 46 days earlier (Table 2). Another interesting recapture was male #79 also found dead in our garden. This male was one of the eight beetles fighting in a ball during Phase IIa, 57 days earlier and 25 meters away in CW (Table 2). It was probably killed by the neighbour's cat.

Mortality during 2007

The total number of dead beetles was 80 (21%), female-to-male-ratio 1 : 1. Cause of death varied throughout the season. Up until June 21, the main cause of death was by predators; after, was caused mainly by human activities. For the corpses photo visit my website (Fremlin 2008a).

I analysed this data during Phases II and III under three categories: predator, human, and other causes of death (Figure 3).

Up until June 21 predator deaths were very high, in particular for the males. Beetle remains suggest that a few were probably caught while on the wing.

After June 21, when the flying activity declined sharply, females suffered a higher death rate from humans than the males. During the same period, May 30 till August 12, overall male and female deaths also show a female sex bias, that is, females suffered a higher death rate in relation to sightings (Table 3). Only 15% of the males were found dead in comparison to 36% of the females, but their numbers were the same.

Table 3. Sightings and dead beetles from May 30 till August 12. Undetermined remains, mostly elytra, are indicated by "?". Sightings female-to-male ratio 1 : 2.4. Deaths female-to-male-ratio 1 :1.

Sightings			Deaths		
♂♂	♀♀	?	♂♂	♀♀	?
233	98	16	35 (15%)	35 (36%)	9

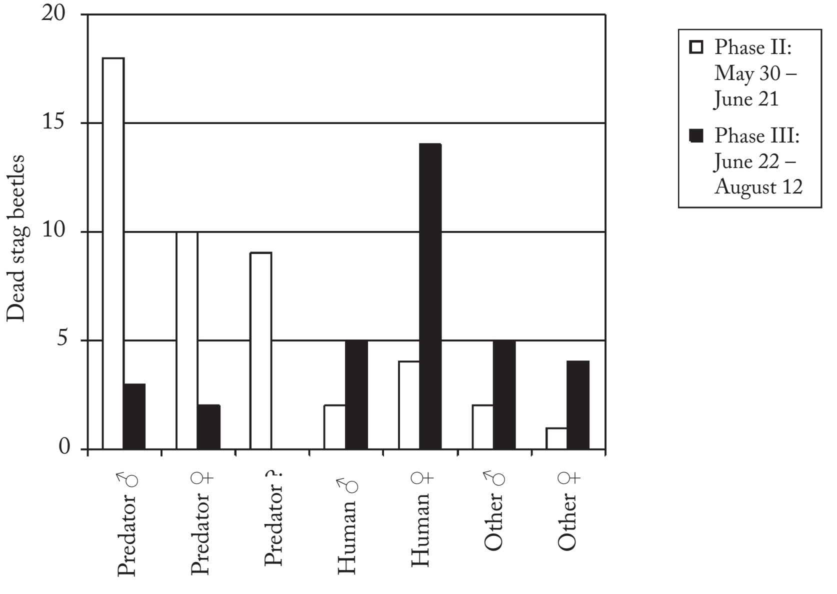

Figure 3. Cause of death during Phases II and III.
"Predator" deaths are easily distinguished by the characteristic body marks left by the predators. Corpses caused by "Human" activities have, at least, a cracked pronotum. "Other" indicates deaths that could not fit either of the other categories. Undetermined remains are indicated by "?".

DISCUSSION

2007 was an exceptionally good year for stag beetles in Colchester; besides it was the culmination of a three year intensive study, when my field skills had improved immensely, hence I carried on monitoring for a much longer period which allowed for a better insight into their behaviour. Coupled with this were the gradual discovery of so many nests in the area and the realisation that all the hotspots were precisely around some of them.

Capture-mark-recapture study

The capture-mark-recapture results allowed me to follow the beetles throughout the season. Many beetles were recaptured, suggesting that some of them do not go very far (Table 2). Moreover these results were also interesting in the sense that there was no sex bias in the percentages of the captured and recaptured beetles, and this probably reflects the consistency of their behaviour (Table 1).

My results compare very well with the study of a *L. cervus* nest in a village 18 Km northeast of Colchester (Hawes 2006), and I have gone into more detail about this elsewhere (Fremlin 2008b). It would be interesting to know if this has also happened in other dispersal studies of sexually dimorphic species, of which I could only find one reference (Beaudoin et al. 2003).

Behavioural observations

Without exception all already mentioned stag beetle surveys, plus the latest one in Bonn (Hachtel et al. 2006), show a repetitive pattern during the season, and a sex bias in favour of the males. And I was able to confirm both results even though I monitored them in a completely different way. My results also compare very well with an identical urban study in the city of Basel, Switzerland (Sprecher 2001).

In this study I have divided the season into several more or less distinct behavioural phases: Phase I, male emergence, Phase IIa, female emergence followed by fierce mating competitions, Phase IIb, no more fights, but still very high flying activity, some females seeking ovipositing sites, Phase III, past the peak season, strong decline in the flying activity, females walking/flying to nests and laying their eggs; males die before the females.

Moreover, it is the females that seem to determine the males' behaviour; for example, in a short time one female attracted 75 males (Cornelius 1868). This happens in particular, soon after emergence, during Phase IIa, they make themselves extremely scarce, very low female-to-male ratio. Paradoxically this is the most critical period after their emergence from such a long time in the soil; all the males want is to mate, but not so the females. The males were going from nest to nest, following and fighting for the females available; thus maximizing their mating chances. Males can detect females up to 60 yards (Harvey 2008), and the distance between recaptures of the 2 males during Phase IIa, 52 m, is within this range (Table 2).

Fights in the wild are almost always reported around one female, which can attract a considerable number of males (Manomov 1991, Klausnitzer 1995, Fremlin 2007). All the fights that I have observed have been during Phase IIa, and remarkably some of them have been around females in crevices. This a very interesting female behaviour observed twice during 2007 albeit only for a very short period. However in 2005 one female stayed in a crevice also in CW for 3 weeks, May 28 – June 18, during which time she attracted not just a lot of frustrated male visitors, but other females turned up as well, and one of which stayed for just a few days (Fremlin 2005). These females covered themselves up with soil during the day, and at night just perched up sometimes with the abdomen up. Other fights have been in the vicinity of nests some of them very recently colonized, or on the point of been so. For instance, in 2005 I have observed some fighting, June 12, around two *Laburnum* stumps which had been cut the previous year, two females and ten males were sighted. Another example is nest *a,* which is in a tree cut late 2005, no emergence holes yet, but during 2007 and 2008, a few females there, during Phase IIa, have attracted the attention of many males for a few days only. Rink has observed exactly the same behaviour around nests in a forest setting (Rink and Sinsch 2007). This contrasts with male behaviour in captivity in which males are very restless, persistent, and fight readily until the end of the season (Harvey 2007, Radnai 1995, Paul Hendriks personal communication, and personal observations). I have not observed this in the wild.

After peak season, Phase III, healthy females do not seem to elicit any male interest. Exceptionally *L. cervus* males show interest in injured or freshly killed females (Bowdrey 1997), right till the end of the season; during 2007 there were two cases, June 9 and July 6, and the latest in the season that I have observed was on July 21 2004. This is now well understood: the females when dead, or injured, sometimes lose the ability to regulate their pheromone release (Harvey 2007).

According to radio-telemetric studies of this species the colonisation of new sites depends on the dispersal ability of the females and amounts to less than one 1 km per generation (Rink and Sinsch 2007). The recapture of one female from nest *a* 149 m away, within 3 days between observations, supports that hypothesis; the females first go to other ovipositing sites, where the males seek them out, and they mate; then they go somewhere else mostly by on-ground movements (Rink and Sinsch 2007). During Rink's telemetric studies most females flew only once, soon after emergence (Rink and Sinsch 2007). However the recapture of the above female possibly indicates that first she flew to nest *a*, and then flew off again, Phase IIb (Table 2). Also during that period there were 4 sightings of flying females including female #9 who was flying in our garden in the afternoon. My other observations of females flying during the day include a female who in the previous year hit our French window, June 7, 9:40 hrs; and sometime ago a blackbird (*Turdus merula*) intercepted a flying female, early afternoon, also in our garden. Coincidentally Harvey in a 3-year study caught substantial numbers of females in hanging traps (Harvey 2007). All this seems to support the hypothesis that females may fly a good deal, even during the day, but as they are less conspicuous than the males they are easily overlooked. Perhaps females encumbered with transmitters are inhibited to fly and prefer on-ground movements only? Indeed in the first telemetric study none of them flew, but they were only two (Sprecher and Durrer 2001). No doubt further telemetric studies, with much bigger samples, will bring more light into this aspect of the female's behaviour.

Did the females recaptured by nest *c* manage to oviposit? The earlier flying one, #9, probably not as her front tibia teeth were still very sharp. However the other female, #10, the one missing her front tarsi, probably did has she had well worn front tibia teeth, an encouraging albeit indirect sign of nidification activity (Arrow 1951). Quite possibly when the females dig they bend back their front tarsi, which would have been useless in the situation; and I have seen them doing that in several occasions. Some dung beetles, Scarabaeinae, have no anterior tarsi at all (Arrow 1951).

Mortality

The variation of their cause of death during the season was an interesting result. First, beetles were killed mostly by predators during their most active flying period; then the females suffered most casualties caused by human activities as they walk much more than the males (Hawes 2004a). And this reflected their varying behaviour during the season, perhaps emphasised by the fact that it was wetter than average, in particular from mid June (Tijou 2008). In order to confirm this result this year in Colchester, students of a nearby secondary school have been doing their own survey, organized by their science teacher. It would also be interesting to analyse the mortality of past surveys before and after June 21 as they would have a much bigger sample than the present one.

The 21% mortality result for 2007 was the highest during the three year study; this was probably the result of improved field skills during a good year. A comparative analysis with other surveys shows that the percentage of live beetles, 94%, 89%, and 79% found in Colchester during 2005-7, agrees with results in Bentley, Suffolk, 1989-1997, 75%, and in the national surveys by PTES, 65% and 91%. However the Road Casualties National Surveys, 33% and 30%, and the Richmond Park, London, surveys, have a significantly lower rate of live beetles, 8% and 7% (Figure 4). The high mortality rate found in the road surveys is a phenomenon strongly linked to the female's behaviour, and again it would be interesting to analyse the data before and after the peak of the season, as females walk much more during Phase III, after the peak.

However the Richmond Park results are very interesting. For the first time an open park was seriously monitored and it proved a very time-consuming and somewhat unrewarding experience because each sighting took 7-24 observer hours. Most sightings, 293 and 235 respectively, were of dead beetles, mostly predated by Corvidae, which are very abundant in the park. This doesn't seem to be a problem in the monitored area, but in Lexden, an adjacent area with larger gardens, many corpses turn up in some of them,

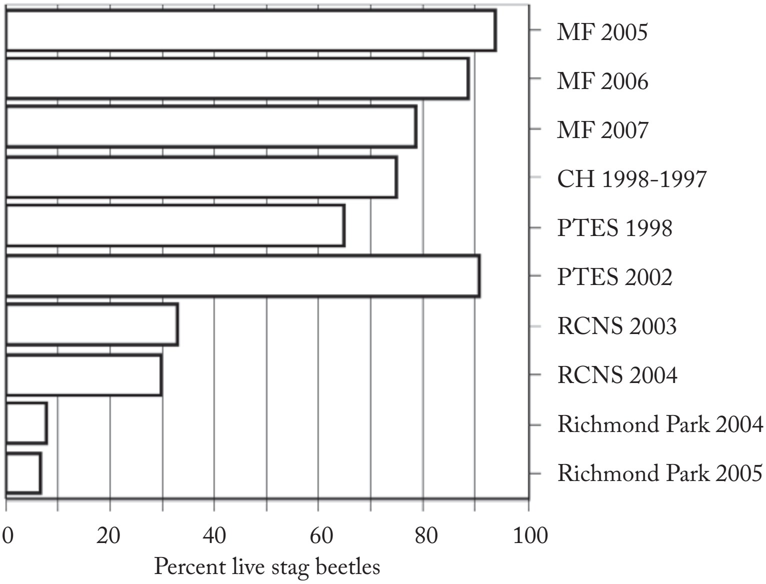

Figure 4. Percentage of live stag beetles found in various surveys in the UK. MF 2005-7 – Maria Fremlin, Colchester, Essex; CH 1998-1997 - Colin Hawes, Bentley, Suffolk (Hawes 2004a,b); PTES 1998, 2002 - People's Trust for Endangered Species National Surveys (Percy et al. 2000; Smith 2003); RCNS 2003-4 - Road Casualties National Surveys (Hawes 2004a); and Richmond Park 2004-5, London (Hatto 2004, 2005).

killed mostly by magpies *Pica pica*, unfortunately at the very beginning of the season (Bowdrey 1997, personal observations), which seems to pose a serious threat to the species.

Habitat

The results of the first PTES survey showed that 70% of the records came from gardens, urban and rural, a somewhat surprising result; see the preface by Gange (Percy et al. 2000).

However the importance of large and relatively old, suburban gardens (pre-1914) as a significant habitat for stag beetles had already been highlighted during the 1997 south London survey (Frith 1999). South London has been subsequently surveyed in 2005 and again the majority of stag beetle sightings were from private gardens; the borough with the highest number of records was Bromley (Margot 2005). In this borough domestic gardens take up about 28% of the land (GLUD 2007). In the monitored part of Colchester, Christ Church ward, domestic gardens take up around 29% of the land (GLUD 2007) and some of them, including ours, are 100 years old or more. Here, and presumably elsewhere, some people are managing their gardens in a very dynamic way which seems to suit this species; this agrees with the suggestion that *L. cervus* populations in Britain result largely from the interactions of humans and trees over time (Whitehead

2007). Perhaps this interaction is partly due to the fact that in this country people change houses quite often; in recent years about 6% of owner-occupied houses in England have been changing hands each year (GLUD 2006-07). For example, the holly tree in nest *a*'s garden was cut for aesthetic reasons soon after the new owners moved in. But this can also pose great dangers for the conservation of this species. Their obvious main threat is loss of habitat due to urban development, closely flowed by habitat disturbance, and this is a very complex situation that deserves to be studied further.

CONCLUSION

With this study I was able to understand better how a saproxylic species has adapted so well to an urban habitat. South-west Colchester has had a very successful urban stag beetle colony over the last 40 years; this is mostly due to the fact that people seem to be always felling trees, and planting new ones, and the females are remarkably quick to colonize them. The males are determined to find and mate with them wherever they happen to be: in the vicinity of nests, alleyways, or even crevices. Many of the beetles do not seem to go very far; felled trees in established gardens provide them with ideal stepping stones less than 100 meters apart. Their behaviour explains the remarkable success of this saproxylic species in not just this urban area, but through their range as well.

Unplanned dynamic management seems to be the ecological solution in urban areas. Therefore the conservation advice for *L. cervus* would be to cut trees for the present generation of beetles and to plant trees for the next generation of cutters. Actively planting new tree/s wherever possible could be added to already existing leaflets (PTES), websites, etc. Constant publicity about the conservation needs of this charismatic species is essential for its urban survival, particularly during its long and vulnerable larval stage. This publicity could be targeted at not just home holders but at all other people involved with housing, for example, gardeners, tree surgeons, builders, and garden centres.

Stag beetles – all they need is love and wood.

Further questions

1. What is the evolutionary advantage to the females of being so inaccessible at the beginning of the season? Is this precisely what made the males evolve bigger and bigger mandibles? Or have the males evolved bigger and bigger armature in tandem with the females getting more and more difficult to court (Emlen and Nijhout 2000)? Only species with exaggerated sexual dimorphism fight for their females (Arrow 1951). For instance, I have not observed this behaviour in *D. parallelepipedus*, the other Lucanidea species present in the area, which is much more nocturnal than *L. cervus*.

2. Which volatiles attract the females to freshly cut stumps? Which volatiles attract the females to ageing trees, where sometimes larvae are found? It has been conclusively proved that they have very well developed sense of smell (Harvey 2007).
3. Did the females seen walking in the alleyway after peak season manage to get to oviposit or not? If not, have they still enough strength to crawl or fly to nests the other side of brick walls?

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