Weather-dependence of *Lucanus cervus* L. (Coleoptera: Scarabaeoidea: Lucanidae) activity in a Colchester urban area

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Abstract

In order to determine the effect of weather conditions on the behaviour of *Lucanus cervus* its seasonal activity was monitored during the three years 2005-2007, always at the same time during the evening crepuscular period, in a small urban area, Colchester, UK, with 204, 159 and 306 sightings respectively recorded.

The onset of activity varied from 15.v to 1.vi; it was, in each case, after a rise in temperature on a dry day preceded by light rains. On average the males came before the females and flew much more.

The inter-relationships between activity and four climatic variables, temperature, humidity, wind and atmospheric pressure were examined. The males become markedly more active at temperatures above 13ºC, preferring less humid conditions and light winds and relatively high pressure, 1015-1025 mb. Males were not seen to fly at temperatures below 12ºC.

Females did not seem to respond much to the weather.

Key words. Atmospheric pressure, humidity, temperature, wind, behaviour, emergence, female-to-male ratio, flight, phenology, saproxylic, stag beetle, urban habitat.

Introduction

Stag Beetle *Lucanus cervus* in England is currently classified as "Nationally Scarce Category B" and is mostly found in urban and semi-urban habitats (Percy *et al.* 2000, Smith 2003); Colchester is a well-known hotspot (Clark 1964, 1965; Bowdrey 1997). These saproxylic beetles emerge in late spring and become markedly more active in the evenings when they come out of their hiding places and seek their mates above ground. The males of this markedly sexually-dimorphic species will fight for the females and mate in open habitats (Klausnitzer & Sprecher-Uebersax 2008, Mamonov 1991), including streets (Fremlin 2003, 2009b).

They are active only for a relatively short period during which they may feed but in the UK they have been very rarely observed to do so (Percy *et al.* 2000, Smith 2003). The females are the last to die after ovipositing in the proximity of suitable decaying wood (Harvey & Gange 2003).

The date of their emergence is variable; a hot year seems to bring about both an early shift of their emergence and of their peak activity (Moretti & Sprecher-Uebersax 2004a,b); cold years have the opposite effect (Hawes 1998). It has been suggested that their emergence might be triggered by a breach of some meteorological threshold (Tullett 1998).

During a national survey in 1998 in the UK over 9,000 sightings were reported between May and October, peaking in June, which had an average temperature of around 16ºC. It was found that they prefer to fly on warm, calm evenings at daytime temperatures of 23 to 25ºC. Males came first and were seen in flight more frequently than the females (Percy *et al.* 2000, Graph 3).

The phenology of *L. cervus* was first investigated in detail in the Basel region, Switzerland (Sprecher-Uebersax & Durrer 1998, Sprecher-Uebersax 2001). For ten years the beetles were monitored and their sightings analyzed for the influence of temperature, humidity, wind and phases of the moon. It was found that their season followed a predictable pattern, with the females being sighted about two weeks after the males; male flight activity occurred at median daily temperatures of 16ºC and higher, and there was a suggestion that the beetles liked warm low humidity conditions, but there seemed to be no clear linear relationship between the four weather parameters and the number of beetles observed.

In a village in Bentley, Suffolk, UK (Hawes 2008), it was found that there was little activity at evening temperatures of 15ºC, or less, and flights were usually at temperatures of 16ºC and higher. In a study around two villages in the Moselle valley, northern Rhineland-Palatinate, Germany, beetles were seen flying at temperatures down to 11ºC (Rink 2006, Rink & Sinsch 2007). Rink also studied the stag beetles' emergence directly from the ground, and found that the males emerged earlier (as Sprecher-Uebersax and others had noted) and that females did not seem to respond to the weather in the same way as the males (Rink 2006, Rink & Sinsch 2008).

Adopting an approach modeled on that of Sprecher-Uebersax (2001), the present study investigates the effect of weather conditions (temperature, humidity, wind and atmospheric pressure) on the seasonal behaviour of *Lucanus cervus* in an urban area in Colchester over a three-year period, with particular emphasis on differences between males and females.

Methods

During 3 consecutive years (2005-2007) stag beetles were monitored in a small suburban area in south-west Colchester, Essex, UK, daily at dusk, from 20.00 to 21.00 hrs Greenwich Mean Time (GMT) (21.00 to 22.00 hrs British Summer Time) from mid-May to early July (Figure 1).

In the monitored area, Christ Church ward, the population density is about 30 people/ha (ONS, 2001) and gardens take up about 29% of the land area (GLUD 2007). The soil is a quick-draining light loam underlain by sand and gravel; the area has one of the lowest rainfalls in the country, 600 mm on average (Tijou 2009). Most properties have large gardens to the rear and small ones facing the road; the back gardens are generally well established, some being 100 years old or more, and often with trees (Figure 1). The breeding grounds in this area are described on Table 1 and elsewhere (Fremlin 2009a,b).

The period was chosen to include the period of maximum activity, and to approximately match the period covered by Sprecher-Uebersax (2001), 21.v-10.vii. The hour was chosen as one in which beetles of both sexes were regularly active; note that it was earlier than the hour covered in Sprecher-Uebersax (2001). All sightings were made and recorded by a single observer (M.F.) who beat the path on a bicycle, alighting when necessary. Beetles were captured, measured, marked, and released and flight was intercepted by hand when possible.

All weather data presented here are taken from an amateur station about 2.3 km NNE of the monitored area, (TL997252, 28 m elevation) (Tijou 2009). In 2006 a LaCrosse wireless weather station WS2300 was installed in the authors' garden (TL986244, 30-35 m elevation). This has furnished data that are generally consistent with those from the Tijou station.

The figures for air temperature, pressure, humidity and wind used in the analysis are averages over the hour during which the monitoring took place, 20.00-21.00 hrs GMT.

Figure 1. Aerial photograph of the monitored area, 0.5km x 0.7km, © getmapping.com. The path followed is the solid line, starting anti-clockwise from **x;** during 2006-2007 it was slightly longer, dotted lines. There is a main road, running approximately NE-SW; the others are minor roads. The land in the lower left corner is an allotment site. Cambridge Walk, running NNE-SSW, is a paved alleyway (with no motor vehicle traffic) between the backs of established gardens, mostly separated from them by fences or walls up to 2 meters in height. Hotspots and nests are labelled ***a*** **–*e***; ***b*** and ***c*** are in Ireton Road, the others border the alleyway (Table 1).

Table 1. Description of the breeding grounds in the monitored area.

	Stumps	Date felled	Location	Years of particular activity
Hotspot ***a***	Horse Chestnut *Aesculus hippocastanum*	2003	Garden on the other side of a brick wall, Cambridge Walk	2005
	Field Maple *Acer campestre*	May 2004		
Hotspot ***b***	Two Common Laburnums *Laburnum anagyroides*	2004	Front garden, Ireton Rd	2005
Nest ***c***	Holly *Ilex aquifolium*	Nov 2005	Front garden, Ireton Rd	2007
Nest ***d***	Two Cherries *Prunus avium*	2002 & 2005	Back garden, Cambridge Walk	2007
Nest ***e***	Sycamore *Acer pseudoplatanus*	2002	Christ Church garden, unfenced, Cambridge Walk	2007
Nest ***f***	Holly *Ilex aquifolium*	2003 or possibly later	Christ Church, garden by footpath	2007

Results

"Emergence" has not been studied in the strict sense of emergence from the ground. However, data have been collected on weather variables for the date of the first sighting, D, and the three preceding days in each year, Table 2. Note the jump in temperature in 2005 and 2006; in both years there was a generally rising pressure. Also in all years the first sighting was on a dry day preceded by light rains.

Table 2. Atmospheric temperature, pressure and relative humidity preceding first appearance. Here as elsewhere they are the average over the hour in which the monitoring took place, 20.00-21.00 hrs GMT. The rain is the daily total (Tijou 2009). D-1 to D-3 are the days preceding D day, the first day in which beetles were sighted.

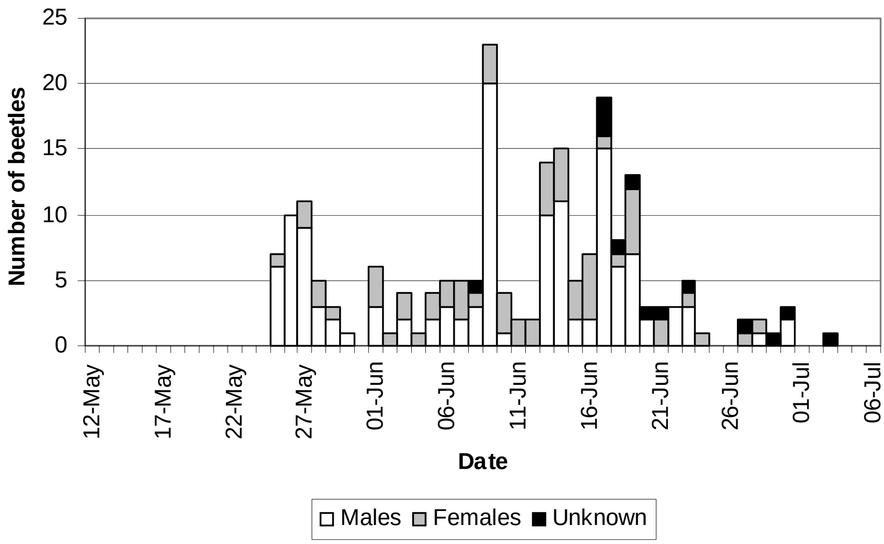
	T ºC	**P mb**	**Rain mm**	**T ºC**	**P mb**	**Rain mm**	**T ºC**	**P mb**	**Rain mm**
D-3	12.3	1003	0.3	8.5	1017	0.3	11.9	1009	2.7
D-2	12.2	1013	0.0	8.1	1020	2.0	11.1	1011	3.7
D-1	13.7	1014	0.3	7.6	1026	0.3	13.1	1016	2.4
D	17.0	1015	0.0	13.7	1028	0.0	13.2	1008	0.0
1st sighting	**25.v.2005**			**1.vi.2006**			**18.v.2007**		

Sightings

Here a digest of our observations is given; for the full set of data on which this paper is based see Fremlin 2009c. Most beetles were found on the roadway or footpaths or on walls and fences; more than half the sightings (56%) were made in the alleyway, Cambridge Walk (Figure 1).

Shown in Figure 2 are the results for 2005. Stag beetles were first sighted on 25.v, when they came out in numbers; it was the first warm day after a relatively long cold period (Table 2).

Figure 2. Daily Stag Beetle sightings for 2005, total 204. Female-to-male ratio 1 : 2.2. Flying sightings: 63 males, 6 females and 12 unknown.



Our first sightings were of 1 pair mating plus 5 males, in the alleyway, and until 14.vi intensive courtship behaviour took place there around one female in a crevice, first sighted on 28.v (Fremlin 2005), a total of seven mating observations, including one on a very cold evening, 9.8ºC, 7.vi (Figure 1, Table 1, hotspot ***a***). At the same time there were other very competitive mating displays nearby (on a fence and a house wall) on 9 and 13.vi (Table 1, hotspot ***b***). There was a mass flight on 17.vi starting at around 20.43 hrs GMT, with 18 flying individuals counted (certainly an under-estimate). 19.vi was the hottest evening, 23.3ºC, of the season; 4 females were seen flying and the stationary female had left. Soon after that there was a general decline in the males' activity. In total, until 6.vii, there were 204 sightings of which 6.4% were of dead beetles.

Males and females appeared more or less together (Figure 3).

In 2006 (Figure 4) the first stag beetle sighting was of a single female on 1.vi, again after a sudden rise in temperature (Table 2), followed two days later by the first male. However, reports of 11 male and 2 female magpie victims from a local nest indicated that the beetles had emerged before 26.v. It was generally a good year but no hotspots were found and only one fighting episode (up a tree) was seen, on 7.vi; also no matings were observed. Overall there were 159 sightings, with 10.7% dead.

Figure 3. Cumulative percentages of all 2005 sightings.

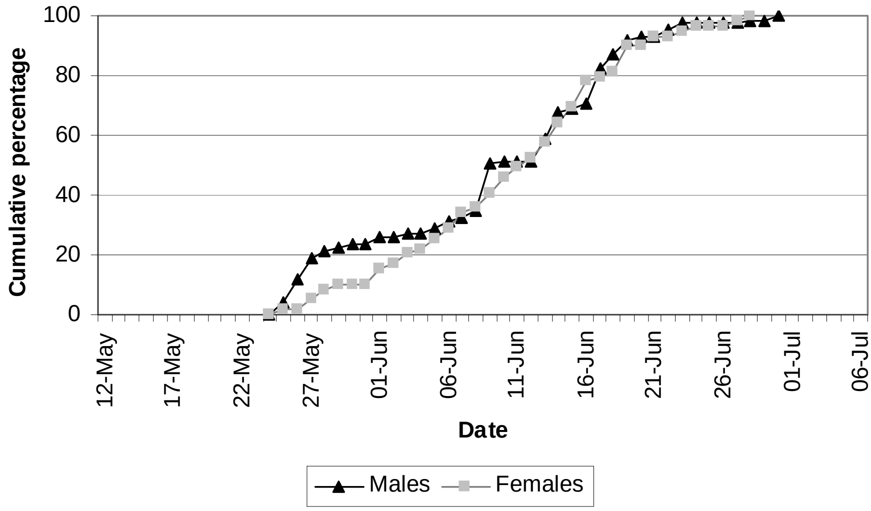


Figure 4. Daily Stag Beetle sightings for 2006, total 159. Female-to-male ratio 1 : 2.4. Flying sightings: 73 males, 1 female and 11 unknown.

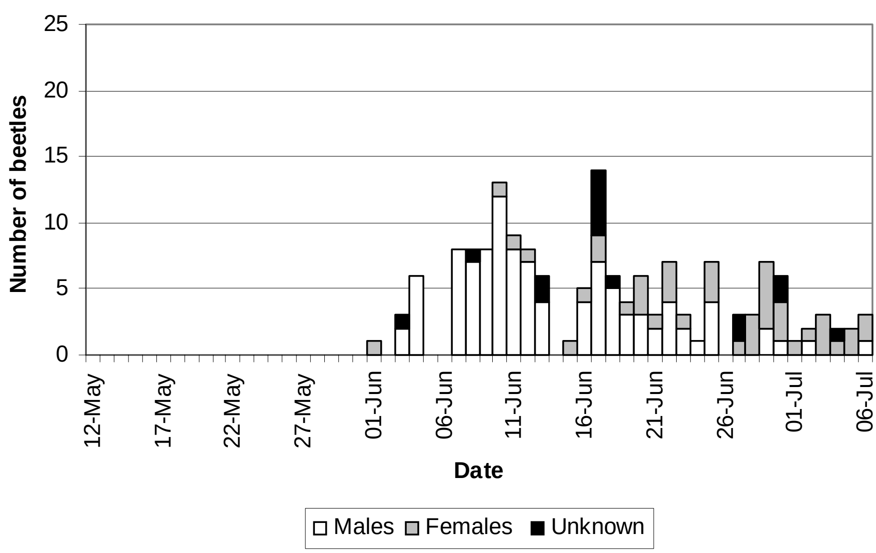
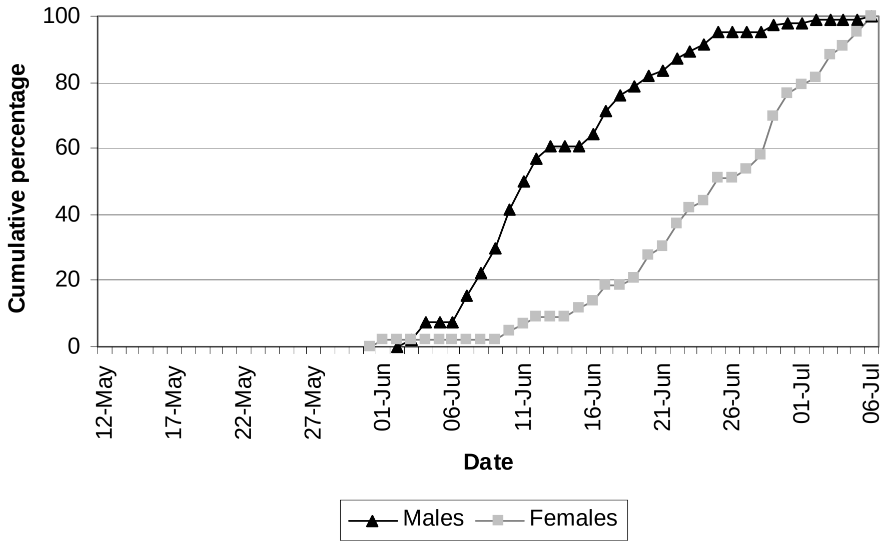


Figure 5. Cumulative percentages of all 2006 sightings.



Males generally appeared earlier in the season than females, Figure 5.

In 2007, April was unusually warm and there were reports of a male sighting in the area (11.iv, Ryder pers. comm.). However, monitoring was started only on 15.v and three days later 5 males were sighted in a couple of places in the alleyway, soon after 20.19 hrs GMT.

In this year there was no sudden change in temperature (Table 2). The first female appeared on 30.v, and after that the beetles were very active. Several episodes of males fighting for a single female up to 10.vi were witnessed, in the alleyway in the vicinity of nests ***d-f*** and by the nest ***c*** (Table 1).

However, the season was rather wet (Tijou 2009); there were 5 nights, 16 and 27.v, 14, 19, and 24.vi, that were not monitored because of rain.

As during the day one female was observed walking in the rain (25.vi, 14.49 hrs), on the night of 5.vii monitoring was carried out in very wet conditions. That night there were 6 sightings, 4 live males, 1 injured female and 1 dead male. Except for the dead male they were all in the rain shadow of fences. In another instance a male stag beetle was seen flying against a moderate wind in light rain (2.vii, 20.36 hrs, 15.3ºC, 84% relative humidity, and 1002 mb pressure).

In spite of the wet weather 2007 was the best year, with a total of 306 sightings; 17.3% were of dead beetles, Figure 6.

As in the previous year males appeared earlier in the season than the females, Figure 7.

Figure 6. Daily Stag Beetle sightings for 2007, total 306. Female-to-male ratio 1 : 3.6. Flying sightings: 68 males, 2 females and 13 unknown.

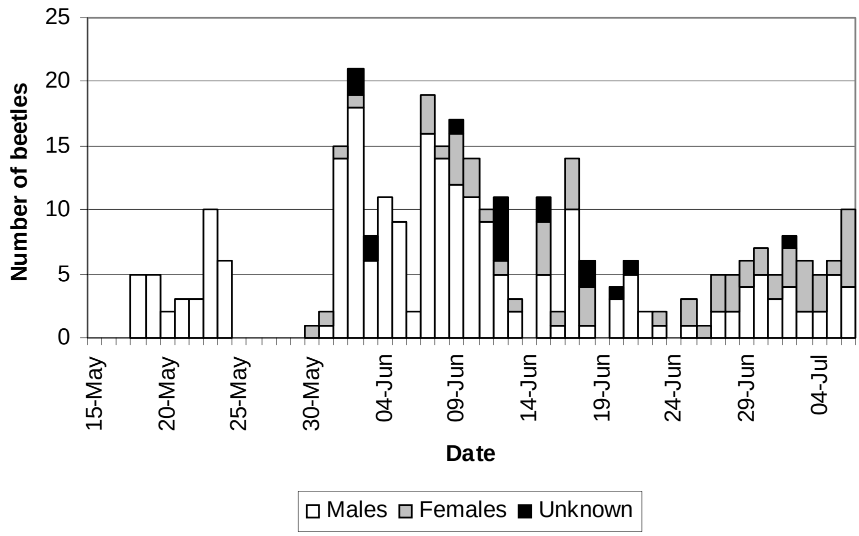
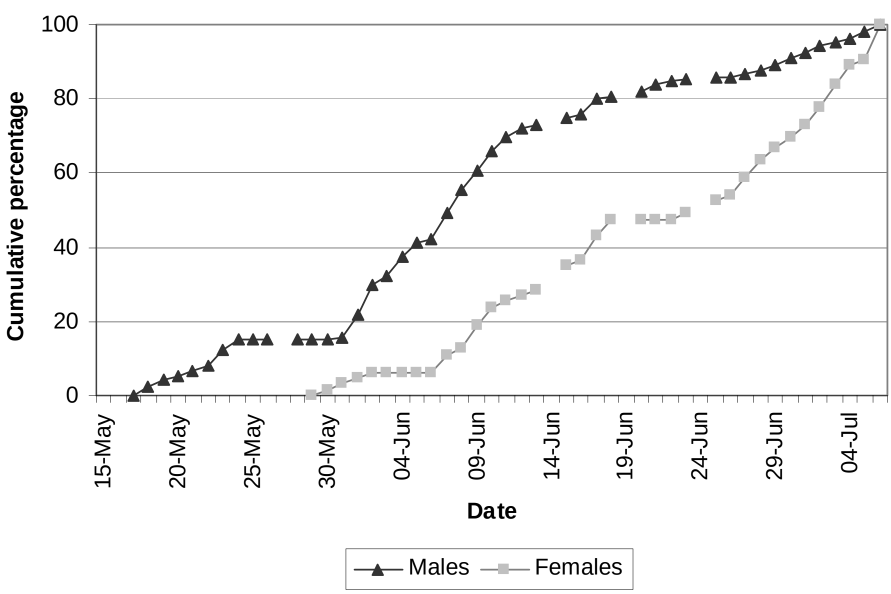


Figure 7. Cumulative percentages of all 2007 sightings. Gaps correspond to days without monitoring due to rain: 27.v, 14, 19, and 24.vi.



Seasonal activity analysis

For the next part of the analysis the period analyzed in each year was from the first day in which at least five beetles were sighted, to the last day in which at least five beetles were sighted (Fremlin 2009c). Only live beetles were considered, all dead and unknown-sex sightings were discarded; these restrictions have reduced the number of sightings by 23%. The overall female-to-male ratio of the analyzed live sexed beetles is 1 : 3.8 (Table 3).

Table 3. Sightings during the monitoring period and considered for the analysis period.

Year	**Monitoring period from first sighting/s**	**Total no. of sightings**	**Analysis period**	**No. of live sexed beetles in analysis period**
2005	25.v – 6.vii	204	25.v – 19.vi	161
2006	1.vi - 6.vii	159	4.vi – 29.vi	119
2007	18.v - 6.vii	306	18.v – 6.vii	238
	Total	669		518

For the analysis of flying beetles, only males were considered as the females flew much less. For the three year period there were only 9 identifiable females in flight compared to 204 males; all these females were observed after the middle of June. In addition, 36 flying beetles could not be sexed with certainty.

For this analysis the weather variables displayed are the integer parts of their average values between 20.00 and 21.00 hrs GMT.

Temperature

The results for the 3 years together, Figure 8, show that there is an apparent step-change in numbers of live and flying males around 13-14 degrees, possibly another between 19 and 20 degrees. The exceptional observations at 9+ºC were made on 7.vi.2005. Males become more active at around 13 degrees, but apparently not so the females.

No male stag beetles were seen flying below 12ºC (Figure 9). Five flying males were seen on 3.vi.2007, in a crepuscular temperature of 13.0ºC. The dramatic leap in the number of male flying stag beetles recorded at the highest temperature is due to a single night on which there was a mass flight, 17.vi.2005. A significant number of non-flying males were seen at temperatures between 9ºC and 13ºC; otherwise the two curves are not far apart.

Humidity

Results of an identical analysis for the humidity show that males seem to prefer relatively low humidity days, Figure 10, whereas the females are much less responsive. Flying males reduce their activity in high humidity, non-flying males are not affected, Figure 11.

Wind

Stag Beetle males appear less on windier days, but the converse seems to happen for the females, Figure 12. Flying males do not like strong winds, Figure 13.

Pressure

There is an apparent step change for the males at 1015 mb; females don't seem to respond the same way, Figure 14. The reaction of flying and non-flying males to pressure is fairly close, except at the high-pressure end, when non-flying males were seen around a stationary female during a cold weather period in 7-8.vi.2005.

Figure 8: The number of days at a given temperature and the average number of live male and female Stag Beetle sightings during 2005-2007 plotted against the temperature. There were no days at 22+ºC. In this figure and all subsequent ones bars bracketing average values indicate standard deviations.

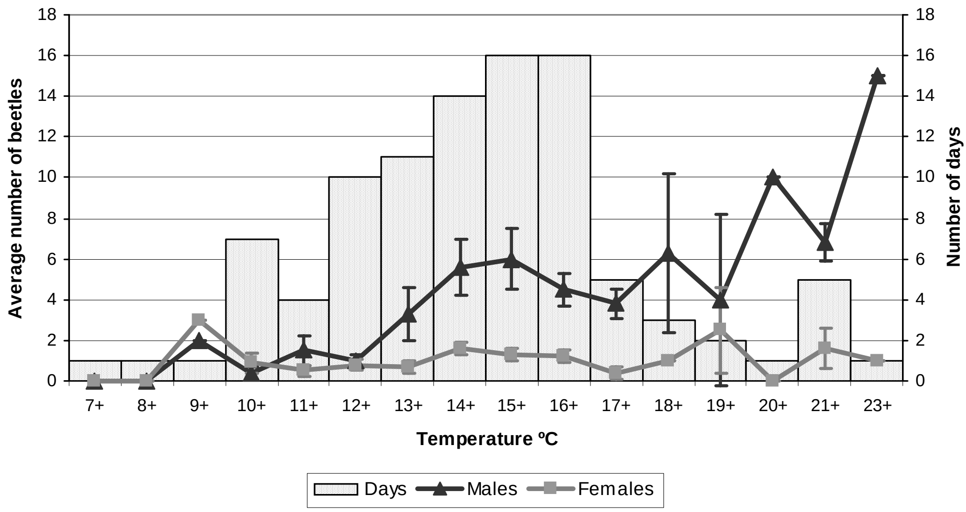


Figure 9: The number of days at a given temperature and the average number of flying and non-flying males sightings during 2005-2007 plotted against the temperature.

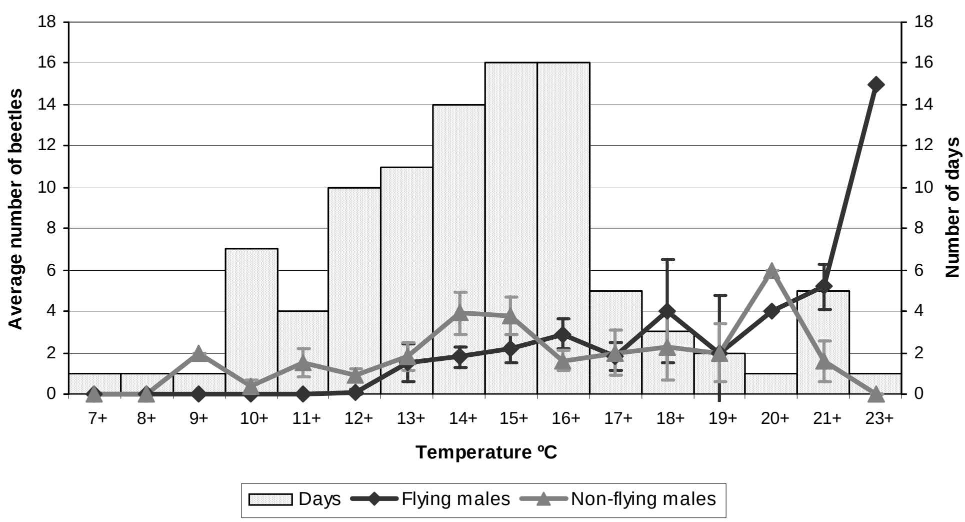


Figure 10: The number of days at a given humidity and the average number of live male and female Stag Beetle sightings during 2005-2007 plotted against the humidity.

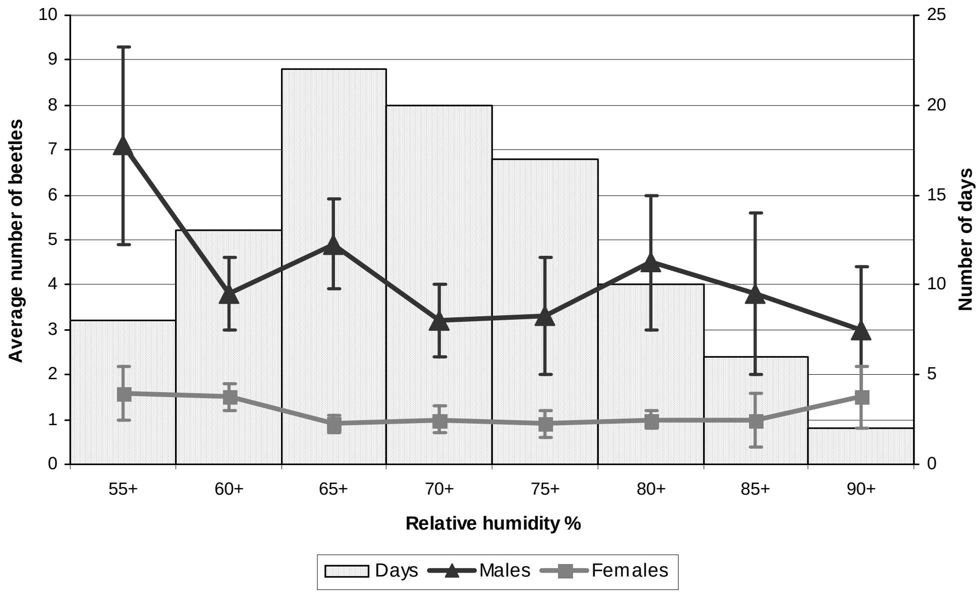


Figure 11: The number of days at a given relative humidity and the average number of flying and non-flying males sightings during 2005-2007 plotted against the relative humidity.

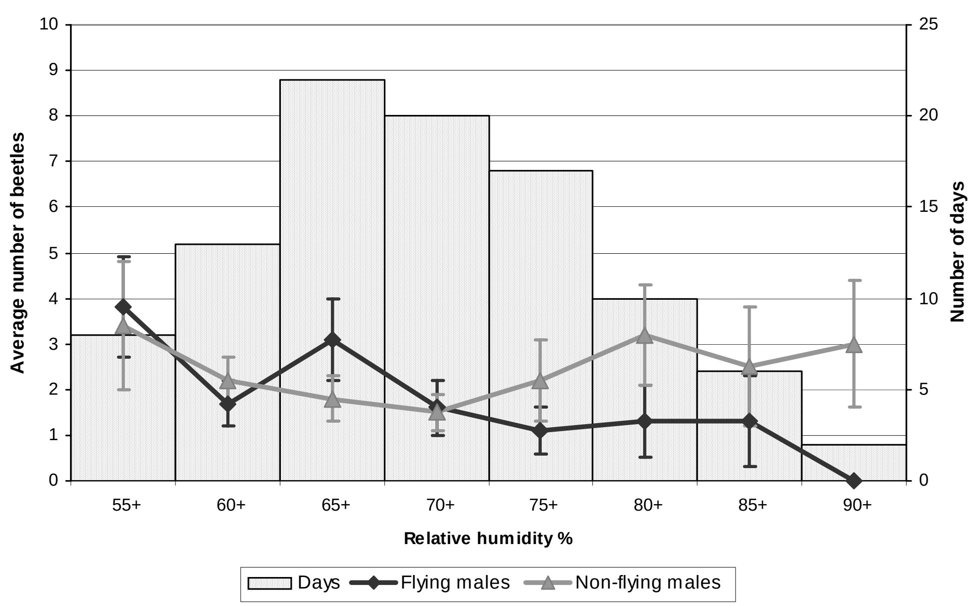


Figure 12: The number of days at a given wind speed and the average number of live male and female Stag Beetle sightings during 2005-2007 plotted against the wind speed.

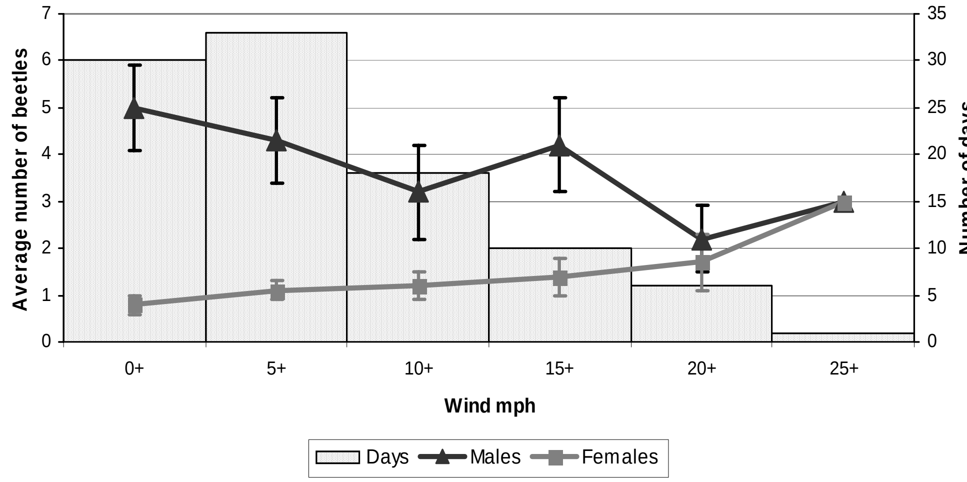


Figure 13: The number of days at a given wind speed and the average number of flying and non-flying males sightings during 2005-2007 plotted against the wind speed.

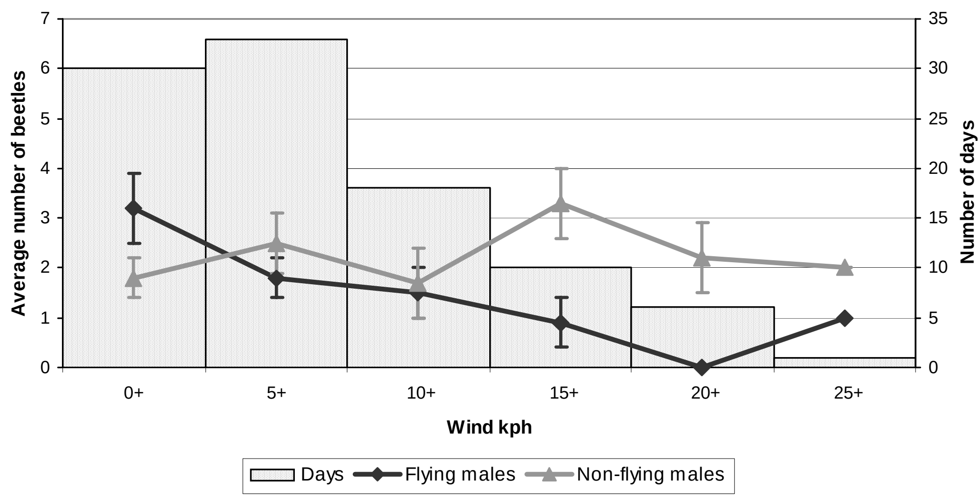


Figure 14: The number of days at a given pressure and the average number of live male and female Stag Beetle sightings during 2005-2007 plotted against the pressure.

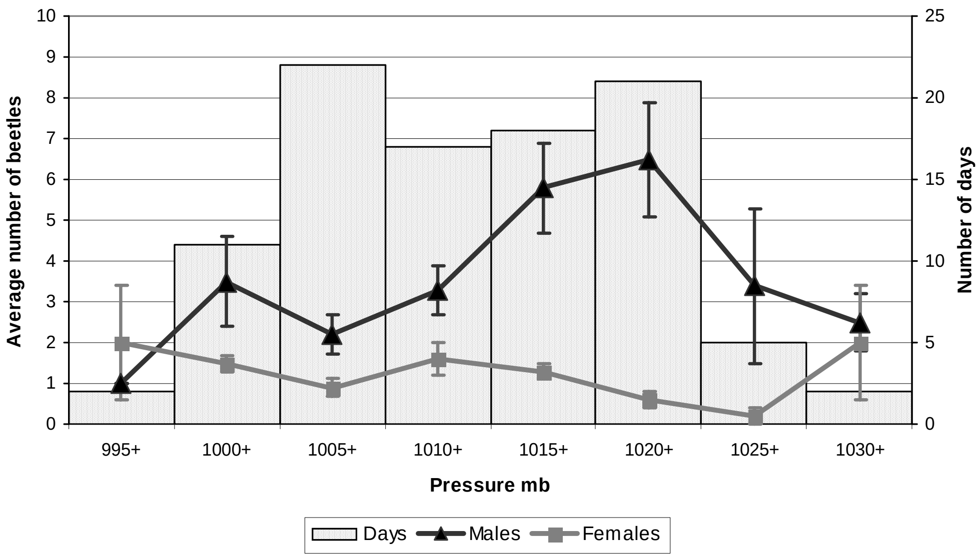
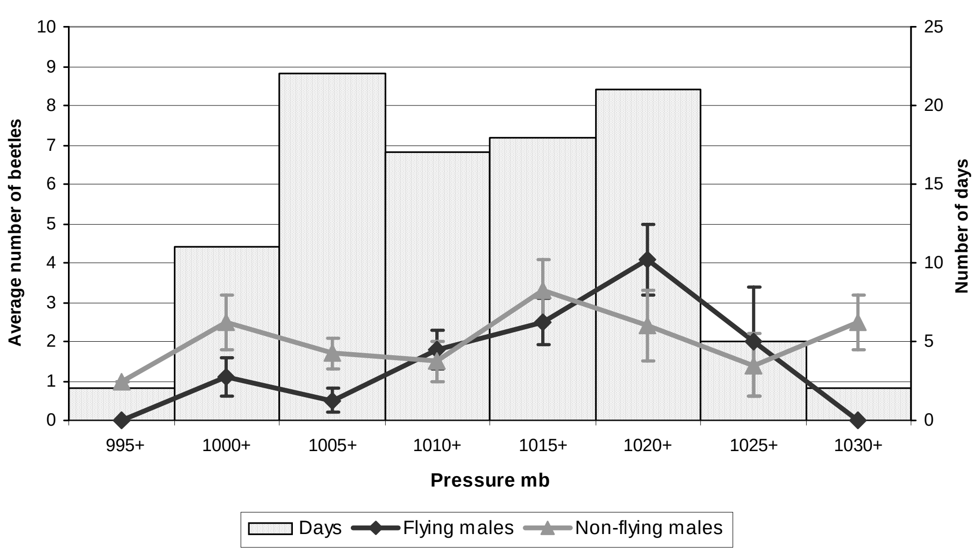


Figure 15: The number of days at a given atmospheric pressure and the average number of flying and non-flying males sightings during 2005-2007 plotted against atmospheric pressure.



Discussion

Our relatively large dataset (more than 200 sightings of *L. cervus per annum* as compared with the 51 sightings of Sprecher-Uebersax (2001) makes it possible to distinguish male and female responses to the variables investigated.

Emergence

L. cervus emergence dates vary a great deal. For instance, Sprecher-Uebersax's ranged from 23.v to 18.vi in the 10 years 1991-2000 (2001). Rink & Sinsch (2008, Table 2) suggest that emergence from the ground may be influenced by the climatic conditions of the 3 preceding days. Our Table 3 indicates that first sightings can be expected after a rise in temperature and on a dry day preceded by light rains. It should be noted that these dates of first appearance probably do not represent true emergence dates as observed by Rink & Sinsch (2008).

Post-emergence activity

The analysis of dependence of behaviour on weather is greatly complicated by the dependence of behaviour on the season. The reduced number of sightings in July as compared with June is not because the weather is different in July. For this reason, our detailed analysis of the relation between sightings and weather variables (Figures 8-15) is restricted to the period in each year in which beetles were relatively abundant.

There were no clear associations between female behaviour and the weather variables. Females evidently behave very differently from males; note that the difference in the number of sightings (Figures 2, 4 and 6) already indicates a large difference in behaviour – females spend more time more or less hidden (Fremlin 2009a). The males fly much more, particularly at the beginning, and as the season progresses this declines rapidly (cf. Rink & Sinsch 2007, Figure 4).

The female-to-male flying ratio we observed was 1 : 23. This is markedly different from ratios previously reported; two PTES surveys (Percy *et al.* 2000, and Smith 2003, pers. comm.) gave 1 : 3.3 and 1 : 2.6 respectively; Rink & Sinsch (2007) suggest 1 : 3; aerial traps actually caught more females than males (Harvey 2007). However, we saw a substantial number of flying beetles of uncertain sex and it may be that part of the discrepancy is due to the observer's difficulty in making definite distinctions in the dusk.

Temperature

The temperature at which males become noticeably more active, 13ºC, is lower than has been suggested in the past (Sprecher-Uebersax 2001, Hawes 2004, 2008), Figure 9.

When comparing our temperature data with the figures given in Sprecher-Uebersax 2001, we should note that we have used evening temperatures (following Rink 2006, Hawes 2004) while Sprecher-Uebersax used daily medians, which are naturally higher. In particular, the exceptional sightings of non-flying males on 7.vi.2005 and of flying males on 3.vi.2007, at evening temperatures of 9.8ºC and 13.0ºC, were on days with daily mean temperatures of 11.8º and 14.9ºC respectively.

Moreover in the urban area studied there were several hiding places where the beetles could benefit from heat stored during the day.

Humidity

Males seem to prefer less humid conditions, Figure 10; but as humidity and temperature are inversely correlated, this may be no more than a reflection of their preference for warm weather.

Wind

Flying males do not like windy conditions, Figure 13, though they sometimes fly upwind at good speeds (pers. obs.).

Pressure

Figure 14 seems to show little variation in female activity with pressure, as with the other variables, but there is a striking pattern in male activity: a steady rise in activity up to 1025 mb, followed by a dramatic drop. If real this would be most interesting.

On detailed analysis, however, we note the following. On all the seven days in which the pressure was above 1025 mb, the temperature was below 16ºC (Fremlin 2009c). This means that the non-appearance of beetles at high pressures in our study may be no more than a reflection of an unusual weather pattern.

Another point arises here. We have already remarked on the appearance of two males on 7.vi.2005 at an exceptionally low temperature of 9.8ºC; on the same day we note that the pressure was 1033 mb. In fact the three females observed at temperatures below 10ºC (Figure 8) were also all seen on that day. Moreover, the males and two of the females were together (hotspot ***a***, Figure 1), and a pair were mating. Conceivably this behaviour was related not only to the proximity of a freshly cut stump (Table 1) but also to the high pressure that evening, but of course a single observation of this kind can do no more than offer a line for future research. A study of plum curculios suggested that pressure might influence the female's odour discrimination (Leskey & Prokopy 2003).

Since our observations were at fixed hours, the light intensity necessarily rose and fell as the season progressed. If such a study were to be repeated, it could be done at a fixed time relative to sunset (for example, starting 40 min after sunset) and it might then be worth while investigating the possible effect of light on the activity of stag beetles, especially the males. Light intensity is known to affect several scarabaeoid beetles (Beaudoin-Ollivier *et al*. 2003, Evans & Gyrisco 1958, Houston & McIntyre 1985, Wensler 1974).

Conclusion

This study was possible because there is a thriving *L. cervus* population in the monitored area (cf. Clark 1964, 1965, Bowdrey 1997). It was found that there are large differences in the responses of males and females to the weather. Besides the known dependence on temperature, our data suggest that the males are affected by atmospheric pressure, appearing more readily at higher pressures.

Our research shows that even in a relatively densely populated area, stag beetle behaviour is governed by similar factors to those operative in village and wooded environments, and may be more easily observed. We hope that it will be a contribution towards the understanding of the climatic factors that govern their crepuscular behaviour.

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References

BEAUDOIN-OLLIVIER, L., BONACCORSO, F., ALOYSIUS, M. & KASIKI, M. (2003). Flight movement of *Scapanes australis australis* (Boisduval) (Coleoptera: Scarabaeidae: Dynastinae) in Papua New Guinea: a radiotelemetry study. *Australian Journal of Entomology* **42**: 367-372. doi: 10.1046/j.1440-6055.2003.00369.x

BOWDREY, J. (1997). The stag beetle *Lucanus cervus* L. (Coleoptera: Lucanidae) in north-east Essex: Results of the 1996 Colchester "Search for Stag Beetles" survey. *The Essex Naturalist* **14**: 79-88.

CLARK, J.T. (1964). The stag beetle in north-east Essex. *The Essex Naturalist*: **31**: 167-172.

CLARK, J. T. (1965). The stag beetle in north-east Essex - second report. *The Essex Naturalist* **31**: 267-*270.*

EVANS, W.G. & GYRISCO, G.G. (1958). The influence of light intensity on the nocturnal emergence of the European chafer. *Ecology* **39**: 761-763.

FREMLIN, M. (2003). A stag night in Colchester, Essex, UK. URL http://maria.fremlin.org/stag_night [accessed on 11.iii.2010].

FREMLIN, M. (2005). Stag beetle mating quiz. URL http://maria.fremlin.de/stagbeetles/quiz-mating.html [accessed on 11.iii.2010].

FREMLIN, M. (2009a). Stag beetle (*Lucanus cervus*, (L., 1758), Lucanidae) urban behaviour. In Saproxylic beetles.–.Their role and diversity in European woodland and tree habitats. *Proceedings of the 5th Symposium and Workshop on the Conservation of Saproxylic Beetles, Lüneburg (Germany), 14-16.06.2008*. Buse J., Alexander K.N.A., Ranius T. & Assmann T. (Eds*). Pensoft, Sofia- Moscow* : 161-176.

FREMLIN, M. (2009b). Stag beetle urban behaviour. 5th Conference on Saproxylic Beetles. URL http://maria.fremlin.org/saproxylic_conference/ [accessed on 11.iii.2010].

FREMLIN, M. (2009c). Phenology data for 2005-2007. URL http://maria.fremlin.org/phenology/data_2005_2006_2007.xls [accessed on 11.iii.2010].

GLUD (GENERALISED LAND USE DATABASE) (2007). *Generalised Land Use Database Statistics for England 2005*. URL http://www.communities.gov.uk/publications/planningandbuilding/generalisedlanduse [accessed on 11.iii.2010].

HARVEY, D. & GANGE, A. (2003). The private life of the stag beetle (*Lucanus cervus*). *Bulletin of the Amateur Entomologists' Society* **62**: 240-244.

HARVEY, D. (2007). *Aspects of the biology and ecology of the stag beetle (Lucanus cervus)*. PhD thesis, Royal Holloway, Univ. London, UK.

HAWES, C.J. (1998). The stag beetle, *Lucanus cervus* L. (Coleoptera: Lucanidae) in Suffolk - a first report. *Transactions of the Suffolk Naturalists' Society* **34**: 35-49.

HAWES, C. J. (2004). The stag beetles *Lucanus cervus* (L.) (Coleoptera: Lucanidae) in the County of Suffolk (England): Distribution and Monitoring. *Proceedings of the 13th Symposium and Workshop on the Conservation of Saproxylic Beetles, Riga/Latvia, 7-11 July 2004. Latvijas entomologos,* **suppl, VI**: 51-67.

HAWES, C.J. (2008). The stag beetle *Lucanus cervus* (Linnaeus, 1758) (Coleoptera: Lucanidae): a mark-release-recapture study undertaken in one United Kingdom residential garden. In *Proceedings of the 4th Symposium on the Conservation and Workshop of Saproxylic Beetles, Vivoin (72) / France, 27th-29th June, 2006.* Vignon V. & Asmodé, J.-F. (eds). *Revue D'Écologie. (La Terre et la Vie),* **suppl. 10**: 139-146.

HOUSTON, W.W.K. &. MCINTYRE, P. (1985). The daily onset of flight in the crepuscular dung beetle *Onitis alexis*. *Entomologia Experimentalis et Applicata* **39**: 223-232.

KLAUSNITZER, B. & SPRECHER-UEBERSAX, E. (2008). *Die Hirschkäfer oder Schröter (Lucanidae). Die Neue Brehm-Bücherei* **551**: 4. 161. Westarp Wissenschaften Hohenwarsleben.

LESKEY, T.C. & PROKOPY, R.J. (2003). Influence of barometric pressure on odor discrimination and oviposition by adult plum curculios (Coleoptera: Curculionidae). *European Journal of Entomology (Czech Republic)* **100**: 517-520.

MAMONOV, G. (1991). The great European stag beetle – its past and its future. *Bulletin of the Amateur Entomologist's Society* **50**: 157-163.

MORETTI, M. & SPRECHER-UEBERSAX, E. (2004a). Über das Vorkommen des Hirschkäfers *Lucanus cervus* L. (Coleoptera, Lucanidae) im Tessin: Eine Umfrage im Sommer 2003. *Mitteilungen der Entomologischen Gesellschaft Basel* **54**: 75-82.

MORETTI, M. & SPRECHER-UEBERSAX, E. (2004b). Cervo volante: un anno eccezionale: ecco i risultati del censimento 2003 (*Lucanus cervus*). *Agricoltore Ticinese* **16**: 10-11.

ONS (OFFICE FOR NATIONAL STATISTICS) (2001). *Population Density (UV02), Neighbourhood Statistics*. URL http://neighbourhood.statistics.gov.uk [accessed on 11.iii.2010].

PERCY, C., BASSFORD, G. & KEEBLE, V. (2000). *Findings of the 1998 national stag beetle survey*. Robb, C. (ed). People's Trust for Endangered Species. London, UK: 1-48.

RINK, M. (2006). *Der Hirschkäfer Lucanus cervus in der Kulturlandschaft: Ausbreitungsverhalten, Habitatnutzung und Reproduktionsbiologie im Flusstal*. Doctoral diss., Univ. Koblenz-Landau, Germany: 1-151.

RINK, M. & SINSCH, U. (2007). Radio-telemetric monitoring of dispersing stag beetles: implications for conservation. *Journal of Zoology (London)* **272**: 235-243.

RINK, M. & SINSCH, U. (2008). Geschlechtsspezifisches Fort pflanzungsverhalten des Hirschkäfers (*Lucanus cervus*). *Mainzer Naturwissenschaftliches Archiv* **46**: 195-210.

SMITH, M.N. (2003). *National Stag Beetle Survey 2002*. People's Trust for Endangered Species, London, UK: 1-14.

SPRECHER-UEBERSAX, E. & DURRER, H. (1998). Über das Vorkommen des Hirschkäfers (*Lucanus cervus* L.) in der Region Basel (Coleoptera). *Mitteilungen Entomologischen der Gesellschaft Basel* **48**: 142-166.

SPRECHER-UEBERSAX, E. (2001). *Studien zur Biologie und Phänologie des Hirschkäfer im Raum Basel: mit Empfehlungen von Schutzmassnahmen zur Erhhaltung und Förderrung des Bestandes in der Region (Coleoptera: Lucanidae, Lucanus cervus L.)*. Doctoral diss., Univ. Basel, Switzerland: 1-196.

TIJOU, S. (2009). *Colchester Weather Site*. URL http://www.tijou.co.uk/weather/ [accessed on 11.iii.2010].

TULLETT, A.G. (1998). *Conservation status and habitat requirements of the stag-beetle, Lucanus cervus (L.), in Britain*. MSc diss. Univ. East Anglia, UK: 1-67.

WENSLER , R.J. (1974). Crepuscular activity of adult *Sericesthis geminata* (Coleoptera: Scarabaeidae): influence of circadian rhythmicity and light intensity. *New Zealand Journal of Zoology* **1**: 197-204.